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Current Trends in Food Web Theory Report on a Food Web Workshop

October 25–27, 1982
Fontana Village Inn, North Carolina

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CURRENT TRENDS IN FOOD WEB THEORY
REPORT ON A FOOD WEB WORKSHOP

October 25 27 1982

Fontana Village Inn North Carolina

Organized and Edited by

D L DeAngelis
W M Post
G Sugihara

HOST OAK RIDGE NATIONAL LABORATORY

SPONSOR NATIONAL SCIENCE FOUNDATION

Date published October 1983

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ABSTRACT

DEANGELIS D L W M POST and G SUGIHARA 1982
Current trends in Food Web Theory Report on
a Food Web Workshop ORNL 5983
Oak Ridge National Laboratory Oak Ridge Tennessee

This report summarizes the Food Web Workshop held at Fontana Village Inn October 25 27 1982 The objective of the workshop was to review and assess recent progress in the understanding of ecological food webs The workshop focused on three main areas (1) what has been observed of food web patterns (food chain length intervality predator prey ratios etc) (2) processes involved in food chains (energy flow and nutrient cycles) and (3) the dynamic behavior of food webs (Lyapunov stability resilience etc)

The introduction reviews some of the important contributions to food web theory during the past decade The synopses of the presentations by invited speakers address many of the specific themes in current thought on food webs

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PREFACE

Two major generalizations guided food web theory until the 1970 s The first generalization asserted that the complexity of food webs conferred on them a stability that simple systems do not have The second generalization involved the second law of thermodynamics (that is the inefficiency of trophic energy conversion) as the primary factor limiting the maximum number of trophic levels in food webs Both of these generalizations have been called into question during the past ten years the first by May (1972 1973) and the second by Pimm and Lawton (1977) These challenges to prevailing dogma have sparked a flurry of hypotheses and subsequent testing of hypotheses with data from real food webs Although no new generalizations have yet solidly emerged to replace the old ones we can probably guess from our current perspective that when new ones do appear they will not be quite so simple and sweeping as the old ones The study of ecological food webs has entered a new era

In view of the current ferment in food web theory it is important that there be more effort to bring together researchers in this area The assimilation and assessment of current results in the field and the planning of future research directions require face to face contact and free exchange of ideas among the principal researchers As a step in improving this sort of interaction a Food Web Workshop was held at Fontana Village Inn on October 25 27 1982 Prominent food web researchers from the United States and Canada were invited to present papers concerning either their recent research in or evaluations of three general areas of food web research (1) food web patterns (food chain length interval ity predator prey ratios etc) (2) processes invoked to explain the patterns (dynamics energy flow etc) and (3) the consequences to ecosystem function (resilience nutrient cycling etc)

This report presents the synopses of the presented papers in addition to a brief chronology of relevant research over the past decade

Food Web Workshop Participants

Invited speakers

Peter A Abrams	University of Minnesota
Robert A Armstrong	State University of New York—Stony Brook
Frédéric Briand	University of Ottawa
Joel E Cohen	Rockefeller University
James A Drake	Purdue University
John W Glasser	University of Georgia
Harold M Hastings	Hofstra University
W Charles Kerfoot	Dartmouth University
Anthony W King	University of Tennessee
John H Lawton	University of York
Simon A Levin	Cornell University
Leo S Luckinbill	Wayne State University
Robert M May	Princeton University
Len Nunney	University of California—Riverside
Robert T Paine	University of Washington
Stuart L Pimm	University of Tennessee
Wilfred M Post	Oak Ridge National Laboratory
Donald R Strong Jr	Florida State University
George Sugihara	Oak Ridge National Laboratory
Robert E Ulanowicz	University of Maryland
Peter Yodzis	University of Guelph

Other participants

Donald L DeAngelis	Oak Ridge National Laboratory
Marshall S Adams	Oak Ridge National Laboratory
Richard B McLean	Oak Ridge National Laboratory
Les Hook	Oak Ridge National Laboratory
Paul Franco	Oak Ridge National Laboratory
Joyce Waterhouse	Oak Ridge National Laboratory
Paul Weldon	University of Tennessee
Marie Turner	University of Tennessee
Steve Ellner	University of Tennessee
Charles E Clark	University of Tennessee
Mel Whiteside	University of Tennessee
Michael Moulton	University of Tennessee
James Tanner	University of Tennessee
Jetta Jaeger	University of Tennessee
Donald Weller	University of Tennessee
Scott Wissinger	Purdue University
Robert B Waide	Center for Energy and Environment Research San Juan Puerto Rico
Tom Gard	University of Georgia
Gary Polis	Vanderbilt University
Gerard Joswiak	Wayne State University
Philip McGillivary	University of Georgia

A BRIEF SYNOPSIS OF FOOD WEB THFORY THE PAST DECADE

Since publication of the milestone book Stability and Complexity in Model Ecosystems (May 1973) the literature on food webs has grown rapidly Much of the recent work has been reviewed effectively by May (1979) Goh (1980) and Pimm (1982) Still a short recapitulation would be useful to put the various papers of the present workshop in proper perspective This chronology will necessarily be incomplete and will not attempt to trace every thread in the fabric of food web theory However we shall at least outline three major lines of development which have their respective starting points in the examination of food web (1) structure (2) dynamics and (3) processes By food web structure we mean the static qualitative positional relationships among species in the web Food web dynamics is concerned with the numerical equilibria and fluctuations of species populations in the web Finally the term processes refers to the flows of energy and bioelements through the food webs

In the following chronology when papers appearing in this volume are referred to the author s name is printed in boldface

Food Web Structure

Although it is one of the most fundamental aspects of ecosystem organization food web structure has only recently received rigorous scrutiny Current interest in the problem is due in large part to the seminal monograph Food Webs and Niche Space (Cohen 1978) in which combinational properties of real niche spaces are used to detect the existence of structure or nonrandomness in their construction Along with providing the first real data base for such studies Cohen observed that most real community niche spaces could be collapsed down into one dimensional representations known as interval graphs Because this property could not be accounted for by a host of null models it was presented as an intriguing empirical regularity that begged explanation

YODZIS in studying various models based on energetic considerations has reported that a new more fully detailed list of previously published (Yodzis 1981) assembly rules might in some cases explain intervality Critchlow and Stearns (1982) have suggested that the observed high frequency of intervality could be an artifact of food webs consisting of small disconnected communities and have suggested a new criterion for collapsing niche spaces called interval diets COHEN offers various criticisms of the Critchlow and Stearns paper which together with recent calculations (Sugihara 1982) suggest that this explanation for intervality may not be correct He further reviews the mathematical literature on food web topology and outlines some new problems for future research

SUGIHARA presents an alternative model of the niche which is applied to Briand s (1983) catalogue of food webs to demonstrate that real niche spaces tend to lack holes This is shown to be a companion property of Cohen s intervality in that both are explicable by a necessary and sufficient assembly rule for food webs

BRIAND uses a multivariable statistical approach to explore differences in food web structures in different environments In particular he reports differences in the shape and connectance of food webs that appear to depend respectively on the dimensionality (2 or 3 dimensions) and variability of the environment

Several studies have indicated that there are features of food webs that may be appreciated by understanding the ways in which they develop This notion may be traced from the Clementsian idea of ontological development of an ecological super organism and the more recent ecosystem organization ideas of Odum (1969) concerned with functional integrity Recent work has examined food web structure determined by assembly or successional processes in terms of population equations This approach allows individual species to respond to their internal dynamics and their interactions with other species

Allen (1975) introduced the concept of mutation into the Lotka Volterra model by consid ering the invasion of a different genotype with slightly altered population parameters He examined conditions under which the superior predator or the superior prey would replace their inferior counterpart leading to an irreversible trajectory through population parameter space Felsenstein (1978) using a similar idea but working with energy flow equations of population growth and predation studied models of evolving ecosystems and the macroevolutionary laws which those model ecosystems obey In all cases that he studied the total energy content of the ecosystem increases with time In simple cases the trophic pyramid converges to a geometric shape which does not lengthen during evolution

Using the concept of invasion articulated by Allen (1975 1976) and Felsenstein (1978) with computer simulations Robinson and Valentine (1979) investigated the effect of a single species colonization on the likelihood of compositional change of an initially randomly con structed system They found that invasability of communities decreased as they became more complex in terms of numbers of species and connectance In a series of papers Roberts and Tregonning (Tregonning and Roberts 1978 1979 Roberts and Tregonning 1980) studied properties of systems constructed by natural processes operating on initially large collec tions of randomly interacting components The resulting smaller systems showed a prepon derance of predator prey interactions and were much more likely to be stable than randomly produced systems of comparable size and complexity

Post and Pimm (1983) have combined the processes of invasion and elimination studied separately by the above mentioned authors into a general assembly algorithm for food webs based on Lotka Volterra population dynamics They found that while there was a contínu ous turnover of species in computer generated food webs the turnover rate slowed with assembly time This is in accord with the empirical observations of Shugart and Hett (1873) However while food webs became more resistant to invasion their stability to perturbations from equilibrium decreased as measured by the inverse of return time to equilibrium DRAKE reports on a similar study in which he looked at assembly of food webs of particu lar structures POST has looked at the impact of the Post and Pimm assembly rules on a measure of food web structure proposed by Ulanowicz (1980) Structure defined in terms of certainty (in an information theory context) of biomass flows through a food web increases under certain conditions related to the relative degree of polyphagy of the potential colon ists

The number of prey per predator in a food web has been of interest since Cohen s (1977) discovery of the relatively constant ratio of 4 predators to 3 prey in natural food webs Glasser (1982a b) developed a theory of trophic strategies from considerations of contempo rary niche theory Using a generalized Verhulst equation GLASSER evaluates ideas about the evolution of efficiencies and strategies of resource use by simulating competition among otherwise identical species with different efficiencies and feeding strategies One result of this work is that the number of species at successive trophic levels is expected to decrease in contradiction to the pattern in natural communities reported by Cohen (1977)

Are some ecological systems less tightly structured than others? An interesting debate has developed concerning the relative roles of chance and competition in patterning certain consumer communities (Connor and Simberloff 1979 Dean and Ricklefs 1979 Force 1980 Sale and Williams 1982) STRONG argues here that phytophagous insect communities at least are loosely structured The problems touched on here are relevant to the study of food webs in general and in particular to the question of whether or not observed patterns are results of density dependent processes or can be explained by random processes

Food web dynamics

Drawing on the general results for random systems of Gardner and Ashby (1969) May (1972 1973) showed that randomly connected ecosystem models decreased in stability (i e local asymptotic or Lyapunov stability) with either increasing numbers of species or with increasing connectance or strength of connections between species In particular May (1972) conjectured that if α represents mean species interaction strength n is the number of species and C is the mean number of connections per species in an ecological model then when $\alpha^2 nC > 1$ the system is usually Lyapunov unstable about an equilibrium point while if $\alpha^2 nC < 1$ the system is usually stable In the present volume HASTINGS provides a conceptual proof of this theorem for randomly assembled linear systems

Much of the work on food web dynamics since 1973 has been an attempt to reconcile May s mathematical observation with the empirical observation that complex real ecosystems do appear to be stable in some sense Several different approaches to solving or avoiding this dilemma have been proposed A few of these are approaches based on the suggestion of May and others that real food webs rather than being random assemblages have (1) functional relationships among the species or (2) structural characteristics that favor stability (3) attempts to show that many unstable systems may not be feasible for other reasons and so will not occur in nature (4) emphasis on persistence or other measures rather than Lyapunov stability as the important attribute of food web stability (5) investigation of the role of spatial extent and spatial heterogeneity in stabilizing complex systems These will be discussed in turn

(1) Stabilizing functional relationships in food webs

The recognition that simple predator prey systems could exhibit instabilities (Rosenzweig and MacArthur 1963 May 1972) led to a search for functional relations involving prey refuges predator searching time predator interference predator switching behavior and other details of trophic interactions that could stabilize such systems (Hassell and May 1973 Oaten and Murdock 1975 DeAngelis et al 1976) It was logical to extend this approach in the attempt to show that May s (1972 1973) results for randomly assembled abstract systems were not relevant to real ecosystems For example Austin and Cook (1974) included predator switching decomposition and other details in the series of models and showed that increasing food web size could be accompanied by increasing stability DeAngelis (1975) demonstrated that a bias towards donor dependence strong consumer self regulation and consumer assimilation inefficiency could all contribute towards a positive correlation between system connectance and Lyapunov stability Nunney (1980) showed that the precise predator prey functional relationships can affect stability characteristics In particular when Holling type 3 responses are prevalent food web stability can increase with connectance

Abrams (1981) questioned the generality of the results of DeAngelis (1975) and Nunney (1980) He showed that for food webs containing the same assumptions but also exhibiting symmetric structure with respect to the predators stability measured as return time to equilibrium following a perturbation in food webs that are Lyapunov stable could actually decrease with increasing connectance

While Abrams (1981) challenge underscores the difficulty in making any generalizations regarding food web stability and complexity some reasonably broad patterns are emerging For example Post and Travis (1979) have noted that the food web properties that DeAngelis (1975) showed as leading to a positive correlation between connectance and stability are characteristics that increase the probability of quasi diagonal dominance in the model Nunney s (1980) use of Holling type 3 functional relationships also increased the likelihood

of quasi diagonal dominance Quasi diagonal dominance ensures Lyapunov stability and has been the focus of considerable interest (Siljak 1975 1978 Goh 1980)

It appears that the study of functional relationships as stabilizing (or destabilizing) factors is a rich area for theoretical and empirical research In the present volume ABRAMS demonstrates the way in which detailed functional feeding relationships involving population densities nonlinearly can generate indirect links in a food web LUCKINBILL describes empirical research on a predator prey chain that exhibits one type of indirect link

(2) Stabilizing structural relationships in food webs

When food webs obey constraints on their structure and the signs of their interactions local stability may be guaranteed for any magnitudes of interactions This type of Lyapunov stability is called qualitative stability (May 1974 Levins 1974 Tansky 1978) In particular it demands that (1) there be no feedback loops with more than two links (2) all feedback loops with two links be negative (3) at least one negative feedback loop of unit length (self regulation) exist and (4) all other unit length feedback loops be at least non positive Powell (1980) has applied qualitative stability to some actual food webs

Various types of hierarchical structure have been investigated as stabilizing mechanisms in food webs (e g McMurtrie 1975) As Paine (1980) has stressed food webs often consist of small modules of a few closely interacting species These species in each module interact much more weakly with species in other modules and the web thus avoids the instabilities predicted for webs in which there are many strong connections In the present volume PAINE reemphasizes the need to consider the strengths of connections as well as their existence and the need to be cautious in drawing conclusions for specific food webs based on abstract concepts such as connectance An example of how real food webs can be highly non random in structure is afforded by the aquatic web discussed by KERFOOT in this volume a delicately balanced system in which a keystone predator facilitates the existence of a sizable subsidiary food chain

An almost entirely neglected area in the subject of food web structure dynamics interaction is the presence of age or life stage structure within the species populations In this volume NUNNEY shows that the consideration of age structure in prey populations each life stage with its own predators can lead to time lags that can be either stabilizing or destabilizing depending of the circumstances

(3) Feasibility

Roberts (1974) defined a feasible food web as one whose parameters are such that all species population numbers are positive at equilibrium He stressed that at least for Lotka Volterra systems feasible systems are more difficult to produce randomly as the number of species increases and suggested that a greater percentage of randomly constructed feasible systems might be stable in the Lyapunov sense Goh and Jennings (1977) showed that the probability of feasibility of a randomly constructed Lotka Volterra web varied as 2^m where m is the number of species but they also showed along with Gilpin (1975) that randomly assembled feasible systems had the same decreasing probability of Lyapunov stability with increasing species number as the whole set of randomly constructed webs feasible and infeasible had

Lawlor (1978) recently raised the question of feasibility again in a more general sense than just with respect to Lotka Volterra systems pointing out that vanishingly few randomly constructed matrices could possibly represent plausible food webs Tregonning and Roberts (1980) have contributed some possible understanding to the way in which real food webs develop They showed that large feasible computer assembled food webs in general

consisted at every subsystem level of subsystems feasible in themselves Food webs could increase in complexity in a stable manner by building successively on smaller feasible food webs Unfortunately this hypothesis does not explain the existence of delicate food webs such as that discussed by KERFOOT where removal of a keystone predator causes mass extinctions

(4) Other measures of stability

Generalizing from his work on marine fouling communities Sutherland (1981) was moved to remark Evidence for stability or instability can be found in any community depending on the reference assemblage specific perturbation and time scale This comment reflects a common feeling among students of food webs that no single definition of stability is sufficient to represent the many modes of behavior observed in ecological communities In particular the Lyapunov stability used by May (1972 1973) and many others might not be the appropriate measure of stability in all situations A number of other concepts have been proposed

If the species of a food web are able to continue their existence despite fluctuations (both extrinsically induced and intrinsic as in limit cycles) in their population levels the system is termed persistent The fact that persistence may be more important than Lyapunov stability and that Lyapunov stability is not required for persistence has been pointed out many times (Lewontin 1969 Holling 1973 Innis 1974 Botkin and Sobel 1974 Waide and Webster 1975 Harrison 1979) Less work has been done on the mathematical formulation of persistence than on Lyapunov stability though Resigno and Jones (1972) and Gard and Hallam (1979) have derived mathematical criteria for predator prey chains

Another approach assumes that existing food webs are Lyapunov stable—they have survived natural selection because of that property However such systems may differ from each other in what has been variously called relative stability resilience or elasticity which is related to the time the systems take to return to equilibrium following a perturbation (note that Holling 1973 defines the term resilience in a different way)

Pimm (1979a b 1980a b) and Pimm and Lawton (1977 1978) have hypothesized that extant food webs are those that have the highest relative stability (the shortest time of return) as well as being Lyapunov stable In this volume PIMM reviews the consequences for food web structure from this assumption One of these consequences originally found by Pimm and Lawton (1977) is that food webs with many trophic levels would tend to have long return times compared to those with fewer trophic levels and hence tend to be selected against DeAngelis et al (1979) and DeAngelis (1980) added a footnote to Pimm and Lawton s work They noted that a high flux of energy per unit standing crop of biomass through a food chain could decrease the return time increasing the relative stability Hence systems with high energy flux could feasibly have more trophic levels This hypothesis has yet to be tested with real data

An interesting development in the study of food web relative stability as a function of connectance is discussed in the present volume by ARMSTRONG He shows that in food webs having certain symmetry properties analytic results can be derived that neatly show the variety of time responses that can occur in a single food web model This appears to be the mathematical analog of McNaughton s (1977) experimental results showing that diversity may enhance the functional stability of a food web while simultaneously decreasing the stability of the web to relative fluctuations in the species populations KING further elaborates this point using computer simulations of grazer dominated food webs of varying complexity He points out that while population stability decreases with complexity biomass stability increases The compensatory effect through the food web is enhanced if the food webs have relatively few plant species per herbivore more competing species and even plant abundances

(5) Spatial heterogeneity

Spatial heterogeneity was long ignored in models of more than one population However in the early 1970 s Cohen (1970) Levins and Culver (1971) Horn and MacArthur (1972) Van dermeer (1973) Comins and Blatt (1974) Maynard Smith (1974) Slatkin (1974) Levin (1974) Steele (1974) Levin and Paine (1974) and Roff (1974a b) pioneered analyses that included the spatial dimension and showed that spatial heterogeneity could both increase the proba bility of coexistence of competing species and stabilize predator prey limit cycles caused by Lyapunov instability It is possible that spatial heterogeneity plays a role in allowing food webs to increase in complexity without their becoming less stable

Food web processes

The flow of energy from the bottom to the top of the trophic ladder and the cycling of nutrients through the web are the two basic processes of a food web Some approaches to understanding the structure of food webs begin with the simple thermodynamic constraints governing these processes For example Elton gave the classical explanation for the rela tively small number of trophic levels observed in a food web According to his idea the inef ficiency of trophic transfer rapidly decreases the amount of calories available as one goes to higher levels in the web causing feeding on the highest level to become progressively unpro fitable at a rapid rate

Dynamic explanations discussed earlier have challenged this classical view that energet ics is responsible for the observed small number of trophic levels but the issue is still unde cided Yodzis (1980 1981) has shown that species assembled according to rules based on trophic efficiencies (which are always less than unity because of the second law of thermo dynamics and other causes of loss) produce food webs similar to those observed in nature not only in the number of trophic levels but also in other characteristics In the present vol ume YODZIS discusses the success of a new variation on this basic model

The cycles that carbon and other nutrients undergo in a food web can be considered enti ties in their own right deserving perhaps as much attention as species receive in traditional food web models In the present volume ULANOWICZ hypothesizes that the number of cycles in a food web may be positively correlated with the health of the ecosystem This is supported by data from a control ecosystem and one perturbed by thermal effluent showing a significant decrease in cycles and length of cycles in the latter

While it is obvious that the study of population dynamics has dominated food web theory during the past decade a synthesis of dynamic theory with the study of processes (see also Finn 1980 Van Voris et al 1980 Ulanowicz 1980 Ulanowicz and Kemp 1979) may be a most promising research area for the next decade

Prospects

Food web researchers face enormous challenges in the years ahead both in pure theory and in applications This latter topic applications of food web theory receives little atten tion in this volume because the task of applying what is known about food webs to the vari ous problems of environmental impact assessment has barely begun LEVIN cogently reviews here the problems environmental scientists face and some of the possible paths to solution

The final words of this work belong to MAY who describes both what we have learned about food webs in the past ten years and what we can strive to know in the next ten

REFERENCES

Abrams P A and T D Allison 1982 Complexity stability and functional response *Amer Natur* 115 639 649

Allen P M 1975 Darwinian evolution and a predator prey ecology *Bull. Math. Biol.* 37 389 405

Allen P M 1976 Evolution population dynamics and stability *Proc. Nat. Acad. Sci.* 73 665 668

Austin M P and B G Cook 1974 Ecosystem stability A result from an abstract simula tion *J Theor Biol.* 45 435 458

Botkin D and M J Sobel 1974 The complexity of stability In S Levin ed Ecosystem Analysis and Prediction SIAM Philadelphia pp 144 150

Briand F 1983 Environmental control of food web structure Ecology 64 253 263

Cohen J E 1970 A Markov contingency table model for replicated Lotka Volterra systems near equilibrium *Amer Natur* 104 547 559

Cohen J E 1977 Ratio of prey to predators in community food webs *Nature* 270 165 167

Cohen J E 1978 Food Webs and Niche Space Princeton University Press Princeton New Jersey 189 pp

Comins H N and D W E Blatt Prey predator models on spatially heterogeneous environ ments *J Theor Biol.* 48 75 83

Connor E F and D Simberloff 1979 The assembly of species communities Chance or com petition *Ecology* 60 1132 1140

Critchlow R E and S C Stearns 1982 The structure of food webs *Amer Natur* 120 478 499

Dean J M and R E Ricklefs 1979 Do parasites of Lepidoptera larvae compete for hosts? No! *Amer Natur* 113 302 306

DeAngelis D L 1975 Stability and connectance in food web models *Ecology* 56 238 243

DeAngelis D L 1980 Energy flow nutrient cycling and ecosystem resilience *Ecology* 61 764 771

DeAngelis D L R H Gardner J B Mankin W M Post and J H Carney 1978 Energy flow and the number of trophic levels in ecological communities *Nature* 273 406 407

DeAngelis D L R A Goldstein and R V O Neill 1975 A model for trophic interaction *Ecology* 56 881 892

Diamond J M 1975 Assembly of species communities In M L Cody and J M Diamond eds Ecology and Evolution of Communities Harvard Univ Press Cambridge Mass USA pp 342 444

Felsenstein J 1978 Macroevolution in a model ecosystem *Amer Natur* 112 177 195

Finn J T 1980 Flow analysis of models of the Hubbard Brook ecosystem *Ecology* 31 562 571

Force D C 1980 Do parasitoids of Lepidoptera larvae compete for hosts? Probably! *Amer Natur* 116 873 875

Gard T C and T G Hallam 1979 Persistence in food webs I Lotka Volterra food chains *Bull. Math. Biol.* 41 877 891

Gardner M R and W R Ashby 1970 Connectance of large dynamical (cybernetic) systems critical values for stability *Nature* 228 784

Gilpin M E 1975 Stability of feasibility predator prey systems *Nature* 254 137 139

Glasser J W 1982a A theory of trophic strategies The evolution of facultative specialists *Amer Natur* 119 250 261

Glasser J W 1982b On the causes of temporal change in communities Modification of the biotic environment *Amer Natur* 119 375 390

Goh B S 1980 Management and Analysis of Biological Populations Elsevier Scientific Publ Co Amsterdam 288 pp

Goh B S and L S Jennings 1977 Feasibility and stability in randomly assembled Lotka Volterra models *Ecol. Model.* 3 63 71

Harrison G W 1979 Stability under environmental stress Resistance resilience persistence and variability *Amer Natur* 113 659 669

Hassell M P and R M May 1973 Stability in insect host parasite models *J Anim. Ecol.* 42 693 726

Holling C S 1973 Resilience and stability of ecological systems *Annu. Rev Ecol. Syst* 4 1 24

Innis G 1974 Stability sensitivity resilience persistence What is of interest? In S Levin ed Ecosystem Analysis and Prediction SIAM Philadelphia pp 131 139

Lawlor L R 1980 Structure and stability in natural and commonly constructed competitive communities *Amer Natur* 116 394 408

Lawton J H and D R Strong Jr 1981 Community patterns and competition in folivorous insects *Amer Natur* 118 317 338

Levin S A 1974 Dispersion and population interactions *Amer Natur* 108 207 228

Levin S A and R T Paine 1974 Disturbance patch formation and community structure *Proc Nat Acad. Sci.* USA 71 2744 2747

Levins R 1974 The qualitative analysis of partially specified systems *Ann. N Y Acad. Sci.* 231 123 138

Levins R and D Culver 1971 Ecological coexistence of species and competition between rare species *Proc Nat Acad. Sci* USA 68 1246 1248

Lewontin R C 1969 The meaning of stability In G M Woodwell and H H Smith eds Diversity and Stability in Ecological Systems Brookhaven Nat Lab Publ no 22 pp 13 24

May R M 1972 Will a large complex system be stable? *Nature* 238 413 414

May R M 1973a Stability and ~~Connectance~~ complexity in Model Ecosystems Monographs in Population Biology 6 Princeton University Press Princeton NJ 235 pp

May R M 1973b Qualitative stability in model ecosystems *Ecology* 54 638 641

McMurtrie R E 1975 Determinants of stability of large randomly connected systems *J Theor Biol.* 50 1 11

McNaughton S J 1977 Diversity and stability of ecological communities A comment on the role of empiricism in ecology *Amer Natur* 111 515 525

Nunney L 1980 The stability of complex model ecosystems *Amer Natur* 115 639 649

Oaten A and W W Murdock 1975 Functional response and stability in predator prey systems *Amer Natur* 109 299 318

Odum E P 1969 The strategy of ecosystem development *Science* 164 262 270

Paine R T 1980 Food webs Linkage interaction strength and community infrastructure *J Anim Ecol.* 49 667 685

Pimm S L 1979a Complexity and stability another look at MacArthur s original hypothesis Oikos 33 351 357

Pimm S L 1979b The structure of food webs *Theor Pop Biol.* 16 144 158

Pimm S L 1980a Bounds on food web connectance *Nature* 284 591

Pimm S L 1980b Properties of food webs *Ecology* 61 219 225

Pimm S L 1982 Food Webs Chapman and Hall Publishers London 219 pp

Pimm S L and J H Lawton 1977 The number of trophic levels in ecological communities *Nature* 268 329 331

Pimm S L and J H Lawton 1978 On feeding on more than one trophic level *Nature* 275 542 544

Post W M and S L Pimm 1983 Community assembly and food web stability *Math. Biosci* (in press)

Post W M and C C Travis 1979 Quantitative stability in models of ecological communities *J Theor Biol.* 79 549 553

Powell R A 1980 Stability in a one predator three prey community *Amer Natur* 115 567 579

Roberts A and K Tregonning 1980 The robustness of natural systems *Nature* 288 265 266

Roff D A 1974a Spatial heterogeneity and the persistence of populations *Oecologia* 15 245 258

Roff D A 1974b The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment *Oecologia* 15 259 275

Sale P F and D McB Williams 1982 Community structure of coral reef fishes Are the patterns more than those expected by chance? *Amer Natur* 120 121 127

Siljak D D 1975 When is a complex ecosystem stable? *Math. Biosc* 25 25 50

Siljak D D 1978 Large Scale Dynamic Systems Stability and Structure North Holland Publishers New York 416 pp

Slatkin M 1974 Competition and regional coexistence *Ecology* 55 128 134

Steele J H 1974 Spatial heterogeneity and population stability *Nature* 248 83

Sutherland J P 1981 The fouling community at Beaufort North Carolina A study in stability *Amer Natur* 118 499 519

Tansky M 1978 Stability of multispecies prey predator systems *Mem. Coll. Sci. Univ Kyoto Ser* B 7 87 94

Tregonning K and A Roberts 1980 The robustness of natural systems *Nature* 288 265 266

Ulanowicz R E 1980 An hypothesis on the development of natural communities *J Theor Biol.* 85 223 245

Ulanowicz R E and W M Kemp 1979 Toward canonical trophic aggregations *Amer Natur* 114 871 883

Vandermeer J H 1973 On the regional stabilization of locally unstable predator prey relationships *J Theor Biol.* 41 161 170

Van Voris P R V O Neill W R Emanuel and H H Shugart 1980 Functional complexity and ecosystem stability *Ecology* 61 1352 1360

Waide J B and J R Webster 1975 Engineering systems analysis applicability to ecosystems In B C Patten ed Systems Analysis and Simulation in Ecology Vol 4 Academic Press New York Pp 329 371

Yodzis P 1980 The connectance of real ecosystems *Nature* 284 544 545

Yodzis P 1981a The stability of real ecosystems *Nature* 289 674 676

Yodzis P 1981b The structure of assembled communities *J Theor Biol.* 92 103 107

Yodzis P 1982 Compartmentalization of real and assembled ecosystems *Amer Natur* 120 551 570

Intertidal Food Webs Does Connectance Describe Their Essence

Robert T Paine

Organisms interact prey and predator (or exploiter—victim) relationships generate trophic links The pattern and detail of these linkages have become basic to most studies of food web design and assemblage stability (i e May 1973 Yodzis 1981 Abrams and Allison 1982 and many others) They underlie in a descriptive sense the issues of complexity and compartmentalization (Pimm and Lawton 1980) Application of the more dynamical concepts of interaction strength (May 1973) and species deletion stability (Pimm 1980) requires detailed and intimate knowledge of the web I will argue that the unit basic to all the above approaches the trophic link (and the derived term connectance) is variable enough so that theoreticians cannot test their views against or draw inspiration from descriptions of pat terns in natural communities Three neglected sources of difficulty will be discussed

Do predictable resources generate a preditable web

Connectance has been shown to vary locally seasonally and geographically (Paine 1980) in one well defined community although the most generalized features of that web retain their essence over a broad spatial scale (28° to 55°N lat) Not all assemblages however are characterized by such uniformity I have studied the major invertebrate prey and their pri mary consumers along the western shore of South America from 20 S to 43 S lat Specifics of the web may be found in Viviani (1975) and Castilla (1981) One of its features is that the predominant sessile prey i e barnacles mussels tunicates and tubeworms are found throughout this range with many beginning about 0 -5 S and extending to Tierra del Fuego Thus the prey species list remains relatively constant although the abundances of specific items shift from site to site Given then a predictable resource base what can be said about the dependent trophic structure and its complexity?

Table 1 provides one view when the diet of the dominant invertebrate predator the sea star *Heliaster helianthus* is examined Although the total number of links remains surpris ingly constant the primary prey category is site specific with barnacles tending to domi nate in the north and mussels to the south Rank order statistics (Spearman test) show no significant correlation (p > 05) between ranked prey in comparisons of the various areas However when prey abundance is ordered by % cover within an area it is always signifi cantly correlated with the rank order of prey in *Heliaster s* diet The obvious implication is that prey availability determines the weight given to each potential trophic pathway by this generalist starfish What is less obvious and unexplained is why *Heliaster* disappears from the community at about 34 S although all its sessile prey continue in abundance to at least 43 S Furthermore no ecologically equivalent replacement species appear When the entire coastline is considered other predators (*Acanthina Cracilabrum Stichaster* for instance) show little concordance as to where they enter or leave the assemblage Such deletions or additions seem to bear no relationship to whether a particular species diet is catholic or spe cialized Connectance in this community is thus variable geographically and it is discourag ing to recogr ize that the presence of a suite of prey has had little apparent infuence on the assembly of their consumers

Spurious links

Some maybe most prey predator links have little significance for the local community This is true because the majority of links usually are established with species at the rare

Table 1 The diet of the starfish *Heliaster helianthus* at four study sites along the exposed rocky shoreline of Chile A plus (+) indicates that an item amounted to less than 1% of the predator s prey items Numbers represent percent of total observed diet

	Iquique (20 15 5 S)	Antofagasta (23 42 S)	Los Molles (32 14 S)	Punta el Lacho (33 30 S)
Mussels				
Perumytilus purpuratus	+	2	4	60
Other mussels (3 spp)	3	22	37	13
Barnacles				
Jehlius cirratus	27	33	1	3
Chthamalu scabrosus	40	+	2	8
Balanoid barnacles (3 spp)	15	19	34	9
Snails (7 spp)	8	17	5	6
Limpets (5 spp)	6	+	16	1
Chitons (4 spp)	+	2	1	1
Urchins (2 spp)	1	+		+
Tubeworms (2 spp)	+	+		
Tunicate				
Pyura praeputialis	+	4		+
No observations	1480	1209	388	3026
No observed links	27	29	18	27

tail of species abundance spectra Thus *Heliaster* although connected to a minimum of 30 species concentrates its effort on only 2-4 It is these latter few not the former majority which are apt to be ecologically important However without biological detail no techniques exist to distinguish the spurious from the rare yet significant

Two examples will help to clarify the problem Levin et al (1977) by implicating a connection to terrestrial food webs have added an impressive three trophic level spur to the marine community described by Paine (1980) Although this spur should be ignored in most reconstructions of connectance its omission emphasizes the necessarily arbitrary and incomplete nature of all such descriptions A better example is found in the debate between Edwards et al (1982) and Menge (1982) in which the former argue that 2 trophic levels can and should be added to a food web generalized by Menge (1976) I believe Menge s rebuttal to be effective Nonetheless the new trophic levels and increase in linkage from 11 to 24 indicate the sensitivity of relatively simple assemblages to the addition of new participants Such additions of importance to theoretical discussions of the web appear to be of little biological consequence

All links are not created equal

Variation in linkage strength in certain aquatic communities is increasingly well documented (Paine 1980 Mann 1983) Where a predator is capable of influencing a prey itself in turn a significant community member cascades of effect ensue I believe one outcome is the development of trophically dependent subgroups (or compartments sensu Pimm and Lawton 1980) These appear to have an individual trophic structure and their local presence can add much descriptive complexity Because the extent of compartment expression or even appear

ance is dynamically coupled to species which are little influenced by their presence it remains uncertain whether they should be evaluated separately or with the rest of the community

The subtlety of the dynamic is suggested by Fig 1 drawn from work in progress (Paine unpubl) The chiton *Katharina tunicata* is a major herbivore which prefers to eat large brown algae but also consumes diatoms and some coralline algae *Katharina* removal leads to a fouling and subsequent increased mortality of coralline crusts and the local disappearance of the more specialized grazers dependent on these crusts *Katharina* must also suppress somehow members of the animal fouling community These eventually establish themselves in chiton removal but not in chitons only present plots and begin to overgrow both coralline and upright fleshy algae After 16 mo chiton removals the surface of some plots is more than 60% fouling community These space occupiers tend to be suspension feeding animals not plants some are characterized by their own specialized predators which were not present previously The net effect is a trend toward replacement of a 2 level by a 3 trophic level subsystem These mutually incompatable units add structural complexity to the local scene their presence however has little known significance for the community s major interactors

The qualitative value of connectance patterns

The sum of these observations on spatial and temporal variations spurious links and linkage inequalities is that I don t believe that quantitative interpretations of linkage patterns in natural communities is warrented It impresses me as a very insecure beginning from which to establish the reality or relevance of rigorous theory

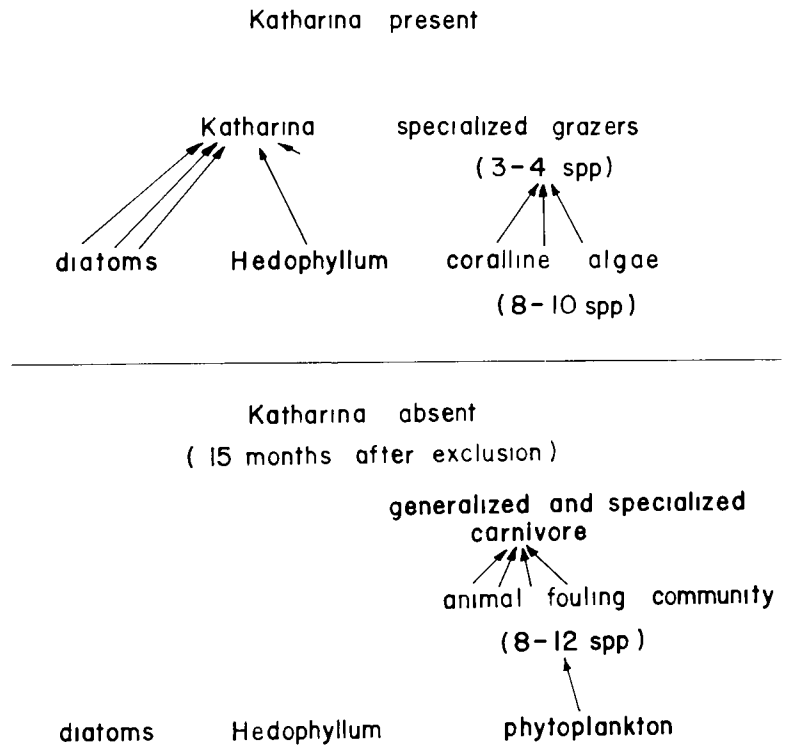

Fig 1 Food web structure with and without the chiton present

Instead I think that links when their implications are properly understood provide the ecologist with a qualitatively simple framework from which to predict the behavior of com plex multispecies systems Two examples drawn from many possible ones support this view Van der Elst (1979) has shown how suppression of large oceanic sharks a measure ini tiated for the benefit of swimmers in South Africa has lead indirectly to a deterioration of an inshore sports fishery The dynamics are understandable and the outcome of human interference even predictable from knowledge of linkage strengths Total web structure and connectance taken by themselves seem immaterial Mann and his coworkers (see Wharton and Mann 1981 for references) have worked out the details of why overexploitation of lob sters in Nova Scotia has produced severe and persistent environmental modification Embed ded in their reconstruction of events are foraging behavior and environmental heterogeneity both of which play major roles and neither of which are usually considered in conjunction with food web dynamics The lobster influence is readily understood in terms of interaction strength and the behavioral quirks of some web members Again general connectance pat terns and webbiness of the community seem unrelated to a qualitative understanding of the assemblage s response to severe perturbation

In conclusion interspecies linkage is a fundamental property of all communities—obviously no species lives in isolation from others One of my hopes for this workshop is that empiricism and theory will be brought a little closer together and that I will leave here with new insights and suggestions for future research directions which will generate data useful to the coming generation of theory

REFERENCES

Abrams P A and T D Allison 1982 Complexity stability and functional response *Amer Natur* 119 240 249

Castilla J C 1981 Perspectivas de investigacion en estructura y dinamica de comunidades intermareales rocosas de Chile central II Depredadores de alto nivel trofico *Medio Ambiente* 35 190 215

Edwards D C D O Conover and F Sutter 1982 Mobile predators and the structure of marine intertidal communities *Ecology* 63 1175 1180

Levin S A J E Levin and R T Paine 1977 Snowy owl predation on short eared owls *Condor* 79 395

May R M 1973 Stability and Complexity in Model Ecosystems Princeton University Press Princeton 235 pp

Menge B A 1976 Organization of the New England rocky intertidal community role of predation competition and environmental heterogeneity *Ecol. Monogr* 46 355 393

Menge B A 1982 Reply to a comment by Edwards Conover and Sutter *Ecology* 63 1180 1184

Paine R T 1980 Foodwebs linkage interaction strength and community infrastructure *J Anim. Ecol.* 49 667 685

Pimm S L 1980 Food web design and the effect of species deletion *Oikos* 35 139 149

Pimm S L and J H Lawton 1980 Are food webs divided into compartments? *J Anim. Ecol.* 49 879 898

van der Elst R P 1979 A proliferation of small sharks in the shore based Natal sports fishery *Env Biol. Fish* 4 349 362

Viviani C A 1975 Las comunidades marinas litorales en al norte grande Viviani *Publ. Ocasional Lab Marina Iquique* 1 1 196

Wharton W G and K H Mann 1981 Relationship between destructive grazing by the sea urchin *Strengylocentrotus droebachiensis* and the abundance of American lobster *Homarus americanus* on the Atlantic coast of Nova Scotio *Can. J Fish. Aquat. Sci.* 38 1339 1349

Yodzis P 1981 The stability of real ecosystems *Nature* 289 674 676

Recent Progress and Problems in Food Web Theory

Joel E Cohen

Introduction

In 1968 I proposed a way to set lower bounds on the dimensionality of trophic niche space by using data on food webs In 1978 I showed that in community food webs in a single habitat the data on trophic niche overlap were consistent with a one dimensional trophic niche space more often than might be expected from some simplified random models of food webs

This note has three parts First I will comment on some recent explanations and criticisms of my empirical finding of a high frequency of interval food webs (Sect 2) Second I will review some recent mathematical progress in the graph theory of food webs (Sect 3) Third I will state an outstanding theoretical question concerning the combinatorial structure of food webs (Sect 4) to explain the observed distributions of the length of maximal food chains I conclude with a list of open problems

Intervality of food webs fact or artifact

Let me review the general structure of the argument I used in 1978 I collected observed food webs I tested each observed food web to see if it had or did not have a certain property which I call property P (The property of interest was intervality but that is irrelevant for the moment) I also constructed a model of food webs that described successfully properties P_1 P_d other than property P of food webs [For example in model 5 of Cohen (1978 p 60) the number of kinds of predators was taken as given (P_1) the number of kinds of prey was taken as given (P_2) the number of predator prey interactions or directed arcs in the food web directed graph was taken as given (P_3) and the number of overlaps among the diets of predators or number of edges in the niche overlap graph was shown (Cohen 1978 p 69) to be very well described by the model (P_4)] Relative to this model the observed frequency of property P (intervality) substantially exceeded the expected frequency I inferred that P remained in need of explanation [It is concluded that the high observed frequency of arrangements of niche overlap that can be represented in a one dimensional niche space [property P] does not result from the operation within the framework of several plausible models [in particular of model 5 that describes P_1 P_4] of chance alone (Cohen 1978 p 92)]

More than one commentary has gone like this Ah yes but if you adjoin to your model additional properties P_{d+1} P_{d+2} P_{d+D} then the model with properties P_1 P_{d+D} fully explains the observed frequency of property P Therefore property P is an artifact of the omission of P_{d+1} P_{d+D} from your model

For example Yodzis (1981a) found that a model which he interpreted in terms of energetic constraints on the assembly of communities could not explain the observed frequency of intervality When Yodzis (1982) constrained the artificial food webs generated from the model to have a number of dominant cliques equal to the number observed the frequency of intervality could be explained [When Yodzis (1981c) chose different parameter values for his original model he was also able to account for the observed frequency of intervality but Lawton and Pimm (1982) pointed out that these new parameter values appear to be biologically senseless]

Similarly Critchlow and Stearns (1982 p 495) observed that the number of block submatrices in observed food web matrices is generally higher and the number of distinct diet

overlaps in observed food web matrices is generally lower than predicted by model 5 They asserted (p 496) without any calculation to justify their claim Failure to account for block submatrices and distinct diet overlaps introduced a bias into the analysis that led directly to the conclusion that interval food webs are improbably frequent No deeper explanation need be sought To justify this claim they would have to show that a model that correctly described the number of block submatrices and the number of distinct diet overlaps would also correctly predict the frequency of intervality They did not show this

In yet another approach Sugihara (1982) showed that the frequency of interval food webs could be accounted for by requiring that the niche overlap graph be a rigid circuit graph or by requiring that a certain simplicial complex constructed to reflect the sharing of food resources by predators have no holes

He incidentally showed that the existence of block submatrices may not suffice to explain the excess frequency of interval food webs The food webs he used are in fact connected components from real community food webs When he randomly assembled model food webs to allow small holes in the simplicial complex that describes resource use he found substantially fewer interval food webs in the artificial sample than in the real food webs This finding appears to contradict at least that part of the unsupported claim of Critchlow and Stearns pertaining to block submatrices However the random model of Sugihara differs from my model 5 on which Critchlow and Stearns based their other calculations in requiring that each compartment (food web in his language) be connected Whether the frequency of intervality would be correctly predicted by my model 5 if a block submatrix structure were imposed on it remains open but doubtful in the light of Sugihara s results

Let me pretend that the logical error in the argument of Critchlow and Stearns did not exist and respond as if all the above workers had proved their points

(a) Such explanations are exactly what I want congratulations! Indeed one purpose of modeling is to explain everything we think we know about food webs It is a happy event when the task of explaining one empirical discovery drives the incorporation of further empirical discoveries into a model

Now however that we have five explanations (two offered by Yodzis two by Sugihara and one asserted only by Critchlow and Stearns) plus qualitative ones offered by others which if any is correct? Can they all be correct? If so how are they to be reconciled? A large number of proofs of the existence of God raises doubts about the infallibility of any one of them though not of course about the existence of God itself the feeling is similar here

(b) Some of the explanations offered appear to push the problem of theoretical explanation one step back Suppose as Yodzis (1982) claimed the frequency of intervality is explained by constraining the number of dominant cliques or as Critchlow and Stearns (1982) claimed by constraining the number of block submatrices and distinct diet overlaps Then what explains the low number of dominant cliques and distinct diet overlaps and the high number of block submatrices in real food webs? Suppose you were trying to explain the variation in men s heights and you observed that almost all the variation could be explained if you knew the heights of their ears This represents some progress but it would be nice to be able to explain the heights of their ears In this regard the proposals of Sugihara (1982) are of special interest because he has tried to derive imputed community properties from an underlying theory of population dynamics

(c) The word artifact is loaded The fraction of food webs that are interval is determined by the food web data If failure to resolve different kinds of organisms biases food web data in the direction of intervality the solution is to refine the observations If the fraction of food webs that are interval can be explained by a tested model that also accounts for other features of food webs it means that our understanding has been enlarged not that intervality is an artifact

In the second half of this section I would like to point out two further misunderstandings in the article of Critchlow and Stearns (1982)

They asserted (p 479) that Cohen s techniques have no necessary connection to niches If two different kinds of predators take a single kind of prey organism under similar circumstances at one stage of the prey s life cycle I cannot see how any useful definition of niche would fail to imply that the niches of the two predators must overlap It seems to me that information about dietary overlap *does* provide some information about niches even if this information is not necessary and sufficient to describe all aspects of niche overlap

They also asserted (p 479) that the interval graph algorithm selected by Cohen is the wrong technique They amplified this assertion later (pp 493 494) The sets which overlap in a food web are the diets of the predators These sets are directly accessible and should be tested for interval representation with the interval diets criterion The interval diet overlaps criterion i e Cohen s interval food web criterion is an inherently more complicated and less precise method of testing a food web for interval diets "

The interval graph algorithm I used is indeed the wrong technique for answering the question Critchlow and Stearns asked whether diets themselves have an interval representation But that is a different question from the slightly more abstract one I was asking To pretend as Critchlow and Stearns have done that they asked the same question I asked only better is to generate confusion rather than progress

In brief Critchlow and Stearns applied the consecutive one s tests to the food web matrix directly I applied the consecutive one s test to the dominant clique matrix derived from the food web matrix Critchlow and Stearns have repeated some well known examples in which the two approaches give different answers Unfortunately these examples are too simple to be of help in deciding which approach is more useful So consider the following example

Suppose a food web C contains 7 kinds of predators p_1 p_2 p_7 (The argument would hold for any number of predators) Suppose C contains $\binom{7}{2} = 21$ kinds of prey For each pair p_i p_j of distinct predators suppose there is a prey species that constitutes the shared diet of p_i and of p_j and that the prey species is different for each distinct pair of predators (This assumption is much stronger and less realistic than what is required to make the following point but is a simple way of describing a food web matrix without the consecutive one s property that has an overlap graph that is a complete graph on 7 points) Then the diet of every predator in C overlaps with the diet of every other predator in C The consecutive diets test of Critchlow and Stearns would infer that the trophic niche space in this case could not be one dimensional because the food web matrix fails the consecutive diets test I believe it is more plausible to infer from the exhaustive pairwise overlapping of diets that there is some common region in trophic niche space that all 7 predators share and therefore that the dimensionality of the trophic niche space need not exceed 1

I hope this example makes it unmistakably clear that the two techniques really are different

Graph theory of food webs

In this section I will describe some mathematical facts developed in the last decade concerning food webs interval graphs and their generalizations Many of these results are due to Fred S Roberts and his students The best single review known to me is by his doctoral student Cozzens from whose thesis (1981) I learned of many of the results stated here

A digraph (= directed graph) is a finite set of vertices (corresponding here to kinds of organisms) and arcs or directed edges If (x y) is an edge then organism x preys on organism y Digraphs are of ecological interest as an approximation to the combinatorial structure of food webs It will be assumed here that all digraphs are acyclic and loopless The niche overlap graph G of a digraph D is a graph with the same vertices as D and an undirected edge between vertices x and y if and only if in D there is a vertex z such that

(x z) and (y z) are arcs of D In other words the trophic niches of x and y overlap if and only if they take some prey in common

The results I shall describe fall into two classes The first class deals with the question When is a given graph the niche overlap graph of some digraph? That is which niche over lap graphs could arise from some food web? The second class deals with the question Given a niche overlap graph when is it the intersection graph of some given family of sets? E g when is it an interval graph?

Roberts (1978) showed that the niche overlap graph of an (acyclic loopless) digraph always has at least one isolated vertex which is a vertex with no neighbors Moreover if G is any graph there is a finite number k such that the union of G with k isolated vertices is the niche overlap graph of a digraph The competition number k(G) of a graph G is the smallest integer k that works i e the least number of isolated vertices that must be adjoined to G to make the union into the niche overlap graph of some (acyclic) digraph Recently Opsut (1982) showed that the computation of a graph s competition number and hence the characterization of niche overlap graphs of (acyclic loopless) digraphs is an NP complete problem This means that the problem is hard

Lundgren and Maybee (1982) have characterized niche overlap graphs They define a col lection S of sets of vertices of G to be a line cover of G if each set in S is either a clique in G or the empty set and every vertex of G is in at least one of the cliques in S Then they prove a graph G with n vertices is a niche overlap graph if and only if the vertices of G can be labeled v_1 v_2 v_n so that G has a line cover $S = \{C_1 \quad C_n\}$ such that if the vertex v_i is in the set C_j then $i > j$ It follows that if G is a rigid circuit graph with an isolated vertex then G is a niche overlap graph of some (acyclic loopless) digraph In particular every interval graph with an isolated vertex is a niche overlap graph

Dutton and Brigham (1982) characterized the niche overlap graphs of digraphs that may have both cycles and loops Roberts and Steif (1982) characterized the niche overlap graphs of digraphs that are loopless but may have cycles

Roberts (1982) reviewed a variety of other applications of the mathematical ideas behind niche overlap graphs It is illuminating to see the ecological applications in this broader con text

I now turn to the characterization of an undirected graph G (in the present context G is a niche overlap graph) as the intersection graph of some family of sets Recall that G is an intersection graph of a family of sets S if there exists a function f that assigns to each vertex v of G a set f(v) in S such that for all vertices x and y of G (x y) is an undirected edge of G if and only if f(x) and f(y) intersect i e have a nonempty intersection

An intersection graph of the family of intervals of the real line is an interval graph The boxicity of a graph G denoted b(G) is the smallest integer k such that G is an intersection graph of boxes (rectangular regions open or closed) in the space of k dimensional real vectors (Roberts 1969) Obviously if G is an interval graph b(G) = 1 Roberts (1978) showed that the boxicity of a niche overlap graph can be arbitrarily high So an observation that many real niche overlap graphs have boxicity equal to 1 is not an artifact caused by considering niche overlap graphs Although a linear time algorithm is known for deciding whether a graph is an interval graph (Booth and Lueker 1976) Cozzens (1981) proved that the computation of the boxicity of a graph is an NP complete problem

Given a graph G with n vertices its adjacency matrix is an $n \times n$ matrix A with 1 everywhere on the main diagonal and for $i \neq j$ with $a_{ij} = 1$ when $(v_i \quad v_j)$ is an edge of G $a_{ij} = 0$ otherwise Mirkin (1972) showed that G is an interval graph if and only if the rows of its A can be permuted so that the consecutive one s property holds for the entries within a column at and below the main diagonal

Another well known characterization is that G is an interval graph if and only if none of its induced subgraphs is in a specified list of forbidden induced subgraphs Steif (1982) showed that if D is the acyclic digraph of a niche overlap graph G that is interval there

can be no forbidden induced subdigraph list that characterizes D However there does exist a list of forbidden *sink* induced subdigraphs for digraphs with interval niche overlap graphs Here a sink induced subdigraph is an induced subdigraph such that for every vertex x in the subdigraph if (x y) is an arc in the main digraph then y is also a vertex in the subdi graph [This corresponds to my (1978) notion of a sink subweb] Thus it is possible to deter mine whether a food web is interval by checking all its sink induced subdigraphs (sink subwebs) against a finite list

Lundgren and Maybee (1982) suggested the nice idea of studying a food web s common enemy graph which is the obvious dual to its niche overlap graph if D is the original food web digraph and D is the graph obtained by reversing the direction of all the arcs of D then the common enemy graph of D is the niche overlap graph of D i e two kinds of organisms have a common enemy if and only if there is a predator that preys on both of them

I showed in 1978 that a community food web has a niche overlap graph that is interval if and only if every sink food web in it has a niche overlap graph that is interval Dually Lundgren and Maybee (1982) showed that a community food web has a common enemy graph that is interval if and only if every source food web contained in it does

Another idea of potential ecological relevance is that of an overlap graph A graph G is an overlap graph if there is a function from the vertices of G to intervals on the real line such that two vertices are adjacent in G if and only if the corresponding intervals intersect *and* neither interval properly contains the other Obviously every overlap graph is an inter val graph but not conversely If one thinks of the intervals corresponding to vertices as one dimensional regions in the trophic niche space overlap graphs have the nice p operty of not allowing the trophic niche of one kind of organism to be contained in the trophic niche of another Gavril (1973) proved that every overlap graph is a circle graph and conversely A circle graph is defined as the intersection graph of a finite collection of chords on a circle

Food chain lengths

The problem of explaining or predicting the length of food chains has long intrigued ecol ogists The recent collection of substantial numbers of food webs in machine readable form presents a new opportunity and challenge for quantitative tests of food chain models So far as I know not a single model has been published that predicts quantitatively the frequency distribution of lengths of maximal food chains in a single food web or collection of food webs

Before anyone rushes out to do battle let me sound a note of caution regarding the data I published the frequency distribution of lengths of maximal food chains in four food webs in 1978 (p 59) When I learned from a manuscript of Peter Yodzis that he had computed these frequency distributions for all 40 food webs in the collection of F Briand I asked for and he kindly sent all 40 frequency distributions Three of my four analyzed food webs are among those in Briand s collection so I compared the frequency distributions computed by Yodzis and me for those three The statistics for my case 28 12 (Briand s 38) Rocky shore Lake Nyasa were identical The statistics for the other two cases shown in Table 1 were not

The differences are probably due to Briand s correction of the data I used In the food web matrix of the Aspen forest Canada Briand (1983 Appendix) reported modifying entries that would explain why Yodzis showed two fewer prey than I did This change affects substantially the frequency of maximal food chains of length two Similarly in the food web matrix of the sandy shore Lake Nyasa Briand reported deleting two columns and one row (these were duplications I did not detect) This change has little effect on the frequency dis tribution of chain lengths

Table 1 Comparison of frequency distributions of lengths of maximal food chains in two food webs as computed by Cohen (1978) and Yodzis

Food web	Aspen forest	Canada	Sandy shore	Lake Nyasa
Author	Cohen	Yodzis	Cohen	Yodzis
Identification number	1 3	25	28 2	39
Predators	22	22	34	32
Prey	19	17	18	17
Interval	Yes	?	No	?
Length of chain		Frequency		
1	2	3	21	20
2	9	17	37	36
3	6	5	11	11
4	7	1	0	0
>4	0	0	0	0

In light of the possible sensitivity of the frequency distribution of maximal food chain length to the details of the food web data it is important to make those data as reliable as possible before too much effort is invested in explaining the quantitative details of these frequency distributions

In spite of this caveat I believe that quantitative tests such as I propose are essential for sharpening our models and for getting rid of the host of speculations that are biologically plausible qualitatively correct and actually wrong

Conclusion open problems

Aside from general exhortations the preceding remarks identify some specific open problems

1 Suppose random food webs are generated by my model 5 and all of them in which the number of block submatrices differs from the observed number are discarded Among those remaining will the frequency of intervality approximate the observed frequency of intervality? In other words will conditioning on the observed number of block submatrices really explain the frequency of intervality as Critchlow and Stearns (1982) claimed?

2 Similarly will conditioning on the observed number of distinct diets explain the observed frequency of intervality?

3 Will conditioning on the number of block submatrices and the number of distinct diets explain intervality?

4 Are the common enemy graphs of real food webs interval about as frequently as would be expected from random models?

5 Are the niche overlap graphs of real food webs overlap graphs (i e representable without proper inclusion of intervals) about as frequently as would be expected from random models?

6 Can dynamic models of the kind recommended by Lawton and Pimm quantitatively explain the frequency distribution of maximal food chain lengths? Can they quantitatively account for the frequency of intervality?

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REFERENCES

Booth K and G Lueker 1976 Testing for the consecutive ones property interval graphs and graph planarity using PQ tree algorithms *Journal of Computer and Systems Science* 13 335 379

Briand F 1983 Environmental control of food web structure *Ecology* 64 253 263

Cohen J E 1968 Interval graphs and food webs a finding and a problem RAND Corporation Document D 17696 PR 30 August 1968

Cohen J E 1978 Food Webs and Niche Space Princeton Princeton University Press

Cozzens M B 1981 Higher and Multi Dimensional Analogues of Interval Graphs Ph D thesis Rutgers University New Brunswick N J March 1981

Critchlow R E and S C Stearns 1982 The structure of food webs *American Naturalist* 120 478 499

Dutton R D and R C Brigham 1982 A characterization of competition graphs In press *Discrete Applied Mathematics*

Gavril F 1973 Algorithms for a maximum clique and a maximum independent set of a circle graph *Networks* 4 261 273

Lawton J H and S L Pimm 1982 Pattern and process in food webs Manuscript May 1982

Lundgren J R and J S Maybee 1982 Food webs competition graphs and associated matrices In press *Discrete Applied Mathematics*

Mirkin B G 1972 Description of some relations on the set of real line intervals *Journal of Mathematical Psychology* 9 243 252

Opsut R J 1982 On the computation of the competition number of a graph In press *SIAM Journal on Algebraic and Discrete Methods*

Roberts F S 1969 On the boxicity and cubicity of a graph In Recent Progress in Combinatorics (W T Tutte ed) New York Academic Press 301 310

Roberts F S 1978 Food webs competition graphs and the boxicity of ecological phase space In Theory and Applications of Graphs (Y Alavi and D Lick eds) New York Springer Verlag 477 490

Roberts F S 1982 Application of edge coverings by cliques Manuscript June 1982

Roberts F S and J E Steif 1982 A characterization of competition graphs of arbitrary digraphs In press *Discrete Applied Mathematics*

Steif J E 1982 Frame Dimension Generalized Competition Graphs and Forbidden Sublist Characterizations B A thesis Rutgers College New Brunswick N J May 1982

Sugihara G 1982 Niche Hierarchy Structure Organization and an Assembly in Natural Communities Ph D thesis Princeton University Princeton N J May 1982

Yodzis P 1981a The structure of assembled communities *Journal of Theoretical Biology* 92 103 117

Yodzis P 1982 The compartmentalization of real and assembled ecosystems *American Naturalist* 120 551 570

Yodzis P 1981c Why are so many niche spaces one dimensional? Manuscript August 1981

Holes in Niche Space A Derived Assembly Rule and its Relation to Intervality

George Sugihara

Introduction

A central problem in ecology involves finding and understanding constraints shaping the assembly of ecological systems This problem has been manifested in studies of energetics (Lindeman 1942) succession (Curtis 1954 Horn 1971 Shugart and West 1980) colonization (Patrick 1968 Paine 1980) and in interpreting biogeographic patterns in the data (Diamond 1975 Heatwole and Levins 1972) Recently Cohen (1978) has expanded the list to include some intriguing graphical properties of food webs This work is important not only for the regularities discovered but because it opens the way for a formal study of mathematical structure in food webs My aim here will be to extend this analytical approach by proposing a new mathematical characterization of the niche and by reporting on two interrelated topo logical results that help to shape the assembly of real communities

Niches Tinker Toys and Crystals

In Cohen s (1978) *niche overlap graph* G(C) consumer species are identified with the ver tices of a generalized graph and two vertices are joined by an edge if and only if they share some resource in common (Fig 1C) This portrait of the niche characterizes the overlap pattern or potential competitive structure of communities Here consumer species are *objects* (vertices) and shared resource is the *relation* (edge) joining these objects

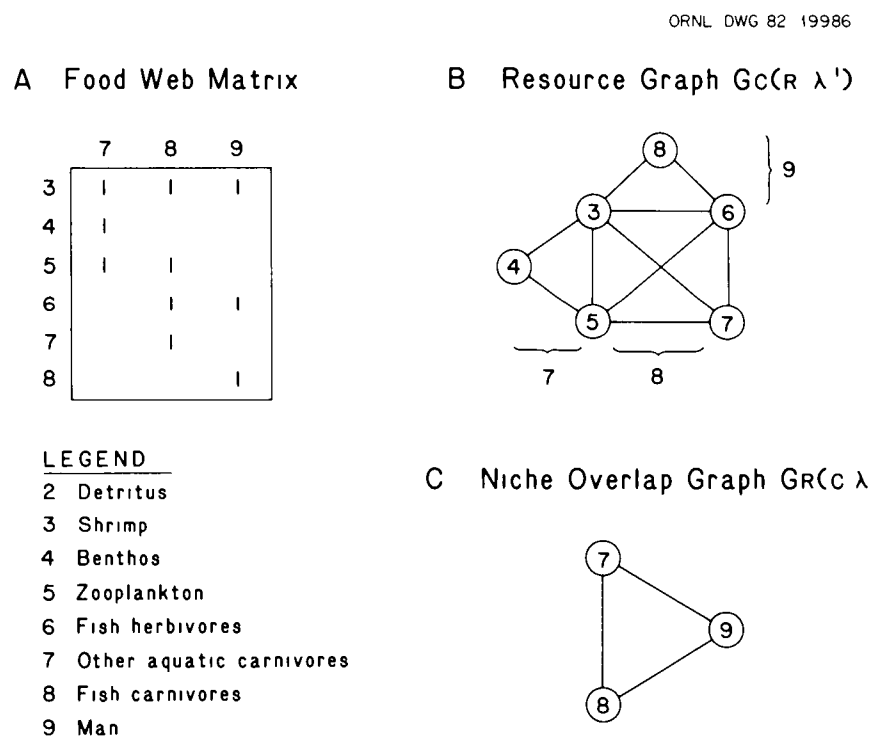

Fig 1 Food web matrix niche overlap graph G(C) [or G_R(C λ) above] and resource graph G^{-1}(R) [or G_c(R λ) above] for Cochin backwater (in Sugihara 1982)

Although it is mathematically well defined the niche overlap graph represents a rarified condensation of the true multidmensional communal niche (sensu Whittaker 1972) For example in Fig 1C although the niche of fish carnivores includes four distinct resource categories it is represented as a single vertex in G(C) Furthermore although it overlaps other aquatic carnivores (7) with respect to two resources shrimp (3) and zooplankton (5) this overlap is collapsed down to a single edge That is individual species hypervolumes (Hutchinson 1958) are collapsed down to single points and multiple resource overlaps are reduced to single edges

A fuller characterization of the communal niche that aligns more closely with the mul tidimensional Hutchinson Whittaker model may be obtained simply by constructing the con jugate or inside out version of the niche overlap graph (Fig 1B) In these so called *resource graphs* (Sugihara 1982) G(R) resources rather than consumers are taken to be the primary objects of interest (vertices) with consumers defining relations (edges) among the resource points (Fig 2) As in the Hutchinson Whittaker model a consumer species is defined as a mapping over the resources it uses In graph theoretical terms this means that a consumer s n dimensional niche may be represented as a *clique* (maximally connected sub graph) over its resource base A species n dimensional niche therefore consists of n resource points all mutually connected In the example above (Fig 1B) the trophic niche of fish carnivores consists of four resource points all mutually joined to form a clique over four vertices

In application G(R) can be viewed as a tinker toy model in which the articulation points or joints correspond to resources and the species niches are represented simply as struts of a given color maximally connecting a set of resource points The community niche is created by linking up the toy species niches so that their labeled articulation points (resources) match The resulting tinker toy model yields a robust geometrical portrait of the multidi mensional community niche

The resource graph model can be modified slightly by inflating it in a higher dimensional space so that the vertices and edges of a species clique identify with the vertices and edges of a *simplex* In geometrical terms this gives rise to a solid tinker toy model where the n dimensional species niches may be thought of as convex polyhedra The n vertices of each polyhedron correspond to the n resources used by that species This generates a powerful architectural description of communities where the polyhedral species niches are joined

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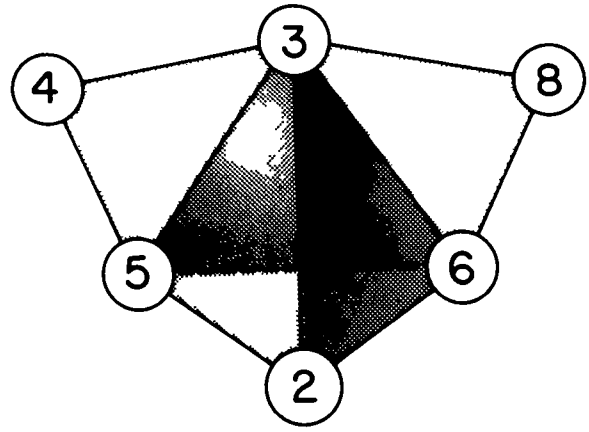

Fig 2 The Cochin backwater community (Fig 1) as a simplicial complex

through shared resource vertices to form a *simplicial complex* K(R) (Fig 2) According to this model a community hypervolume may be broadly visualized as a multidimensional crystal having clusters of crystal faces which correspond to individual species niches

Holes in Niche Space

We shall now apply this characterization of the niche to data to determine how real crystalline species niches fit together to form a community complex In particular we shall determine if natural ensembles are packed densely as a simple solid or if they are constructed loosely to contain holes as in a multidimensional swiss cheese (Fig 3) This is viewed as the converse of the well known species packing problem and asks if any minimal constraints come into play in assembling communities

An analysis of corrected data (Sugihara 1982) compiled originally by Briand (1983) reveals that most if not all real communities tend to be packed conservatively in a manner that precludes holes (Fig 4) This data set spanning 40 different food webs contains 73 nontrivial communities (containing more than two species) A community here is defined as a connected component in G(C) The surprising result is that out of the 73 distinct communities represented none had p dimensional holes with $p \geqslant 2$ (a hollow sphere contains a two dimensional hole) and only two had one dimensional holes This is indeed surprising in view of the fact that randomly assembled simplicial complexes having the same component simplexes as in the Briand data will generate an expected 22 06 communities with holes (Sugihara 1982) Therefore real communities although rich in their detailed mosaic patterns tend to be packed simply and this dense packing represents a nonrandom element of structure that is specific to ecological assemblages

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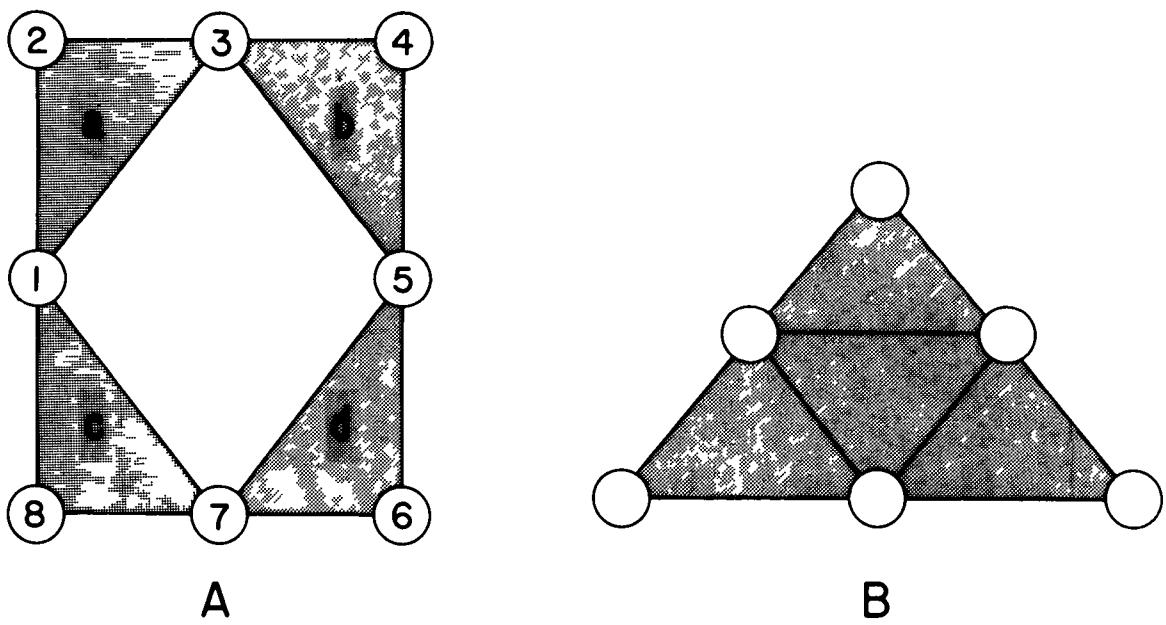

Fig 3 Two alternative packing schemes in K(C) In both cases all species are defined on three sources In B species are packed conservatively while in A they are packed loosely leaving a hole in the complex

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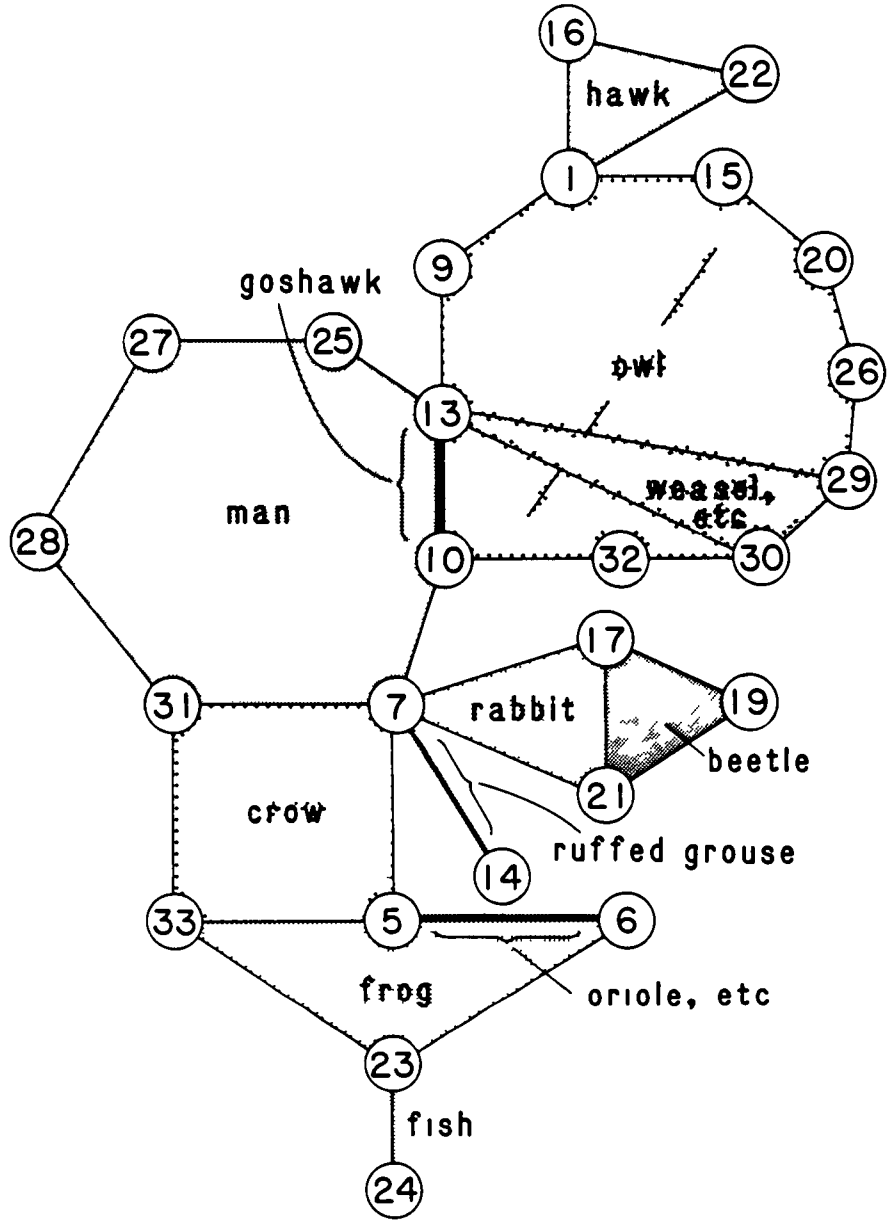

Fig 4 Bird s Aspen Parkland Community (Sugihara 1982) A representative example of K(C) modified for purposes of illustration so that shaded polygons correspond to species

Aside from its interest as a fundamental topological property of communities the primary biological significance of this result is the implication that resources in the environment are ordered or correlated with each other by various means (e g spatially taxonomically by size) and that this ordering is perceived similarly by all of the species involved For example consider an insectivorous lizard community where the prey sizes may be grouped into the categories large middle and small As seen in Fig 5 the appearance of a

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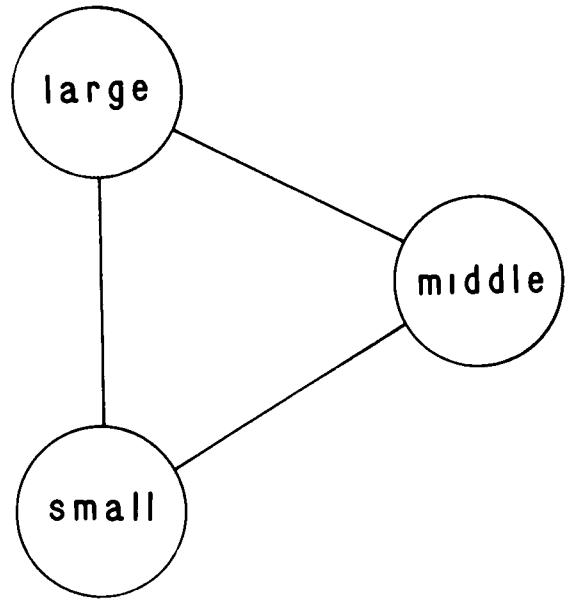

Fig 5 A hole may be created if a local ordering in the resource set is not obeyed Here each species consumes two resources and is described by an edge connecting two resource points One species eats small and middle sized insects another eats middle and large insects and the third (hole maker) eats large and small insects

lizard on the scene that eats only large and small insects while avoiding the middle sized ones will create a hole On the other hand if this lizard obeyed the size ordering and also took in middle sized prey items the hole would be filled One should not be misled by this grossly simple example because some of the orderings can be quite subtle (Sugihara 1982)

It is worthwhile to mention that the observed lack of holes in K(R) marches with the additional finding that species niches tend to be strung together in a tree like fashion (Sug ihara 1982) Both of these properties the absence of holes and the underlying tree structure in the niche are consistent with an evolutionary scenario for communities in which there are interchangeable species having equivalent ecological roles (Sugihara 1982)

In the next sections we shall see how the lack of holes in K(R) relates to other topologi cal regularities namely Cohen s intervality and how both may be underpinned by a simple mathematical assembly rule

Assembly

Recently Yodzis (1981) has proposed an intriguing list of *a priori* assembly rules that are designed to explain certain features of real food webs (Cohen 1978) As a complement to this inductive approach I will here mention an assembly rule that can be mathematically deduced from a specific property of the final niche overlap graph G(C)

In simple terms the assembly rule requires that species be incorporated into a commu nity conservatively by attaching to single guilds rather than by bridging multiple guilds (see Fig 6) Here the term guild identifies with the graphical usage clique (maximally con nected subgraph) That is species of a given guild are represented as mutually connected vertices in G(C)

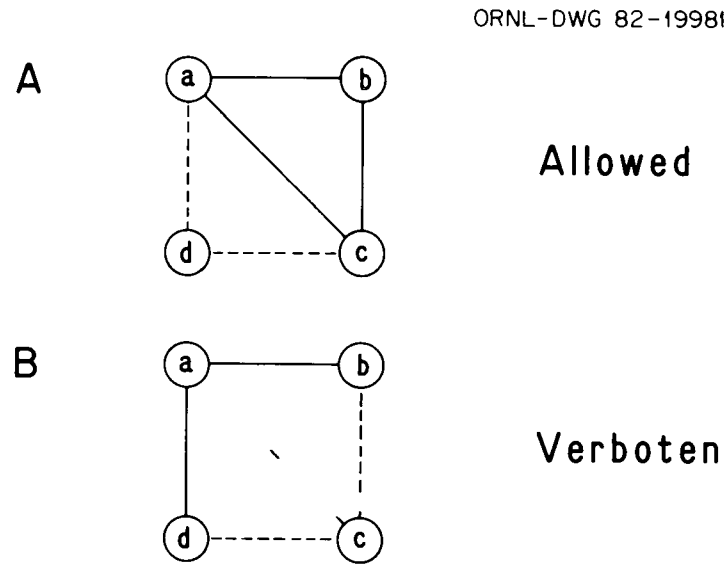

Fig 6 Two alternative incorporation sequences in G(C) In A the last species d is added to a single guild (clique) in B species c is added by bridging two guilds (a d) and (a b)

Put briefly the assembly rule is derived from the observation that all of the niche overlap graphs G(C) in Briand s corrected collection possess the rigid circuit property [no circuits of length ≥4 without a chord i e triangulated (see Fig 7)] (Dirac 1961 Sugihara 1982) Interestingly graphs having this property can always be collapsed into smaller rigid circuit graphs by successively eliminating points whose *neighbors form a clique* (extreme vertex) (Rose 1970) Conversely one may always build a rigid circuit graph by adding such extreme vertices If each additional vertex joins to more of the vertices already present than any subsequent vertex then provided the final graph is rigid they must have been extreme vertices In biological terms if each additional species is a relative specialist (overlaps with more species already present than any subsequent species) and the final overlap graph is rigid they must have been incorporated into single cliques or guilds This conservative assembly rule can be shown to be both necessary and sufficient provided that the final niche overlap graph is rigid and species are added in order of increasing relative specialization as described above

Assembly and Holes

The deduced assembly rule can be applied to explain the lack of holes in the simplicial complex model of the niche

Suppose that a guild or clique in G(C) is defined by a common resource V_0 (This is true in about all observed cases) Then it is easy to show that requiring successive species to be attached to single guilds means that the distance (number of edges) between V_0 and some other resource in the attachment set V_j must be less than two in K(R) This in turn preempts the possibility of holes in the community complex Therefore rigidity in the niche overlap graph and the absence of holes in K(R) emerge as companion properties in that both can be explained by a common assembly rule

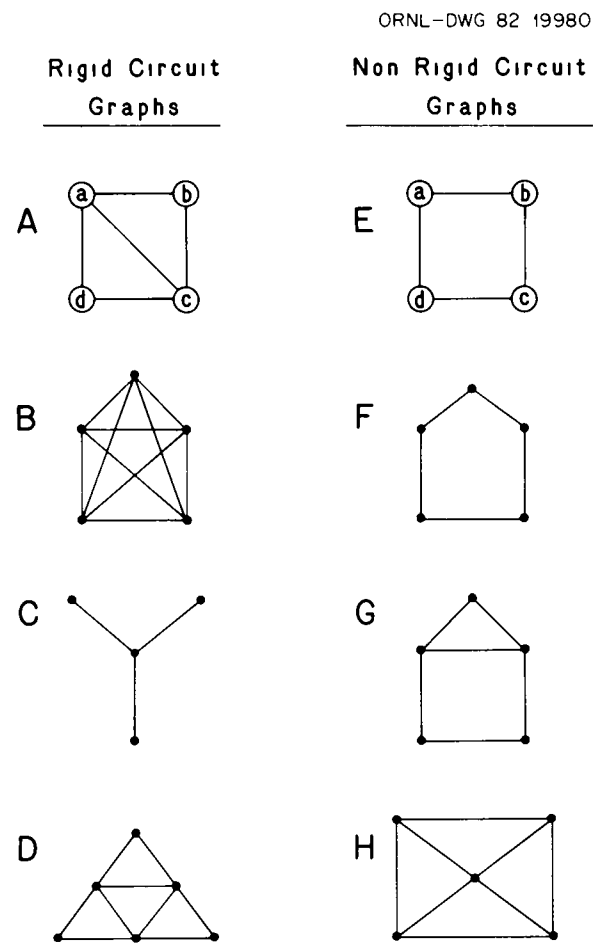

Fig 7 The rigid circuit property no circuits of length ≥4 without a chord

Assembly and Intervality

In his monograph Food Webs and Niche Space Cohen (1978) reported that it is possible to collapse real niche overlap graphs into one dimensional representations known as inter val graphs far more often than would be expected at random (Fig 8) As of date no firm explanation has been found for this intriguing discovery (but see Yodzis in this volume)

The necessary and sufficient conditions for a graph G to be interval are as follows (Lek erkerker and Boland 1962)

1 G must be rigid cricuit

2 G must not be asteroidal

The first property has already been described and the second condition requires roughly that a graph not be too large and tentacled

Because real niche overlap graphs tend to be rigid one might ask whether satisfying this condition by itself might not be sufficient to explain the high frequency of intervality That is could the nonasteroidal condition be superfluous?

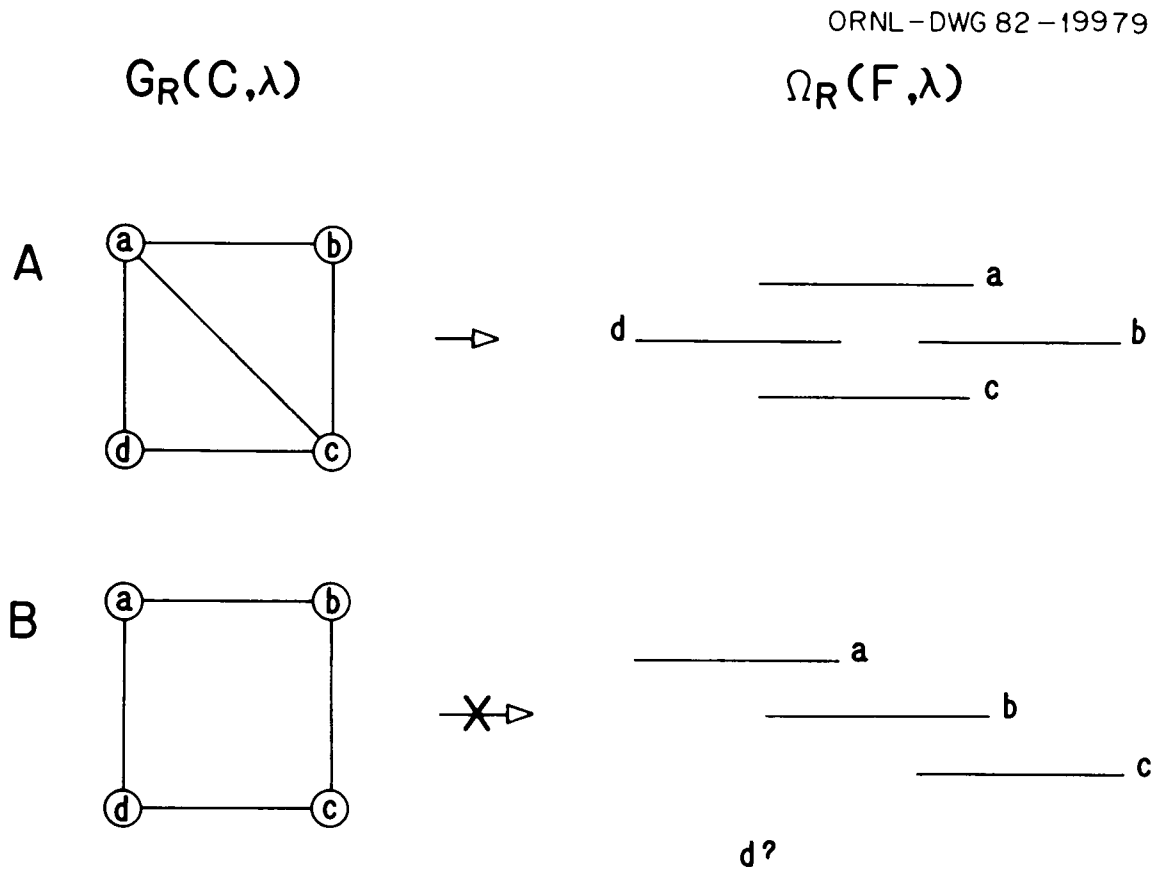

Fig 8 An illustration of intervality The niche overlap graph A can be reduced to a set of overlapping intervals on the line whereas B cannot

To test this idea random rigid circuit graphs were constructed for Briand s webs using the described assembly rule The results obtained (1000 simulations for each community) show a striking agreement with the natural frequency 62 communities were observed to be interval and 62 35 were predicted to be interval by random assembly (Z = 0 326) There fore our assembly rule and rigidity *per se* appear to be sufficient to explain the high fre quency of interval niche overlap graphs Thus intervality *per se* is not selected for but emerges as a consequence of the more fundamental rigid circuit property Rigidity in turn is tied to the lack of holes cited earlier and both can be explained by our necessary and suf ficient assembly rule

Robustness

That the empirical regularities described thus far (no holes and the companion property rigid circuits) should show up at all is surprising in view of the fact that they are based on such a wide diversity of food webs Paine (1980) has pointed out that a possible shortcoming of analyzing such food web properties is that they are based on simple binary portraits of the niche with no reference to the strength of linkages or the thresholds chosen for deciding the presence or absence of interactions among species Accordingly one might expect that

any topological properties discovered should be sensitive to the threshold chosen for deciding the existence of interactions Yet the appearance of these regularities across studies which must have used different thresholds suggest that they might be robust

To test this idea the set of community matrices assembled by Cody (1974) representing eleven different bird assemblages worldwide were examined to determine whether recruiting successively weaker linkages (lower α values in the matrix) would change the rigid circuit structure of the corresponding niche overlap graph Figure 9 shows two representative sequences As can be seen the rigid circuit property is preserved at all thresholds In all out of a total of 959 edges added only 27 resulted in nonrigid circuits and most of these became triangulated with the addition of the next few edges (Sugihara 1982) In fact if a small measurement error of 0 05 is allowed in Cody s estimates one could argue that all 959 edges could be added in a manner that preserves rigidity in G(C) Therefore rigidity and the accompanying lack of holes emerge as robust properties of communities

It is interesting to note that this robustness implies that the utilization surfaces for communities must be *quasiconvex* That is they must be capable of shedding water without forming pools or hollows (every point on the surface must have a directional derivative that is less than or equal to 0) Such quasiconvexity (rigidity at all levels) might help to explain the observation that real communities are more dynamically stable than randomly permuted ones (Lawlor 1980 Yodzis 1980)

REFERENCES

Briand F 1983 Environmental control of food web structure *Ecolog* 64 253 263

Cody M 1974 Competition and the Structure of Bird Communities Princeton Univ Press

Cohen J E 1978 Food Webs and Niche Space Princeton Univ Press Princeton

Curtis J T 1954 The Vegetation of Wisconsin Univ of Wisconsin Press Madison

Diamond J M 1975 Assembly of species communities pp 342 344 IN Cody M L and J M Diamond (eds) Ecology and Evolution of Communities Belknap Press Cambridge

Dirac G A 1961 On rigid circuit graphs *Abh. Math. Sem. Univ Hamburg* 25 71 76

Heatwole H and R Levins 1972 Trophic structure stability and faunal change during recolonization *Ecology* 53 531 534

Horn H S 1971 The Adaptive Geometry of Trees Princeton Univ Press Princeton

Lawlor L R 1980 Structure and stability in natural and randomly constructed competitive communities *Amer Natur* 116 317 338

Lekerkerker C G and J C Boland 1962 Representation of a finite graph by a set of intervals on the real line *Fund. Math. Polska Akad. Navk* 51 45

Lindeman R L 1942 The trophic dynamic aspect of ecology *Ecology* 23 399 418

Paine R T 1980 Food webs linkage interaction strength and community intrastructure *Journal of Animal Ecology* 49 667 685

Patrick R 1968 The structure of diatom communities in similar ecological conditions *Amer Natur* 102 173 183

Shugart H H and D C West 1980 Forest succession models *Bioscience* 30 308 313

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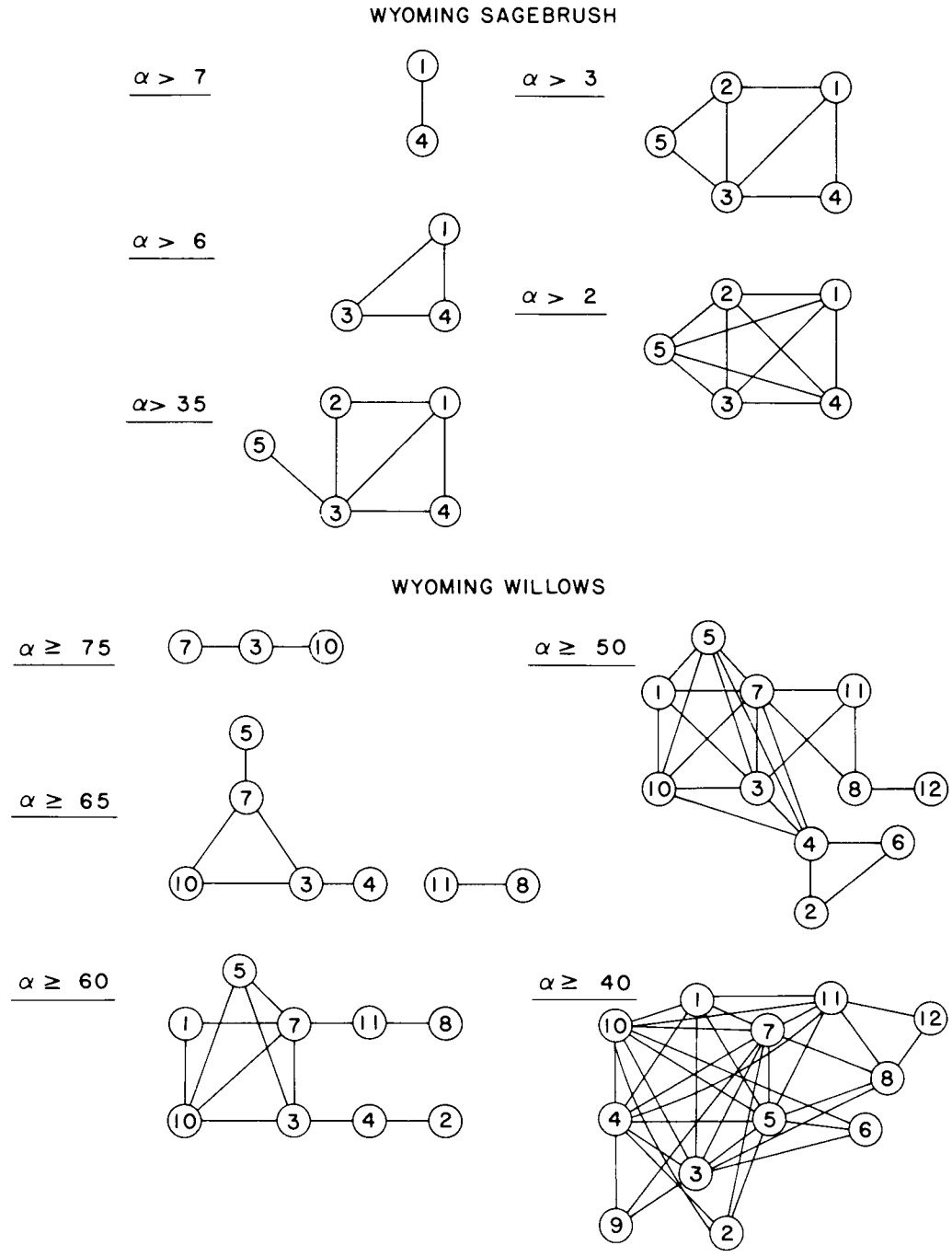

Fig 9 Real niche overlap graphs at various thresholds ($\alpha_j \geq t$) tend to be rigid

(A) Cody s (1974) Wyoming Sage Brush community

(1) Brewer s sparrow (3) Vesper sparrow (5) Brewer s blackbird
(2) Cliff swallow (4) W C Sparrow

(B) Cody s (1974) Wyoming Willows community

(1) C hummingbird (5) C C sparrow (9) Cliff sparrow
(2) Wilson s warbler (6) Trail s flycatcher (10) W C sparrow
(3) Yellow throat (7) Lincoln s sparrow (11) Fox sparrow
(4) Yellow warbler (8) Song sparrow (12) Swainson s thrush

Sugihara G 1982 Niche Hierarchy Structure Organization and Assembly in Natural Communities Ph D Thesis Princeton Univ

Whittaker R H 1972 Evolution and the measurement of species diversity *Taxon* 21 213 0251

Yodzis P 1980 The connectance of real ecosystems *Nature* 284 544 545

Yodzis P 1981 The structure of assembled communities *J Theor Biol* 92 103 117

Biogeographic Patterns in Food Web Organization

Frederic Briand

Due to the low number of real food webs generally known from the published record we have been so far unable to appreciate the part if there is any played by the abiotic environment in shaping trophic structure

To tackle the problem I first assembled a collection of 40 real community webs On that basis I established that trophic structure is markedly affected by the degree of variability independent of predictability of the physical environment Thus food webs in fluctuating systems are characterized by a significantly lower connectance than webs representative of more constant environments (Briand 1983)

The same collection also revealed some striking relations between habitat type and food web organization In particular forest pelagic and intertidal communities emerged as distinct groups in the space defined by connectance species richness and herbivorous fraction This however could only be described as a qualitative trend since the number of webs representing each biome was too small to allow statistical analysis (Briand 1983)

To pursue the question further I extended my collection of community webs to 62 These are representative of a wide variety of environments from all latitudes (see Table 1) The statistics of the main food web parameters given in Table 2 indicate a large degree of variance for most indices As an aside it appears worth noting that as many as 51 webs (i e 82% of the collection) are interval graphs which provides additional support to the findings of Cohen (1978)

A principal component analysis of all food web variables reveals that three factors account for more than 76% of the variance in the data The product SC (species richness × upper connectance) ranging from 2 3 to 20 8 is by far the major contributor to the first factor Average chain length and fraction of strict herbivores—the latter indicative of food web width —contribute the most to the second factor but in exactly opposite ways In other words the widest food webs will tend to be the shortest and vice versa Lastly fraction of top carnivores weighs the most on the third factor Interestingly neither fraction of omnivores (those organisms feeding on more than one trophic level) nor fraction of specialists appear among the major discriminating variables

Table 1 Biogeographic classification of 62 food webs

Environmental variability	
fluctuating	43
constant	19
Latitude	
tropical	14
temperature	38
high latitude	10
Environment	
totally aquatic	32
totally terrestrial	9
interface	21

Table 2 Basic statistics for 62 food webs

Variable	Mean	Range
no of organisms	17 85	5 45
lower connectance	0 26	0 05 0 60
connectance	0 43	0 18 0 85
trophic links	33 29	6 95
potential competitive links	38 39	1 257
average chain length	2 86	1 85 5 92
max chain length	5 19	3 9
% herbivores	32 68	5 55
% top carnivores	22 44	6 42
% interm consumers	54 05	20 79
% omnivores	27 44	0 64
% specialist consumers	41 10	0 88

Note upper connectance takes potential competition into account lower connectance does not (see Briand 1983 for details)

Next predefined groups of food webs corresponding to distinct habitat types and environmental regimes were compared using discriminant analysis This revealed profound and significant distinctions in trophic structure notably between

1 fluctuating (low sc) and constant (high sc) systems ($p < 0\ 0001$) This confirms a theoretical speculation of May (1981) and suggests that feeding optimization imposes structural changes when the level of environmental perturbation is relatively high (see Bri and 1983)

2 pelagic (longer food chains) and sublittoral benthic (shorter) systems ($p = 0\ 004$) This may be due to a lower assimilation efficiency in benthic systems where the energy transfer is largely detritus based

3 two dimensional (shorter wider) and three dimensional (longer thinner) systems ($p = 0\ 009$)

4 pelagic three dimensional aquatic (more generalists) and three dimensional terrestrial (more specialists) systems ($p = 0\ 015$)

5 intertidal and sublittoral (high sc) systems ($p = 0\ 015$) For reasons outlined in (1) above

Clearly then habitat tvpe geometrical configuration and temporal variability of the environment are leading factors as far as food web structure is concerned In conclusion (see Fig 1) I propose as a working hvpothesis that there exist four different sets of community assembly rules corresponding to four major biomes (intertidal sublittoral pelagic and 3 D terrestrial i e forests) to which we may soon add a fifth (2 D terrestrial i e tundra grassland desert) once representative webs become available

Acknowledgments

I am grateful to Peter Yodzis who kindly provided me with some of the computer programs

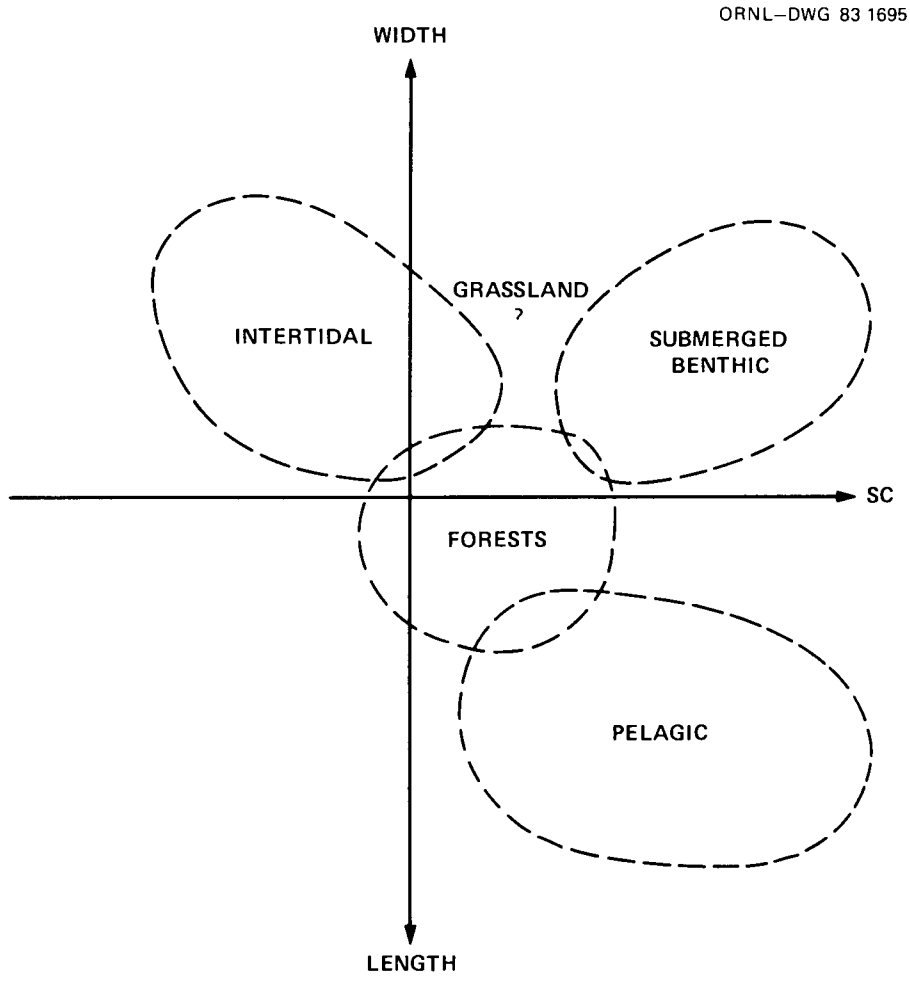

Fig 1 Schematic segregation of major biomes based on three food web characteristics sc food web width and average food chain length

REFERENCES

Briand F 1983 Environmental control of food web structure *Ecology* 64 253 263

Cohen J E 1978 Food Webs and Niche Space Princeton University Press Princeton New Jersey 189 pp

May R M 1981 Patterns in multi species communities IN R M May (ed) pp 197 227 *Theoretical Ecology* W B Saunders Philadelphia

Community Assembly Energy Flow and Food Web Structure

Peter Yodzis

Introduction

Ever since the eloquent paper of Hutchinson (1959) it has been part of ecology s conventional wisdom that the lengths of food chains in nature are constrained by energetic considerations—each link in a food chain corresponding to roughly a 10% transfer efficiency Pimm and Lawton (1977) suggested that such a viewpoint implies that more productive habitats should harbour longer food chains with roughly speaking each order of magnitude increase in primary production permitting one additional food chain link and Pimm (1982) has argued in some detail that this is not in fact observed

But a large increase in primary production will very likely lead to an increase in species diversity at all levels including top predators Therefore if a new super predator is to make use of the total additional production by *all* top predators (as required in the Pimm-Lawton argument) it will not only have to be able to survive on a marginal energy intake but it will have to be some kind of super generalist as well Energy flow cannot easily be dismissed as a structuring agent

Indeed there is rather direct observational support for the notion that energy flow is important for food web structure I have recently shown (Yodzis 1983) that in the food web collection of Briand (1983) there is a clear tendency for food chains to be longer when built above energetically efficient groups like invertebrates than when built above energetically profligate groups like endotherms (in contrast to the findings of Pimm 1982)

I have been investigating (Yodzis 1981 1982) the structure of model food webs which arise from the random assembly of ecosystems by sequentially arriving species each of which has energetic requirements which must be met by consumption from some of the species already present

A preliminary set of rules defining such a stochastic process gave very encouraging results but suffered from several deficiencies (Yodzis 1981) While good fits were obtained for the statistics species richness proportion of herbivores ratio of number of prey to number of predators proportion of dietary specialists number of trophic links number of potential competitive links connectance and average maximal food chain length these fits required in some cases grossly unrealistic values of ecological efficiency and primary production In addition the assembly process had to be terminated in an unsatisfactory *ad hoc* way Moreover the predicted frequency of interval food webs (Cohen 1978) was significantly lower than the observed frequency and the extent of omnivory (Pimm 1980) was not considered at all

I present here a new set of assembly rules which overcome all these difficulties at least for food webs from fluctuating environments

The rules are as follows Given three real parameters (N P E) with N a positive integer P a positive real number and $0<E<1$

1 The community starts from N basal species each with production P A sequence of additional species then enters the community

2 A newly arrived species has a total required energy intake say e which is chosen from the interval $(1\ 10^5)$ according to the probability density

$$p(e) = \begin{cases} C_1(e-1) & 1<e<10 \\ C_2/e & 10<e<10^5 \end{cases}$$

where the constants C_1 and C_2 are determined by requiring that p(e) should be continuous and that its integral over the interval (1 10^5) should be equal to 1

3 The new arrival chooses a sequence of distinct species already in the community say $\{s_1\ s_2\ s_3\ \}$ as follows For each s_i the probability to be chosen for each species present but not yet in the sequence is proportional to its total unutilized production

For each species s_i the new arrival is allowed to utilize a randomly chosen fraction $f_i\ \epsilon\ (0\ 1)$ of that species total production

In general each s_i will already have other species feeding on it In case the fraction of s_i s production which is not already being utilized in this way is smaller than f_i f_i is changed so that it is equal to the total unutilized fraction of s_i s production

Then if P_i is the total production of s_i the new arrival has available to it an energy f_iP_i from species i for each i

4 The sequence defined in step (3) terminates as soon as the cumulative sum

$$T = f_1P_1 + f_2P_2 +$$

exceeds e In case T never reaches e even after all species present are included in the s_i the new arrival cannot enter the community and another species tries to enter instead starting from step (2) If the sequence does terminate but T>10e the last f_i is adjusted so that T=10e

5 The total energy intake of the new species is then T Every species except for the N basals is assumed to have an ecological efficiency (Slobodkin 1960) E Thus the new species has after taking its place in the community a total production ET which is available to subsequently arriving species

6 Because E<1 there will come a point in this sequence of newly arriving species at which the total unutilized production in the community is less than 1 This is not sufficient to support any further species [rule (2)] so the assembly process must terminate

These rules define a three parameter family of *assembled communities* and their corresponding *assembled food webs*

In order to determine whether assembled food webs are reasonable models for the food webs observed in nature we must for each given real food web ask whether there exist parameters N (equal to the number of basal species in the real food web) P and E such that the real food web could plausibly have been chosen at random from the statistical subuniverse of assembled food webs with those parameter values I have explored this question for the collection of 40 community food webs culled from the literature by Briand (1982) this is the most complete published food web collection

As test statistics I use the quantities S (species richness) p_h (proportion of herbivores) R (ratio of the number of prey species to the number of predator species) p_s (proportion of specialist predators) I_t (number of trophic interactions) I_o (number of loop forming omnivore links) I_c (number of potential competitive interactions C_l (lower connectance) C_u (upper connectance) and L (average maximal food chain length) The following procedure was used to test the hypothesis that a given real food web could plausibly have been chosen at random from the set of all assembled food webs with parameters (N P E) Using a pseudo random number generator and the parameters N (equal to the number of basal species in the real food web) P and E 100 webs were assembled according to the rules in Section 2 For this sample of 100 model food webs the range of each test statistic was calculated If the value for the real web of more than one test statistic lay outside the calculated range the hypothesis was rejected Otherwise it was accepted

Table 1 lists the Briand food webs for which acceptable fits were obtained cases in which one test statistic was out of range are marked with an asterisk Most of the webs could be fitted with several different values for P and E For listing in Table 1 and for

Table 1 The Briand communities as assembled communities

Case	Primary production	E	Intervality	Expected intervality
1	1400	01	1	1 00
2	9000	01	1	84
3*	3600	001	0	94
4*	12000	01	0	90
5	95	01	1	1 00
6*	72000	01	0	53
7	24000	01	1	63
8	4000	01	1	85
9	800	1	1	89
10	63	1	1	1 00
11	300	01	1	97
12	12000	001	1	98
13	12000	001	1	98
14	4000	01	1	99
15	9000	01	1	99
16	3200	01	1	90
17	1800	1	1	58
18*	3200	001	0	65
19	12000	01	1	90
20*	18000	01	0	82
23	40000	01	1	87
24	1200	01	1	87
25	90000	001	1	83
26*	36000	001	0	34
27	8000	01	0	80
34	200	1	1	83
37*	24000	001	1	84
40	3000	001	1	1 00

subsequent calculations those parameter values were used for which the mean species richness of the assembled webs was closest to the actual value It will be seen that the efficiencies E and the range of total primary production (=NP) used for the fits are realistic

Briand (1982) classifies the habitats in which these food webs were found as fluctuating (Case Nos 1 28) or constant (Case Nos 29 40) He bases his distinction on the convention that any system described in the original report as subjected to substantial variations in temperature salinity ph water availability or any other major parameter was labelled fluctuating Briand (1982) and Yodzis (1982) have documented significant statistical differences between webs from these two kinds of habitat

Of the 28 Briand food webs from fluctuating environments 25 were modeled as assembled webs of the 12 Briand webs from constant environments only 3 could be so modeled (Table 1) Assembled food webs are excellent models for real food webs from fluctuating environments at least on the basis of the test statistics used here but in constant environments other processes (perhaps succession) beyond the simple assembly contemplated here seem to be at work

The third column of Table 1 contains a 1 for each Briand web which is interval (Cohen 1978) a 0 for each web which is not Of the 28 food webs listed in Table 1 22 are interval

In order to test whether this frequency of intervality is consistent with the assembly process as envisaged here 100 webs were assembled for each set of parameter values listed in Table 1 and tested for the intervality property The fourth column of Table 1 shows for each Briand web the fraction of the corresponding 100 assembled webs that were interval

If the real food webs were obtained by random sampling from the statistical universe of assembled food webs (with appropriate parameters) one would expect (summing the fourth column of Table 1) that 23 72 of them would be interval This does not deviate significantly (P= 31) from the observed value 22 according to Cohen s (1978 pp 76 79) z test Among the 25 webs in Table 1 from fluctuating environments one expects 21 05 to be interval a nonsignificant deviation(P= 21) from the observed value 19

The eleven test statistics used here (counting intervality as a test statistic) include all quantities which have been claimed in the literature (to the best of my knowledge) to express structure in real food webs For food webs from fluctuating environments it appears that all of this structure can be explained on the basis of a simple and primitive process of community assembly subject to energetic constraints

This is not to deny the possibility that other processes may play a role It could very well be that additional structure beyond that already documented will be found and will require some other explanation Indeed it could even be that the explanation I am suggesting though effective in terms of the present data is wrong My claim is that at our present level of empirical understanding for fluctuating environments nothing beyond simple community assembly as articulated here is *required* by way of explanation

Theoretical ecology has far too often traded in generalizations so sweeping that they are from the very start doomed to failure in the complex world of biological communities In the face of such complexity it may be a sounder procedure to try instead to articulate appropri ate *distinctions* The really interesting finding of this work on community assembly may well be its confirmation of Briand s (1982) distinction between food webs from fluctuating and from constant environments and the further light it sheds on that distinction

REFERENCES

Briand F (1983) Environmental control of food web structure *Ecology* 64 253 263

Cohen J E (1978) Food Webs and Niche Space Princeton Princeton University Press

Hutchinson G E (1959) Homage to Santa Rosalina or why are there so many kinds of animals *Am Nat* 93 145 159

Pimm S L (1989) Properties of food webs *Ecology* 61 219 225

Pimm S L (1982) Food Webs London Chapman & Hall

Pimm S L and J H Lawton (1977) The number of trophic levels in ecological communi ties *Nature* 268 329 331

Slobodkin L B (1960) Ecological energy relationships at the population level *Am. Nat* 94 213 236

Yodzis P (1981) The structure of assembled communities *J theoret Biol.* 92 103 117

Yodzis P (1982) The compartmentation of real and assembled communities *Am. Nat* 120 551 570

Yodzis P (1983) Energy flow and the structure of real ecosystems (Ms)

The Causes of Foodweb Structure Dynamics Energy Flow and Natural History

Stuart L Pimm and J H Lawton

Introduction

Elsewhere we have suggested that dynamical constraints are important in shaping food webs (Kirkwood and Lawton 1981 Lawton and Pimm 1978 Pimm 1979a b 1980a b c Pimm and Lawton 1977 1978 1980) The importance of dynamical explanations has recently come under attack from at least 3 sources (1) Auerbach (1979 1983) has suggested that some food web patterns are inevitable consequences of creating random food webs with simple constraints (2) Stenseth (1983) has argued that simple natural history constraints on feeding ecologies are capable of explaining more patterns that we had anticipated (3) Yodzis (1981) has produced model food webs that by suitable adjustments and subject to only energetic constraints can be made to match real food webs in a variety of features Our objective is to list some food web patterns to review the arguments about their causes and to reply to them where necessary

A catalogue of patterns

The patterns within real food webs include these

(1) A miscellaneous group of patterns that distinguish real food webs from models where interactions are placed entirely randomly These include the absence of loops of the kind A eats B eats A A eats B eats C eats A etc and absurdities such as predators without prey

(2) Webs are not too complex Connectance C decreases with the number of species in the web n so that on average the product Cn is a constant (Rejmanek and Stary 1979) or nearly so (Yodzis 1980)

(3) Food chains are short typically a food web has three or four trophic levels (Hutchinson 1959 Pimm 1980b 1983 Pimm and Lawton 1977)

(4) We define omnivores to be species that feed on more than one trophic level Typically food chains have one omnivore per top predator and not the two or three that are possible in systems with four trophic levels (Pimm 1980b Pimm and Lawton 1978)

(5) Omnivores when they occur usually feed on species in adjacent trophic levels Thus in systems with four trophic levels species feeding on herbivores and plants are common so are species feeding on carnivores and herbivores But species that feed on plants and carnivores are very rare (Pimm and Lawton 1978)

(6) Food webs dominated by insects and their predators and parasitoids have more complex patterns of omnivory than webs dominated by the larger invertebrates Hence insect dominated systems are exceptions to patterns (4) and (5) (Pimm 1980b Pimm and Lawton 1978)

(7) There are systems where dynamics do not involve the predator affecting the prey s mortality (for example systems with detritivores and scavengers rather than herbivores and carnivores) Although these systems are not well documented they apparently also have complex patterns of omnivory (Macfadyen 1979 Pimm 1982) scavengers for example eat corpses derived from a variety of trophic levels

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(8) Compartments are defined by clusters of interactions between species within com partments but few weak or no interactions between species in different compartments Webs are only occasionally compartmented Where such compartments exist they correspond to major habitat divisions (Pimm and Lawton 1980) Within habitat webs are not more com partmented than one would expect by chance (Pimm and Lawton 1980) (We note parenthetically that compartments are not identical to the cliques of Cohen (1978) there may be many cliques in a web)

(9) The patterns of overlaps in the prey used by a set of predators can be interval or non interval (see Cohen 1978 for details) The frequency of interval webs in nature is higher than chance alone dictates

Dynamical constraints

Suppose that following a perturbation one requires the species densities in these models to approach quickly their multispecies equilibrium Then eight patterns (1 2 3 4 5 6 7 and 8) contribute significantly to this requirement being satisfied If we assume that natural systems must meet the same requirement then our models predict what patterns should (and should not) be observed in nature (May 1981 Kirkwood and Lawton 1981 Pimm 1979b 1982 1983 Pimm and Lawton 1977 1978 1980) Indeed patterns 2 4 5 6 7 and 8 were predicted by dynamical studies before data were assembled to test the predictions

Dynamical constraints are not the only ones that explain the patterns just listed Simple biological realities (pattern 1) have considerable impact on the stability of models Random webs containing biologically absurd trophic patterns are much less likely to be stable than models of similar size and complexity without loops or predators without prey But to argue that dynamical constraints are the causes of these patterns seems to expand the meaning of stability to the point where it becomes trivial It is correct but not really useful to argue that dynamical constraints exterminate predators that lack a food supply or eliminate spe cies that feed only upon each other!

Some of the other patterns of web design are also consistent with basic natural history requirements and promote stability when incorporated into model systems Hence deciding whether web structures are a consequence of dynamical constraints or are generated by nat ural history considerations which fortuitously promote stability is not going to be easy

Nonetheless some patterns seem necessarily explained by dynamics these are 3 4 5 and 6 Thus dynamical restrictions appear to generate at least half the patterns observed And some more patterns (2 9) may often follow as a consequence of these other patterns

Biological restrictions

Patterns that are non dynamic in nature

Simple biological sense explains some patterns A predator must feed on at least one prey species yet cannot feed on all the species it encounters in a community With an upper and lower limit to the numbers of species that a predator can exploit pattern (2) is inevita ble Suppose that the average number of interactions per species is k The total number of interactions is thus kn and the connectance is kn/n(n 1) or k/(n 1) This result is practically indistinguishable from that predicted by dynamics and seems a much simpler explanation (Pimm 1980a)

Similarly pattern (8) (compartments between not within habitats) is likely to be a con sequence of species in different habitats requiring different adaptations This process in turn restricts their feeding to one habitat Finally pattern (7) is probably a consequence of the lack of such restrictions when animals die carcasses offer much the same challenges irrespective of the trophic positions of their former inhabitants

In summary patterns 1 2 7 and 8 all tend to enhance the stability of model and hence presumably real food webs Although these patterns can be predicted from dynamics models their existence in the real world is more readily explained by elementary biological phenomena

Patterns of omnivory

Patterns 4 5 and 6 are most difficult to explain Stenseth (1983) believes that they can be explained by more biologically acceptable criteria than dynamical constraints His argument is in two stages mechanism and predictions

Mechanisms Stenseth (1983) writes To me the stability hypothesis is unacceptable since it is difficult to understand what selective mechanisms produce the predicted webs If possible an hypothesis based on the principles of natural selection ought to be developed We think that the mechanism behind dynamical constraints is as consistent with natural selection as the one Stenseth proposes The theoretical possibility that one species may per sist in a habitat occupied by certain combinations of species but not in a habitat occupied by alternative sets is accepted without question in competition theory where it is regarded as being consistent with natural selection (Diamond 1974 MacArthur 1972) Dynamical constraints on web structure are conceptually identical with theories of competitive exclu sion involving sets rather than pairs of species The only difference is that in food webs some of the pairwise species interactions are trophic not competitive The difference between Stenseth s arguments and dynamical constraints comes from the predictions they make about food web structures

Predictions Stenseth s arguments lead to two predictions as follows

(i) Omnivory should be commoner at higher than lower trophic levels for two reasons First omnivorous top carnivores can take a similar resource meat from two trophic levels This must be easier Stenseth argues than being omnivorous lower in the food chain and hence being forced to feed on two very different resources meat and plants Second species low in the food chain will tend to be controlled by their own enemies top carnivores in con trast must be food limited When resources are relatively abundant optimum foraging predicts that species should specialize on the most profitable resource When resources are scarce species should generalize and take what they can So again Stenseth s arguments anticipate that omnivory should be more likely at higher trophic levels for these species are the most severly resource limited

(ii) These same optimum foraging arguments predict that omnivorous carnivores should feed on carnivores and plants at least as often as omnivorous carnivores feed on herbivores and plants The difficulties of feeding for both types of omnivore are likely to be compara ble but the top carnivore is more likely to be solely limited by the abundance of its food (and so be less choosy) than the carnivore which is also limited in part by its predators

Now we have previously reviewed these arguments (Pimm and Lawton 1978) In the sample of webs we analyzed omnivory involving top carnivores feeding on both plants and on carnivores is statistically very rare (contrary to Stenseth s prediction ii) yet omnivores feeding on animals at adjacent trophic levels are both equally common (contrary to his pre diction i) Both these results however are consistent with predictions based on dynamical constraints

State models

Both Yodzis and Auerbach propose that realistic model food webs incorporating mini mum sensible biological constraints can be constructed without recourse to dynamics

Auerbach s main point is that short food chains (pattern 3) are more common than long food chains in static models However real food webs still contain significantly fewer trophic levels than random analogues constrained to be as similar as possible in all other ways to actual food webs according to the recipes outlined by Pimm (1980b) Auerbach s approach generates short food chains but they are not short enough

The models formulated by Yodzis (1981) include simple energetic constraints Webs are constructed by the sequential addition of species each of which has energetic requirements that must be met by consuming some of the species already present Energy enters the web via primary producers with productivity P

Yodzis grows his webs using standard assembly rules of which two are critical His assembly rule 5 states that Every species except the N primary producers have an ecologi cal efficiency (Slobodkin 1960) Thus once established species make a fraction of their own consumption available to the next level in the food chain

Assembly rule 6 states because $E < 1$ there comes a point in the sequence of arriv ing species at which every species in the community has an unutilized production of less than 10 The next arrival takes all the unutilized production from all the species where this is greater than 1 The assembly process then stops

Yodzis study is elegant because it provides the simplest possible realistic way of build ing model food webs devoid of dynamics Given N the number of primary producers his method is to search a wide range of values of net primary productivity P and ecological efficiency E until his model systems are as similar as possible in structure to the 40 food webs assembled by Briand Yodzis (1981a) finds an impressive level of agreement between randomly constructed static webs and real webs in 8 properties

A number of things worry us about Yodzis model The first is his claim to explain pattern (3)—the length of food chains The second is the range of values used for E and P which forces us to question all his conclusions

Assembly rule 6 is on Yodzis own admission (p 110) arbitrary The elegant thing to do would be to let the process continue under rules (1) (5) until it terminates Unfor tunately if one does this one finds too many species arriving toward the end of the sequence the result is food webs with *unrealistically long food chains*" (our italics)

The claim to generate model food webs with the same number of trophic levels as real food webs verges on being circular

Our second worry is even more fundamental In order to get so close an agreement between real and model webs Yodzis varies E and P from web to web This results in values for ecologically efficiency in the range 10^{-1} to 10^{-8} with a mean of $8\,7 \times 10^{-3}$ and net primary productivities P stretching over 11 orders of magnitude Real world values of E and P bear little resemblance to these figures Ecological efficiencies less than 10^{-1} are unusual particularly in webs dominated by ectotherms (Kozlovsky 1968 Lawton 1981) Ecological efficiencies as low as or lower than 10^{-3} imply that virtually all population production passes to the decomposer food chain not to the next trophic level There is no evidence that consumers are universally so inefficient Similarly we know of no evidence of net primary productivities ranging over 11 orders of magnitude 5 is extreme (Lieth 1975) We therefore believe that Yodzis model fails not because it incorporates simple energetics principles but for the same reason that Auerbach s model fails both lack dynamics

REFERENCES

Auerbach M J 1979 Some real communities are unstable *Nature* 279 821

Auerbach M J 1983 Stability probability and topology of food webs In Abele L G Strong D R Jr and Simberloff D S (eds) Ecological Communities Conceptual Issues and the Evidence Princeton University Press Princeton pp 99 99

Cohen J R 1978 Food Webs and Niche Space Princeton University Press Princeton

Diamond J M 1974 Assembly of species communities In Cody M L and Diamond J M (eds) Ecology and Evolution of Communities Belknap Press Cambridge Mass pp 342 444

Hutchinson G E 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* 93 145 159

Kirkwood R S M and J H Lawton 1981 Efficiency of biomass transfer and the stability of model food webs *J Theoret. Biol.* 9 225 237

Kozlovsky D G 1968 A critical evaluation of the trophic level concept I Ecological Effi ciencies *Ecology* 49 48 60

Lawton J H 1981 Moose wolves *Daphina* and *Hydra* on the ecological efficiency of endotherms and ectotherms *Am. Nat.* 117 782 783

Lawton J H and S L Pimm 1978 Population dynamics and the length of food chains *Nature* 272 189 190

MacArthur R H 1972 Geographical Ecology Harper and Row New York

Macfadyen A 1979 The role of the fauna in decomposition processes in grassland *Sci. Proc Royal Dublin Soc. Series A* 6 197 206

Pimm S L 1979a Complexity and stability another look at MacArthur s original hypothe sis *Oikos* 33 351 357

Pimm S L 1979b The structure of food webs *Theoret Popul. Biol.* 16 144 158

Pimm S L 1980a Bounds on food web connectance *Nature* 284 591

Pimm S L 1980b Properties of food webs *Ecology* 61 219 225

Pimm S L 1980c Food web design and the effects of species deletion *Oikos* 35 139 149

Pimm S L 1982 Food Webs Chapman and Hall London

Pimm S L 1983 Food chains and return times In Abele L G Strong D R Jr and Sim berloff D S (eds) Ecological Communities Conceptual Issues and the Evidence Prince ton University Press Princeton pp 99 99

Pimm S L and J H Lawton 1977 The number of trophic levels in ecological communities *Nature* 268 329 331

Pimm S L and J H Lawton 1978 On feeding on more than one trophic level *Nature* 275 542 544

Pimm S L and J H Lawton 1980 Are food webs compartmented? *J Anim. Ecol.* 49 879 898

Rejmanek M and P Stary 1979 Connectance in real biotic communities and critical values or stability in mode ecosystems *Nature* 280 311 313

Slobodkin L B 1960 Ecological energy relationships at the population level *Am. Nat.* 94 213 236

Stenseth N C 1983 The structure of food webs preedicted from optimal food selection models an alternative to Pimm s stability hypothesis *Oikos* (in press)

Yodzis P 1980 The connectance of real ecosystems *Nature* 284 544 545

Yodzis P 1981 The structure of assembled communities *J Theoret. Biol.* 92 103 117

Variation in Niche Breadth with Trophic Position On the Disparity Between Expected and Observed Species Packing

John W Glasser

Introduction

In a note and subsequent monograph about food webs Joel Cohen (1977 1978) extracted several interesting observations from information that had been published by other investigators The data described in the note were neither sink nor source food webs (i e they described neither trophic relations among predators and their prey nor among prey and their predators) but rather were relatively unbiased accounts of the producers and consumers in natural communities Dr Cohen (1977) compared the numbers of predators and prey counting as both creatures that fed upon others and were themselves eaten and found that there were more different kinds of predators than prey The data from 14 communities could be described by the linear regression

$$m = 1\,79 + 0\,71n \tag{1}$$

where m and n are the numbers of kinds of prey and predators respectively Because this regression coefficient has a standard deviation of 0 07 Dr Cohen concluded that the approx imate ratio of prey and predators is 3 4

This observation is somewhat enigmatic The numbers of species at trophic level n S_n may be written as a quotient of the available energy and average population requirements

$$S_n = \frac{I \prod_{j=0}^{n-1} E_j}{\frac{1}{S_n} \sum_{i=1}^{S} R_i N_i} \tag{2}$$

The numerator is a product of the rate of solar input I and the intervening transformation efficiencies E_j and the denominator is the average product of individual energy require ments R_i and population sizes N_i Though this expression is useless for computational pur poses it has heuristic value Clearly the numbers of species at successive trophic levels must decrease unless the mean product of individual rations and population sizes decreases faster with trophic position than the available energy decreases

I am not aware of systematic observations relating individual rations or population sizes to trophic position but higher level consumers generally are larger and scarcer than lower level ones (Colinvaux 1978) Large animals live longer and move about with relative impu nity thus assuring sufficient encounters between opposite mating types at smaller popula tion sizes Although assimilation efficiencies may increase with successive transformations of solar energy (Ricklefs 1979) ecological efficiencies need not follow suit The longer more active adult lives that large animals lead reduce their growth efficiencies especially if they are homeothermic (Wiegert personal communication) Thus despite an inverse relation between population size and trophic position an increase in the number of species at succes sive trophic levels seems improbable Moreover it is possible to generate the opposite expec tation from contemporary niche theory (Vandermeer 1972)

Preliminaries

I will begin with an observation first made by Svärdson (1949) The size of a population and its niche breadth are directly related Figure 1 shows the niche breadth trajectories of three model species that are growing independently in the same heterogeneous environment Both axes are scaled The abscissa is the ratio of population size and environmental carrying capacity which is an index of relative resource abundance and the ordinate is niche breadth as a proportion of the maximum The breadths of the fundamental and intraspecific first partial niches of these three species their minima and maxima respectively are the same but their trajectories from one limit to the other differ reflecting differences in the strategies by which they exploit alternative resources The model species whose niche breadth trajectories increase rapidly and slowly as resources become scarce are obligate generalists and specialists respectively while the model species whose niche breadth trajectory increases at an intermediate rate is facultative specializing when resources are abundant and generalizing progressively as they become increasingly rare

Figure 2 also shows the niche breadth trajectories of three model species that are growing independently in the same heterogenous environment These species differ not in strategy (all are facultative) but in their efficiencies of resource use Generalists should be equally efficient at using all available resources and specialists particularly efficient at using subsets of those available The niche breadth trajectories of facultative strategists with equal efficiencies of resource use resemble those of generalists while the trajectories of those with unequal efficiencies resemble specialists The algorithms that implement these strategies ideas about the environmental conditions under which each evolved testable contemporary correlates in the form of expected spatial and temporal distributions and detailed experimental designs capable of evaluating them have been published recently (Glasser 1982a) as have some consistent empirical observations (Glasser 1982b)

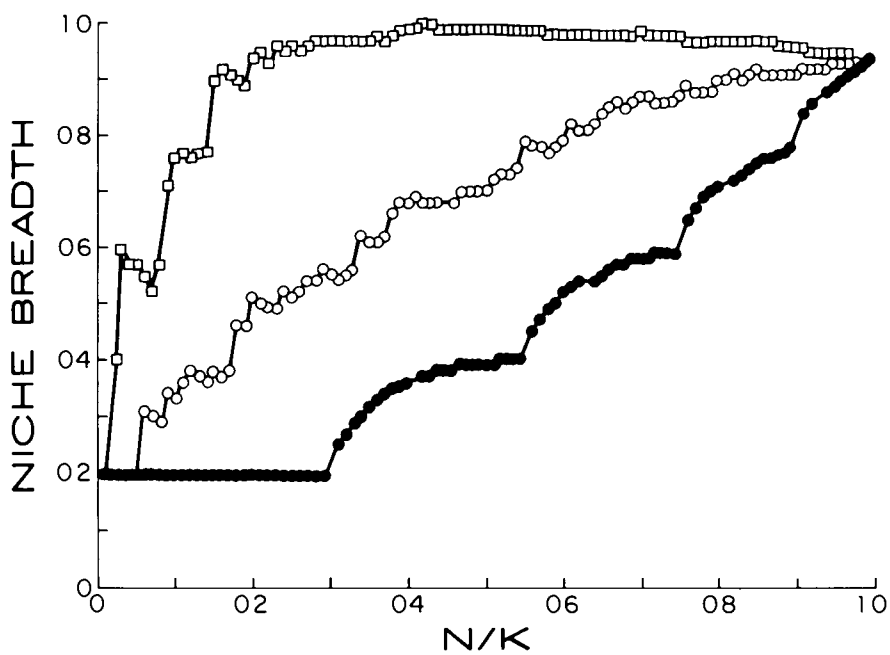

Fig 1 Scaled niche breadth as a function of the ratio of N and K from the growth of model populations differing only in their strategies of resource exploitation (from Glasser 1982a reproduced by permission of the University of Chicago Press)

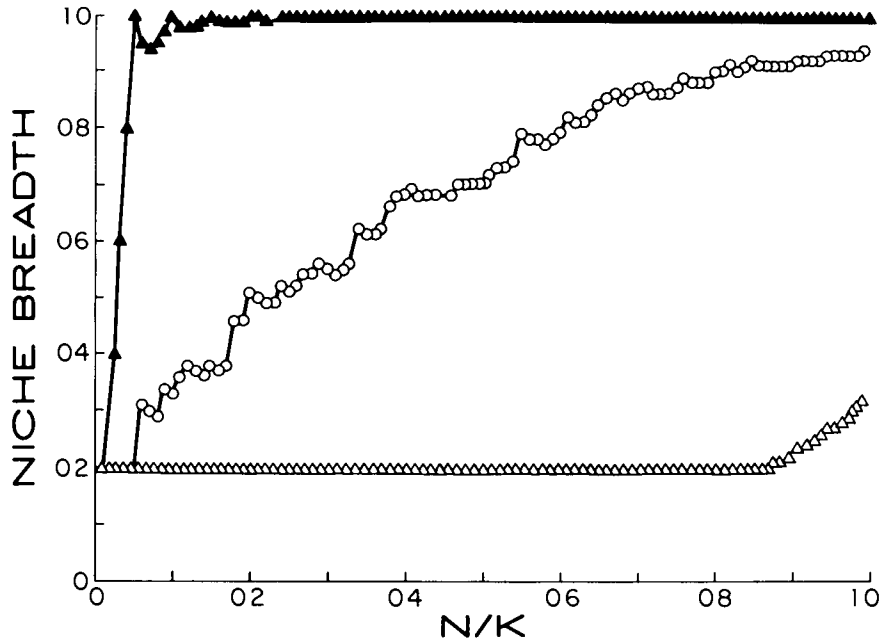

Fig 2 Scaled niche breadth as a function of the ratio of N and K from the growth of model populations of facultative specialists differing only in their efficiencies of resource use The niche breadths of facultative strategists with even efficiencies (i e $e_{ij} = T^{-1}$ for j = 1 to T) increase rapidly with the ratio N/K while those of facultative strategists with uneven ones (i e $e_{i1} = 0\ 9$ $e_{i2} = 0\ 04$ $e_{i3} = 0\ 03$ $e_{i4} = 0\ 02$ $e_{i5} = 0\ 01$) increase slowly (from Glasser 1982a reproduced by permission of the University of Chicago Press)

Although the next two points differ from conventional wisdom in ecology they are so intuitive that I will not digress to justify them now If you disagree grant them for sake of argument and object later The first is that unequal efficiencies develop only when resources are abundant relative to consumer requirements and the second is that consumers would be obligate strategists if this relationship were constant Because it is not consumers will be facultative those evolving where resources are relatively scarce will be equally adept at using any available resource while those that evolve where resources are relatively abundant will be particularly adept at using predictably available subsets (Glasser 1982a)

The next idea was first stated by Heatwole and Levins (1972) As communities develop sucessive trophic levels are colonized sequentially It is appropriate to use Simberloff s man grove data (Simberloff and Wilson 1969) to illustrate this notion because in criticizing Heatwole and Levins (1973) analysis of trophic relations among the arthropods recolonizing after defaunation Simberloff (1976) overlooked the validity of their conclusion Figure 3 shows the recolonization of one of the relatively large distant islands by herbivores car nivores and parasites Not only are successive trophic levels colonized sequentially but the resulting trophic structure persists until the overshoot that marks the transition between Wilson s (1969) non interactive and interactive species equilibria Together with the insights from contemporary niche theory enumerated previously this observation permits develop ment of a species packing mechanism that leads one to expect more species of prey than predators in natural communities

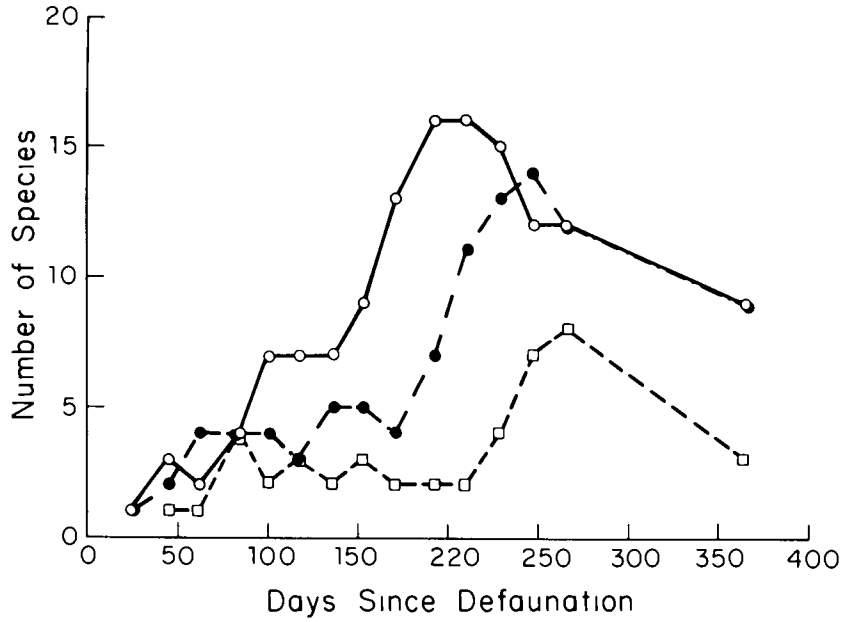

Fig 3 Recolonization of a defaunated mangrove island (E9) located between the keys and Gulf coast of Florida by arboreal arthropods herbivores (solid line) predators (line of alternating dashes and dots) and parasites (dashed line) These data are from Simberloff and Wilson (1969) and the trophic assignments are from Heatwole (personal communication) From Glasser and Price (1982) reproduced by permission of Academic Press Inc (London) Ltd

The expectation

Consider the colonization of any trophic level in a hypothetical community The population sizes of successful colonists would increase rapidly at first and with them their niche breadths Were this to continue available trophic resources would become saturated and both the population growth rates of extant species and the colonization rates of new ones would decline However at all trophic levels save the last these species would themselves soon constitute trophic resources capable of sustaining higher level consumers (Fig 4) As these colonized successfully they would reduce the population sizes of their prey reducing their niche breadths and liberating resources that could permit extant prey species to increase in abundance or sustain propagules of species previously unable to colonize

This mechanism leads to the tighter packing of more species at lower trophic levels because the resources of prey species are more often abundant relative to their requirements than are the resources of their consumers In other words communities are less saturated at lower trophic levels than at higher ones (Glasser 1982a) Consequently the efficiencies of lower level consumers are more unequal than those of higher level ones and their niche breadth trajectories are more sensitive to changes in relative resource abundance such as occur when their population sizes are reduced by predators (Fig 2)

A momentary digression is necessary before presenting evidence that is consistent with this species packing mechanism and discussing how it differs from Dr Cohen s observation The algorithm that implements my facultative strategy chooses the resource whose current abundance weighted by the efficiency with which the consumer converts it into

individuals is greatest Another way of putting this is that intrinsic preferences represented by the conversion efficiencies are weighted by the current abundances of alternative resources Consequently a resource that is not used as efficiently as another may be consumed preferentially if it is sufficiently abundant which it may become during the normal course of events Thus preference has an extrinsic component as well as an intrinsic one In contrast preference is determined solely by intrinsic factors in the strategy that goes by the presumptuous title of optimal foraging Careful attempts to disprove that theory (e g Jaeger and Barnard 1981) have succeeded in demonstrating that prey frequency affects selection

Although the species packing mechanism that I outlined works regardless of consumer strategies it works best if consumers are facultative because their choices are determined by the frequencies of alternative prey to an extent that depends on the strength of intrinsic preferences Consequently abundant prey species are likely to be consumed dispropor tionately by colonizing predators (Fig 4 again) Because these species have the broadest niches this pattern of consumption liberates more resources qualitatively as well as quanti tatively than any other would

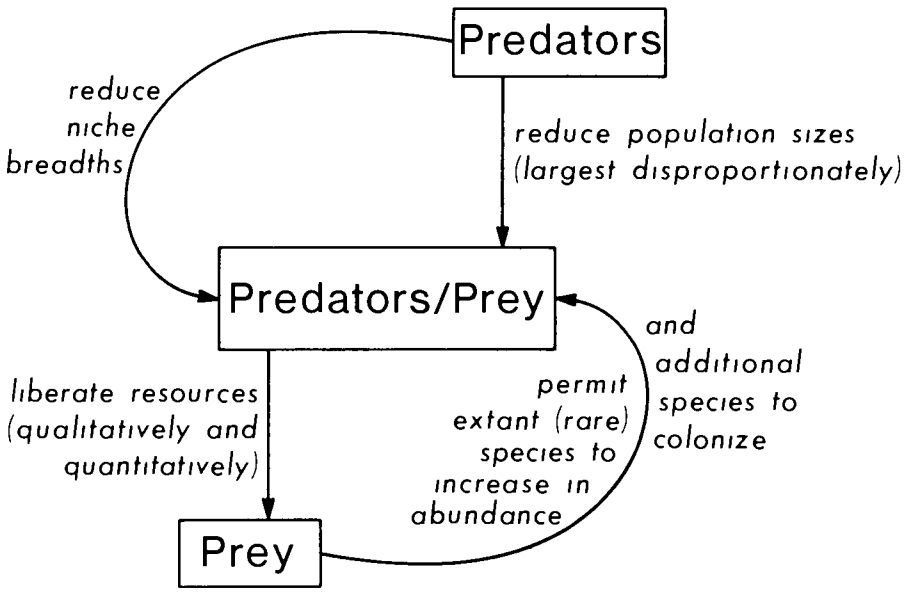

Fig 4 Direct and indirect effects (straight and curved arrows respectively) of pre dation on prey resource use and their consequences for species packing (from Glasser 1983a)

Figures 5 and 6 illustrate temporal patterns that are consistent with this theory in the number of species of sessile invertebrates and the distribution of space among them during the colonization of ceramic tiles that Sutherland (1974) immersed in an estuary during May and August of 1971 The number of species per tile increased to about seven and evenness decreased at first but then increased to high levels in both cases One would expect progres sively less even distributions of space among species to result from competition for attach ment sites or unfiltered water but only until facultative predators discovered the patch and began consuming the competitive dominants disproportionately Tiles enclosed in small

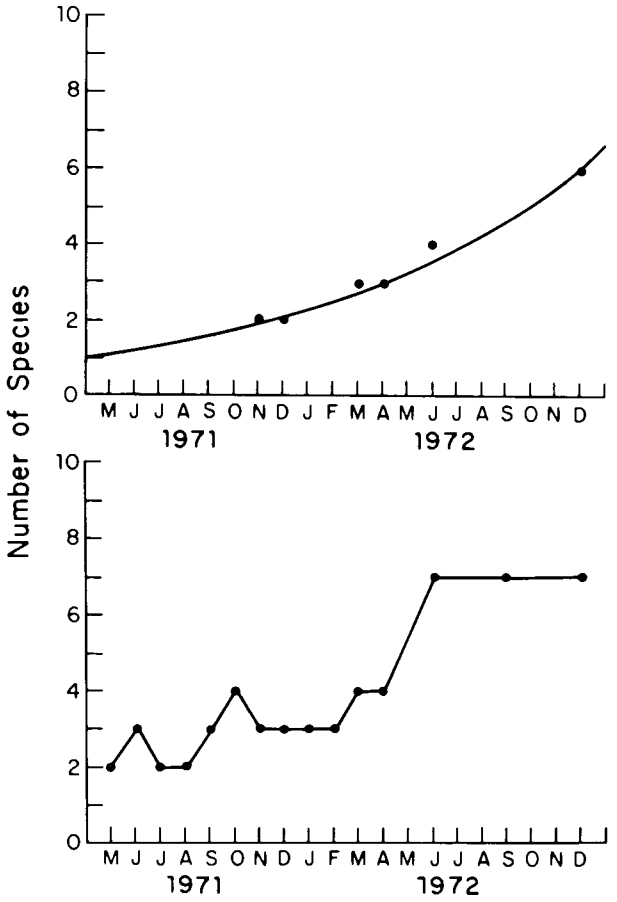

Fig 5 Temporal changes in the numbers of benthic species during community development on plates submerged during August (top) and May (bottom) of 1971 (data from Sutherland 1974 Figs 1 and 2) The equation for the curve is Y = 1 005 exp 0 009X [F = 38 0 N = 12] From Glasser 1982b reproduced by permission of the University of Chicago Press

mesh nets were characterized by fewer species less even distributions of space among them and more violent fluctuations than these suggesting that larval fishes are the heroes of this story Although Robert Paine might disagree I think that the rocky intertidal system works the same way I doubt for instance that *Pisaster* just happens to prefer *Mytilus californianus* or that *Thais* preference for *Balanus cariosus* is fortuitous As competitive dominants in their respective guilds these prey species are predictably available if not abundant Hence I would expect facultative consumers to prefer them even if they were less frequent than alternative prey which seems rarely if ever to be the case

Resolution of the disparity

What can be said about the disparity between observed and expected species packing? That either the observation or the theory is wrong if not both? Not necessarily The theory deals with trophic resources to which I referred as species to facilitate its exposition Dr Cohen enumerated kinds of predators and prey where kinds ranged from size classes or life

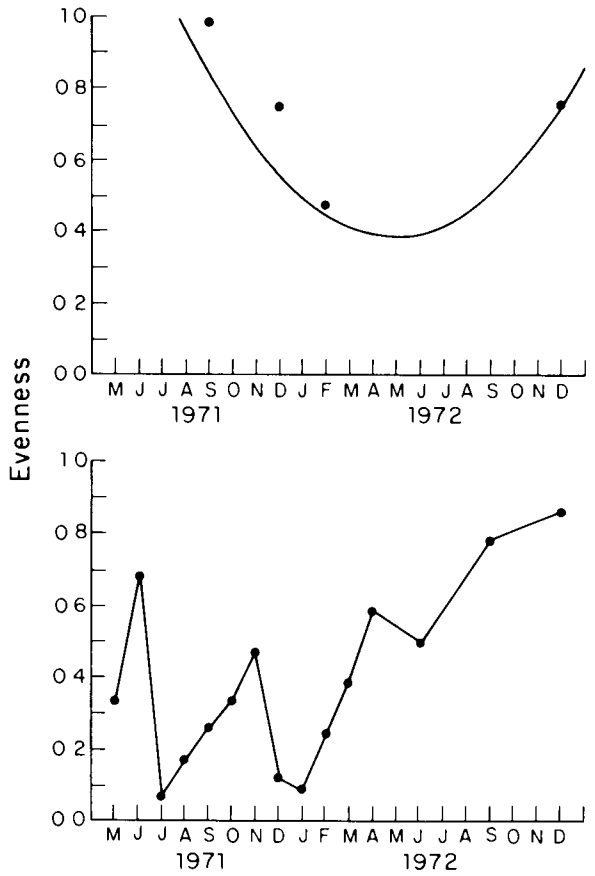

Fig 6 Temporal changes in the distributions of space among benthic species during community development on plates submerged during August (top) and May (bottom) of 1971 (data from Sutherland 1974 Figs 1 and 2) The equation for the curve is Y = 1 59 − 0 19X + 0 007X² [F = 8 3 N = 11] From Glasser 1982b reproduced by permission of the University of Chicago Press

history stages within single species to collections of species related by functional or taxo nomic criteria Are the partitions made by biologists and resource consumers similar? I sus pect that they are not that biologists are inclined to split among higher level consumers and lump among lower level ones (cf Pimm 1982) and that consumers themselves have the opposite inclination but I do not know how to begin answering this question I am limited to arguing for the plausibility of those portions of my theory that depart from conventional wisdom most significantly This will be accomplished using a multiple resource consumer model first to evaluate my assertion that facultative consumers are better adapted to varia ble environments than obligate ones and second to elucidate a particularly well studied resource consumer interaction

A model

The model is a generalization of Verhulst s (1838) logistic in which the number of indivi duals of a species that the environment can sustain is determined as the quotient of the

amount of some limiting resource or its rate of supply and the species per capita require ments In this multiple resource generalization the carrying capacity of the ith species K_i is a sum of T such quotients

$$K_i = \sum_{j=1}^{T} A_j/\alpha_{ij} \tag{3}$$

where A_j is the abundance of the jth resource or its rate of supply and α_{ij} is the amount or rate at which resource j is required by each individual of species i This per capita require ment may be written as a quotient of the individual ration R_i and efficiency with which the jth resource is used by the ith species e_{ij} That is

$$\alpha_{ij} = R_i/e_{ij} \tag{4}$$

Substituting for the carrying capacity in Verhulst s equation and generalizing to many species

$$\frac{dN_i}{dt} = r_i \sum_{j=1}^{T} n_{ij} \left[1 - \sum_{k=1}^{S} \frac{\alpha_{kj} n_{kj}}{A_j}\right] \tag{5}$$

where dN_i/dt is the population growth rate of species i r_i is its biotic potential or intrinsic rate of natural increase n_{ij} is the number of individuals of the ith species that is using the jth resource and S is the number of species in the guild of potential competitors The effect of the kth species on the specific growth rate of the ith to which Peter Abrams (1980) has referred as the intensity of competition is

$$\frac{\partial\left[dN_i/N_i dt\right]}{\partial N_k} = -r_i \sum_{j=1}^{T} \frac{f_{ij}\alpha_{kj} f_{kj}}{A_j} \tag{6}$$

where f_{ij} and f_{kj} are proportions of the populations of species i and k that are using the jth resource That is

$$f_{ij} = n_{ij}/N_i \tag{7}$$

where $N_i = \sum_{j=1}^{T} n_{ij}$ If each element in the S × S matrix of these partial derivatives is divided by the diagonal element in the same row the community matrix (Levins 1968) results

It is possible to use this model to evaluate ideas about the evolution of efficiencies and strategies of resource use by simulating competition among otherwise identical species with different efficiencies or strategies in environments to which organisms with particular com binations are expected to be best adapted Table 1 shows some results of a set of such experiments in which the current abundances of alternative resources were allowed to vary stochastically The rows designate treatments experiments in which the coefficients of envi ronmental variation ranged from 0 to 100 percent and the columns designate model spe

Table 1 Final frequencies $\overset{*}{N}_i / \sum_{k=1}^{S} \overset{*}{N}_k$ where $\overset{*}{N}_i = \sum_{j=1}^{T} \left[\left(A_j - \sum_{k \neq i}^{S} \alpha_{kj} n_{kj} \right) / \alpha_{ij} \right]$ by species from experiments in which the coefficients of environmental variation ranged from 0 to 100 percent (from Glasser 1983b)

Coefficient of variation of mean resource abundance	Species final frequencies					Sample sizes
	1	2	3	4	5	
0	27(0)	22(01)	16(00)	17(0)	17(0)	3
1	26(02)	23(01)	17(00)	18(00)	18(00)	4
10	25(02)	25(01)	16(00)	18(01)	17(00)	6
100	23(01)	24(01)	17(01)	18(01)	18(01)	14

Note Numbers in parentheses are standard errors 0 indicates no error and 00 indicates an error smaller than 005 which would not round off to 01

cies 1 and 5 are an obligate generalist and specialist with efficiencies that are equal and range over two orders of magnitude respectively and 2 3 and 4 are facultative strategists 2 and 4 with the same efficiencies as 1 and 5 and 3 with efficiencies that range over one order of magnitude The entries are equilibrium frequencies and their standard errors and the numbers of experiments upon which each is based are shown in the last column Although obligate generalists fare well under the conditions of this experiment their equilibrium frequencies decrease while those of the facultative strategists with equal efficiencies increase with the coefficient of environmental variation corroborating the expectation

I conclude that the resources of most consumers fluctuate in abundance relative to their requirements for them from the observation that resource abundances fluctuate and the conjecture that few populations track their resources perfectly Together with these simulation results this reasoning suggests that most consumers should be facultative Are they? Let us look at a particularly well studied resource consumer interaction that between *Pemphigus* aphids and one of their hosts narrowleaf cottonwood (Whitham 1980) Eggs that overwinter on the trunks and main branches hatch in spring and females move to the newly opened leaves settling near their bases Leaves are not colonized randomly but larger ones are preferred the largest even if they are already occupied This preference for large leaves is explicable in terms of individual fitness

Whitham (1980 Fig 6) showed that the stem mothers as these females are called on large leaves become larger and produce greater numbers of offspring parthenogenetically than those on smaller leaves These data permit one to calculate the per capita requirements as leaf area per unit of stem mother mass or progeny number Although these could be employed to estimate parameter values for larger and smaller leaves the relationship between efficiency and leaf size is more tractable mathematically The desired transformation is accomplished by choosing individual rations R arbitrarily and dividing them by the observed per capita effects α_{ij} Figure 7 shows two estimates of the efficiencies with which leaves of three sizes are used and first and second order polynomial regressions I used the linear model to extrapolate beyond these estimates to other available leaf sizes shown on Fig 8 The curve drawn through the circles is the actual frequency distribution of available leaves while that drawn through the squares is the frequency distribution of leaf use by model consumers Whitham (1980) does not provide the latter data but he does give the number of galls per available leaf This is shown on Fig 9 by the curve through the triangles The model leaf loading is shown by the curve through the squares

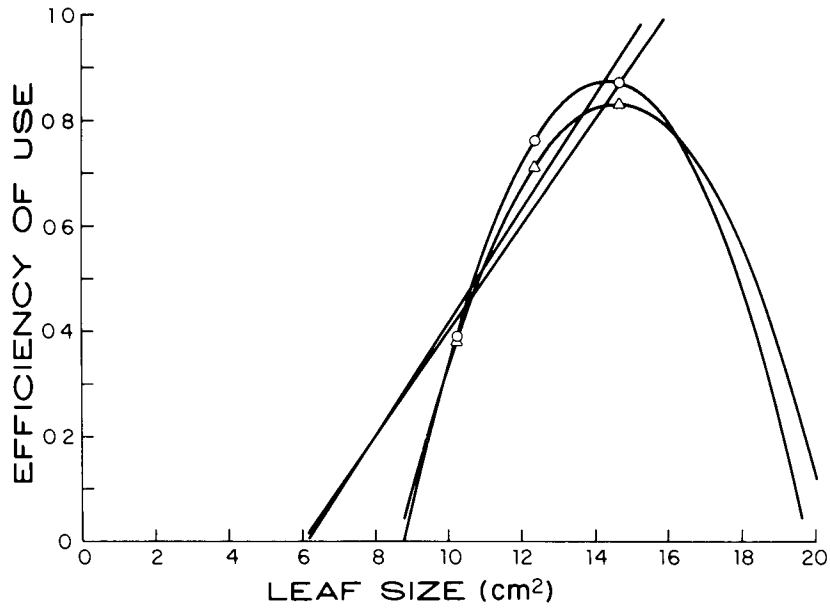

Fig 7 First and second order regressions of two estimates one based on maternal weight (circles) and the other on progeny number (triangles) of the efficiencies with which narrowleaf cottonwood leaves of three sizes are used by *Pemphigus* aphids (from Glasser 1983b) The equations are

	Independent variable	
Regression	**Maternal weight**	**Progeny number**
First order	$Y = 0\ 11X - 0\ 66$	$Y = 0\ 1X - 0\ 61$
Second order	$Y = 0\ 83X - 0\ 03X^2 - 5\ 07$	$Y = 0\ 69X - 0\ 02X^2 - 4\ 22$

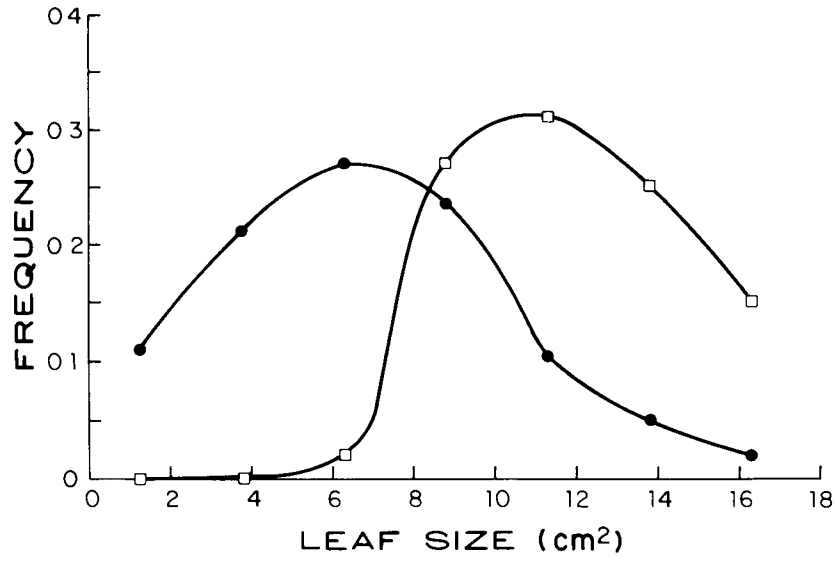

Fig 8 Frequencies of narrowleaf cottonwood leaves of various sizes available (solid circles) and used by a model facultative consumer whose per capita leaf requirements were estimated from Whitham s (1980 Fig 6) data (open squares) From Glasser 1983b

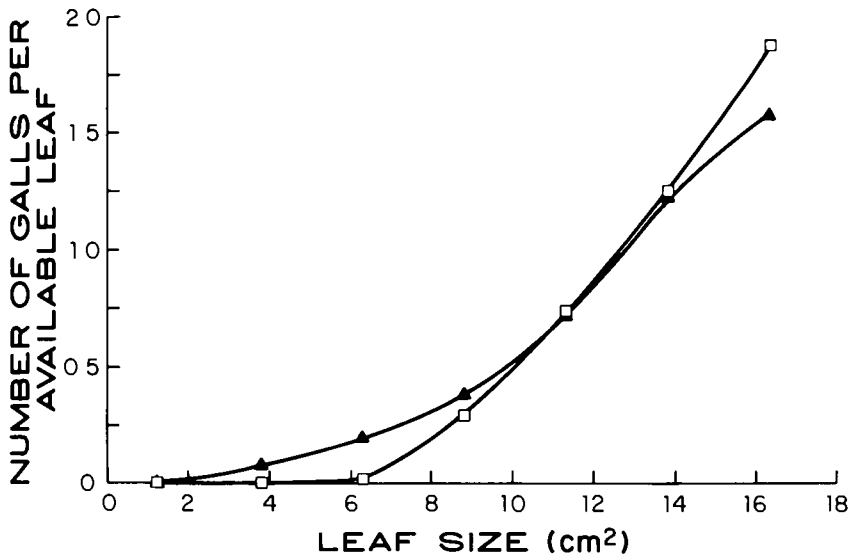

Fig 9 Observed numbers of galls per available leaf of various sizes (solid triangles) and leaf loading by a model facultative consumer whose per capita leaf requirements were estimated from Whitham s (1980 Fig 6) data (open squares) From Glasser 1983b

What does this say about the aphids strategy of resource use? Unfortunately nothing Figure 10 shows the niche breadth trajectories resulting from simulations using parameter values estimated from Whitham s (1980) data but my algorithms for obligate generalists and specialists and facultative strategists Because these trajectories converge the leaf loading at equilibrium is the same irrespective of strategy Dynamic data are required in order to distinguish these alternatives but presently we have only static data All is not lost how ever because Whitham (1980 Fig 6) observed that stem mothers adjust their densities on leaves of varying sizes such that their average fitness on each is the same Although indivi duals should choose gall sites that maximize their individual fitnesses in that event average fitness would increase with leaf size The fitnesses of distally located individuals would be similar fitness increases proximally and large leaves have more galls than small ones

Whitham (1980 p 463) attributes the decrease in the fitnesses of distally located indivi duals to agonistic interactions among stem mothers the dominant ones of which occupy the proximal locations with individuals of decreasing rank located at increasing distances from the leaf base The nature of the disparity between the observed and expected leaf packing (Fig 9 again) under representation on the smallest leaves and over representation on the largest ones (near perfect agreement being limited to the range of leaf sizes from which the extrapolation was made) suggests that this hypothesis is worthy of serious consideration I imagine that the disparity could be eliminated or reduced considerably by modeling interfer ence as well as exploitation because interference would increase the relative value of unoccupied small leaves and decrease that of multiply occupied large ones Be that as it may the present agreement is surprisingly good for a strategic model (*sensu* May 1973)

Although this multiple resource consumer model and the theory that it quantifies facili tate understanding such complex phenomena I have not been able to rationalize the dispar ity between observed and expected species packing

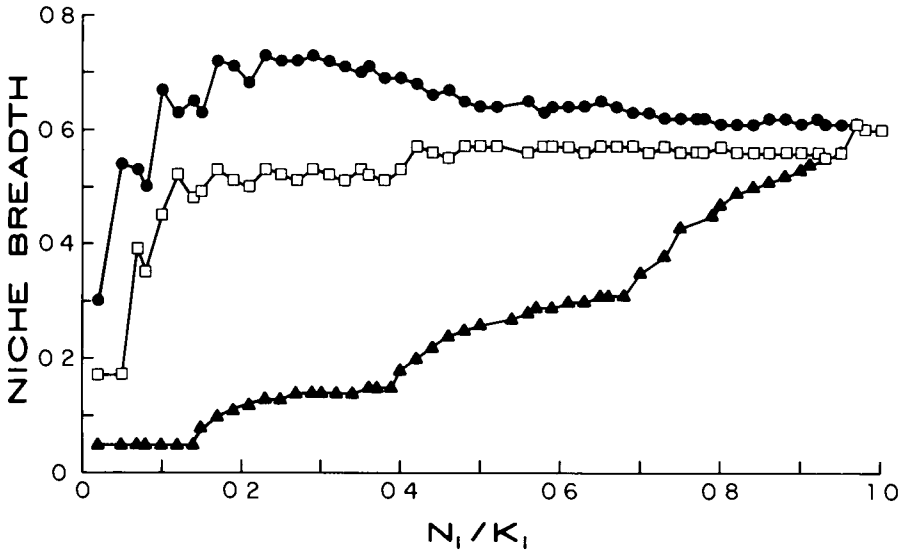

Fig 10 Niche breadth trajectories of model obligate generalists (solid circles) and specialists (solid triangles) and facultative strategists (open squares) whose per capita requirements for leaves of various sizes were estimated from Whitham s (1980 Fig 6) data (from Glasser 1983b)

REFERENCES

Abrams P A 1980 Some comments on measuring niche overlap *Ecology* 61 44 49

Cohen J E 1977 Ratio of prey to predators in community food webs *Nature* 270 165 167

Cohen J E 1978 Food Webs and Niche Space Princeton University Press Princeton N J 189 pp

Colinvaux P A 1978 Why Big Fierce Animals Are Rare An Ecologist s Perspective Princeton University Press Princeton N J 265 pp

Glasser J W 1982a A theory of trophic strategies the evolution of facultative specialists *Amer Natur* 119 250 262

Glasser J W 1982b On the causes of temporal change in communities modification of the biotic environment *Amer Natur* 119 375 390

Glasser J W 1983a Variation in niche breadth with trophic position on the disparity between expected and observed species packing *Amer Natur* 122 in press

Glasser J W 1983b Evolution of efficiencies and strategies of resource exploitation *Ecology* in press

Glasser J W and H J Price 1982 Niche theory new insights from an old paradigm *J theor Biol.* 99 437 460

Heatwole H and R Levins 1972 Trophic structure stability and faunal change during recolonization *Ecology* 53 531 534

Heatwole H and R Levins 1973 Biogeography of the Puerto Rican Bank species turnover on a small cay Cayo Ahogado *Ecology* 54 1042 1055

Jaeger R G and D E Barnard 1981 Foraging tactics of a terrestrial salamander choice of diet in structurally simple environments *Amer Natur* 117 639 664

Levins R 1968 Evolution in Changing Environments Princeton University Press Princeton N J 120 pp

May R M 1973 Stability and Complexity in Model Ecosystems Princeton University Press Princeton N J 265 pp

Pimm S L 1982 Food Webs Chapman and Hall London 219 pp

Ricklefs R E 1979 Ecology Second Edition Chiron Press Inc New York N Y 966 pp

Simberloff D S 1976 Trophic structure determination and equilibrium in an arthropod community *Ecology* 57 395 398

Sutherland J P 1974 Multiple stable points in natural communities *Amer Natur* 108 859 873

Svärdson G 1949 Competition and habitat selection in birds *Oikos* 1 157 174

Vandermeer J H 1972 Niche theory *Ann. Rev Ecol. Syst.* 3 107 132

Verhulst P F 1838 Notice sur la loi que la population suit dans son accroissement *Correspondence Mathematiques et Physiques* 10 113 121

Whitham T G 1981 The theory of habitat selection examined and extended using *Pemphigus* aphids *Amer Natur* 115 449 466

Wilson E O 1969 The species equilibrium *Brookhaven Symp Quant. Biol.* 22 38 47

Stability of Community Interaction Matrices

Harold M Hastings

1 Introduction

M R Gardner and W R Ashby (1970) observed that large randomly assembled linear (cybernetic) systems are less likely to be stable than smaller systems R M May (1972) applied a precise statement and proof using E P Wigner s (1959) statistics of random matrices These results appeared to challenge the classical wisdom that more complex ecosystems tend to be more stable than simpler systems and MacArthur s (1955) explanation that stability depends upon multiple energy pathways in complex systems In addition Lawlor (1978) and May (1974) observed that ecological constraints such as shortness of food chains made real ecological interaction matrices far from random

We (Hastings 1982a) provided a simpler proof of the May Wigner stability theorem (see Sect 2 below) which allows analysis (cf Hastings 1982b) of the role of ecological con straints These constraints may tend to make real ecosystems more stable than random sys tems see Sect 4 below

We also argue following May (1974) and Harrison (1978) that replacing one interaction (say predator eating prey) by a family of similar interactions with proportional decreases in interaction strength tends to enhance stability This reconciles MacArthur s (1955) thesis that multiple energy pathways enhance stability with May s stability theorem

Finally our proof of the May Wigner theorem yields a straight forward analysis of the role of Gaussian noise upon dynamics of these model ecosystems near equilibrium

We acknowledge helpful discussions with Drs D Cohen R M May and G Sugihara Many of these results were also presented at the Conference on Population Biology Edmon ton Alberta June 1982 and will also appear in their proceedings (in press)

2 The May Wigner Stability Theorem

We state and sketch a proof of the May Wigner Stability Theorem for difference equa tions Consider a community of n interacting species Let x denote the difference between the population level of the 1st species and its equilibrium value Let $\underline{x} = \left(x_1\ x_2 \quad x_n\right)$ or its transpose when appropriate Let $M = \left(M_{ij}\right)$ be the community interaction matrix M_{ij} represents the effect of species j upon species i The dynamics of such a community near equilibrium may be represented by the difference equation

$$\underline{x}(t+1) = M\underline{x}(t) \tag{1}$$

Random interaction matrices are parametrized by the *mean square interaction strength* α^2 the *size* n and the *connectance* C C denotes the fraction of the entries in M that are not zero these entries are located independently so that the number of non zero entres in each column represents a sample from a binomial distribution $b(n\ C)$ The non zero entries are chosen independently from a symmetric distribution with variance α^2 and fourth moment of order α^4

May Wigner Stability Theorem

Let M be an nxn matrix of connectance C and mean square interaction strength α^2 Let $P(\alpha\ n\ C)$ be the probability that the corresponding differential system (1) has a stable

equilibrium at 0 Let $\epsilon > 0$ Then $P(\alpha\ n\ C) \to 1$ as $n \to \infty$ provided $\alpha^2 nC < 1 - \epsilon$ conversely $P(\alpha\ n\ C) \to 0$ as $n \to \infty$ for $\alpha^2 nC > 1 + \epsilon$

We announce here a direct proof for matrices with connected underlying graphs More precisely the underlying graph of M (with one edge joining i and j if M_{ij} or M_{ji} is non zero) is asymptotically almost surely connected if $C \geqslant (1 + \epsilon) \log n/n$ and asymptotically almost surely not connected if $C \leqslant (1 - \epsilon) \log n/n$ for any fixed positive ϵ (Bollobás 1979 see p 143) We assume the former condition holds in particular the theorem holds for any constant C

Outline of proof (Hastings 1982a) For motivation recall the Gerschgorin circle theorem if every column sum (sum of absolute values of entries in a column) of M is less than 1 then all eigenvalues of M are less than 1 in size and the system of difference equations $\underline{x}_{t+m} = M\underline{x}_t$ is stable

In our case the expected *Euclidean* norm of each column is $\alpha\sqrt{nC}$ so we compute $\|M\underline{v}\|^2$ for all *unit* vectors $\underline{v}$

$$\|M\underline{v}\|^2 = \sum_{j=1}^{n} \|\underline{M}_j\|^2 v_j^2 + \sum_{\substack{j\ k=1 \\ j \neq k}}^{n} \left(\underline{M}_j\ \ \underline{M}_k\right) v_j v_k \tag{2}$$

Here $\underline{M}_j$ denotes the jth column of M and $\|\ \ \|$ denotes the Euclidean norm

Assume $\alpha^2 nC < 1 - \epsilon$ Then asymptotically almost surely each column of M has at most $(1 + \epsilon/2)\,nC$ non zero entries whose mean square is bounded by $(1 + \epsilon/2)\,\alpha^2$ Thus the first sum in (2) is asymptotically almost surely bounded by $1 - 3\,\epsilon^2/4$ In the second sum in (2) each term has mean 0 and variance $\alpha^4 nC^2 < 1/n$ Since $\sum\left(v_j v_k\right)^2 < \left(\sum v_j^2\right)^2 = 1$ the second sum is of order $1/n$ and thus asymptotically almost surely for all unit vectors $\underline{v}$ $\|M\underline{v}\|^2 < 1$ Stability follows

Instability in the case $\alpha^2 nC > 1 + \epsilon$ is shown similarly

3 The effect of noise

We extend the basic model (1) to include noise (random fluctuations) as follows

$$\underline{x}(t + 1) = M\underline{x}(t) + \Delta\underline{w}(t) \tag{3}$$

where the increments $\Delta\underline{w}(t)$ are selected independently from a symmetric distribution of fixed variance α^2 We now compute the effect of these fluctuations upon the distribution of $\underline{x}(t)$

Let M be a random matrix as defined above Our proof of the May Wigner stability theorem shows that multiplication by M is expected to multiply Euclidean lengths by $\alpha\sqrt{nC}$ If $\alpha^2 nC < 1$ for large t

$$\underline{x}(t + 1) = \Delta\underline{w}(t) + M\Delta\underline{w}(t - 1) + M^2\Delta\underline{w}(t - 2) +$$

$$+ M^{t-1}\Delta\underline{w}(1) + M^t\underline{x}(0) \approx \sum_{r=0}^{t-1} M^r \Delta\underline{w}(t - r) \tag{4}$$

Thus since the increments $\Delta\underline{w}(t)$ are independent for large t $\underline{x}(t + 1)$ has expected value 0 and variance $\alpha^2/(1 - \alpha^2 nC)$ (If in addition the increments are bounded say by b then $\|\underline{x}(t + 1)\|$ is bounded by $b/(1 - \alpha^{1/2} nC)$ for large t)

Thus if $\alpha^2 nC$ is small this variance has order α^2 and is unlikely to cause the system to crash in ecological time however if $\alpha^2 nC$ is near 1 $\underline{x}(t + 1)$ has variance $\gg \alpha^2$ and crashes become likely

4 Discussion

We have outlined a simple conceptual proof of the May Wigner stability theorem and used the proof to analyze the effect of noise upon fluctuations about the equilibria We conclude by briefly summarizing three additional ecological consequences of a detailed analysis of the May Wigner Theorem

(1) *Multiple energy pathways and Lyapunov stability* Increases in connectivity can increase stability provided that they yield sufficient decreases in interaction strength Suppose following MacArthur s (1955) discussion of multiple energy pathways that the mean interaction strength α is inversely proportional to the mean number of interactions per species nC Then $\alpha^2 nC$ is proportional to $1/(nC)$ and increasing complexity increases stability (May 1979 Hastings 1979 Harrison 1978)

(2) *Structural stability* Although as we have just observed Lyapunov stability of suitably scaled systems increases with increasing complexity their structural stability decreases with increasing complexity More precisely suppose that the a random matrix satisfying the hypotheses of the May Wigner stability theorem is perturbed so that the mean non zero interaction is μ $\mu \neq 0$ An argument similar to the proof of the May Wigner stability theorem shows that stability requires $|\mu| nC < 1$ or

$$|\mu| < 1/nC$$

for large n Thus both cooperative ($\mu > 0$) and competitive ($\mu < 0$) effects can destabilize large systems In addition evolution toward greater Lyapunov stability through greater parallelism (multiple energy pathways) is likely to be limited by the requirements of structural stability Thus as May (1974) argued environmental fluctuations limit the complexity of ecosystems but the limiting factor is structural stability rather than Lyapunov stability These considerations may also be useful in models in developmental biology

(3) *Ecological constraints* Lawlor (1978) and May (1972 1974) observed that community interaction matrices are far from random because of ecological constraints involving the length of food chains no loops conditions organization into loosely compiled subsystems etc These constraints tend to enhance stability for two reasons They reduce the variance in the number of non zero elements per column and also reduce the size of the covariance or interaction terms M_j M_k in (2) Thus the asymptotic stability results hold for relatively small values of n Cf Hastings (1982b) for further ecological discussion

REFERENCES

Bollobás B 1979 Graph Theory Graduate Texts in Math 63 Springer Verlag New York

Gardner M R and W R Ashby 1970 Connectance of large dynamic (cybernetic) systems critical values for stability *Nature* 228 784

Hastings H M 1979 Stability considerations in community organization *J Theoret. Biol.* 78 121-127

Hastings H M 1982a The May Wigner stability theorem for connected matrices *Bull. Amer Math. Soc (new series)* 7 387-388

Hastings H M 1982b The May Wigner stability theorem *J Theoret. Biol.* 97 155-166

MacArthur R H 1955 Fluctuations of animal populations and a measure of community stability *Ecology* 36 533-536

May R M 1972 Will a large complex system ever be stable? *Nature* 238 413-414

May R M 1974 Stability and Complexity in Model Ecosystems 2nd ed Princeton University Press Princeton

May R M 1979 The structure and dynamics of ecological communities In Population Dynamics R M Anderson B D Turner and L R Taylor eds Blackwell London pp 385-407

Wigner B 1959 Statistical properties of real symmetric matrices with many dimensions In Proc Fourth Canad Math Cong ed MacPhail M S U Toronto Press Toronto pp 174-184

Dynamic Patterns of Randomly Assembled Food Webs

W M Post

Introduction

Empirical studies have demonstrated a wide variety of food web structures (Cohen 1978 MacDonald 1979 Rejmanek and Stary 1979 Yodzis 1981) Research towards a theoretical understanding of food web structure is already well underway (Lawton and Pimm 1978 Pimm 1979a b 1980a b Pimm and Lawton 1977 1978 1980 Sugihara 1982) On the other hand several studies have indicated that there are features of ecological communities that may be best appreciated by understanding the ways in which they develop (Yodzis 1981 Roberts and Tregonning 1980 Tregonning and Roberts 1979 Robinson and Valentine 1979) We will contribute here to this second body of theory by considering food webs as the result of an assembly process

We have developed a computer model of food web assembly based on population dynam ics A system of Lotka Volterra equations for species biomass growth is elaborated accord ing to a small number of ecologically plausible rules including colonization and extinction During the assembly process we concentrate on the following questions

1 Does the rate of colonization change with the total number of accumulated successful colonizations?

2 How will the populations of successful colonists change with time?

3 How will the local stability of the food web change with time?

4 Does the structure of the food web as measured by its ascendency (Ulanowicz 1980) change with time?

Methods

The computer program begins with a community composed of six non interacting auto trophs This simple community is subject to invasion by another species drawn at random from a finite species pool Invasion is considered to be successful if the food web augmented by the additional equation and interaction terms representing the colonist population passes a number of tests

1 The new species biomass must be able to increase when it is rare and the other species are at equilibrium

2 The colonizing species does not complete a loop

3 The new food web has a finite number of equilibria (the community matrix is nonsingu lar)

4 The new food web is locally stable in the neighborhood of its new equilibrium

When a colonist invades it may cause some of the other species to assume negative equilib rium population biomasses Those populations with negative biomass are deleted from the food web and the resulting equilibrium densities are checked again This process is repeated until a food web is obtained with positive biomasses for all the remaining species The first colonist is followed in turn by other colonists that prey upon members of the food web and may themselves be eaten by previous colonists Ranges of the predator prey interaction

strengths and their probability of occurrence are specified at the beginning The program continues to introduce potential colonists until 200 colonization attempts have been com pleted At this point the simulation is ended The entire process is repeated 100 times for each set of interaction parameters The design of the simulations is shown in Table 1

Table 1 Design of the simulation runs[a]

Run	P_{prey}	P_{pred}
1	0 1	0 1
2	0 5	0 1
3	0 9	0 1
4	0 1	0 5
5	0 5	0 5

[a] P_{prey} is the probability that a spe cies already present in the food web will be a prey of the colonist P_{pred} is the probability that an existing species will be the colonist s predator

Results

We use the number of attempted colonizations (whether or not they are successful) as a measure of time during an assembly We present our results as a function of this measure which we call successional time

The difficulty of colonization (defined as the mean number of unsuccessful colonization attempts that occur between two successful colonization events) increase approximately linearly with time itself (Fig 1) The rate at which the difficulty of colonization increases with time differs between runs Colonization is most difficult when the probability is highest that an existing species is the predator of the colonist ($P_{pred} \geqslant 0\ 5$) Colonization is easiest when the probability of an existing species being a prey to the colonist (P_{prey}) is low

The number of species approaches an equilibrium in all runs (Fig 2) Where the proba bility of an existing species being a prey to the colonist is 0 1 (which means the invader nearly always feeds on only one species) the equilibrium number of species is greater than the original six autotrophs Where this probability is greater (0 4 0 9) the equilibrium num ber of species is less than the original six autotrophs

Combining these two results we see that after the number of species in the web has reached equilibrium the difficulty of colonization continues to increase This indicates that the characteristics of a colonist determined by the set of parameters involving its own pop ulation and those involving interactions with its prey and predators change during succes sional time Statistical analyses of these parameters however show no patterns through time

Establishment of new colonists modifies the local stability of the food web An inverse measure of local stability is the time it takes the difference between species densities and their equilibrium densities to fall to a specified fraction of the difference immediately fol lowing a preturbation This return time can be measured as

$$T_r = -1/Re\left(\lambda_{\max}\right)$$

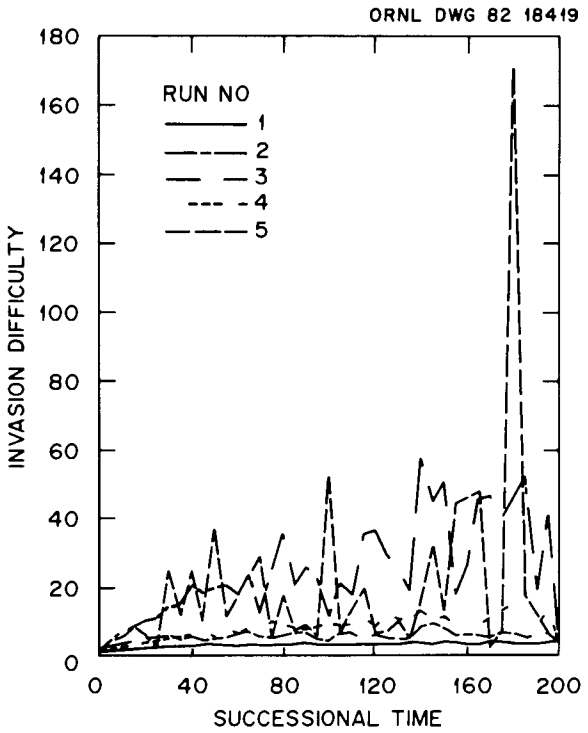

Fig 1 Plot of the invasion difficulty with successional time The different lines on each subplot represent the time course of runs with different values of P_{pred} and P_{prey} (see Table 1) The effect prey species has on predator species j a_{ji} was chosen randomly over the uniform interval (0 0 5) The effect of predator j on prey i a_{ij} was chosen randomly over the uniform interval (0 0 2 0) Successional time on the ordinate is expressed in units of attempted colonizations whether or not they are successful

where $\mathrm{Re}\left(\lambda_{\max}\right)$ is the real part of the maximum eigenvalue of the food web s stability matrix Figure 3 shows that the return time increases with succession indicating a decrease in local stability

The dynamic patterns we observed during the simulated succession may be attributable to structural changes A measure of food web structure should indicate ways in which the general architecture of the food web might be constrained enabling us to interpret the results on invasion difficulty and stability We examined the measure of average mutual information or ascendency proposed by Ulanowicz (1980) In our system the information is biomass flow to sustain predators Also since we do not allow loops ascendency becomes largely a measure of specialization or certainty with which biomass leaving species i will go directly to species j Ascendency is one component of the development capacity of the food web Development capacity is defined as the maximum uncertainty associated with the biomass flows or

$$C = -T \sum_i Q_i \ln\left(Q_i\right)$$

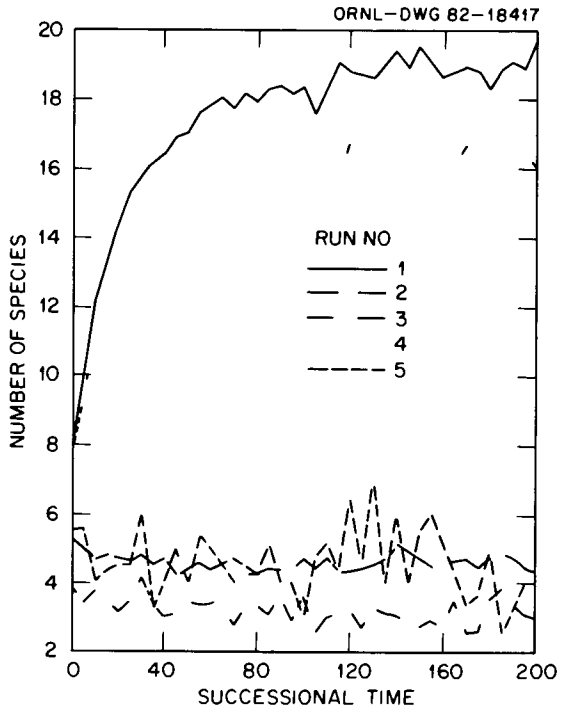

Fig 2 Plot of the number of species with successional time See Fig 1 legend for additional details

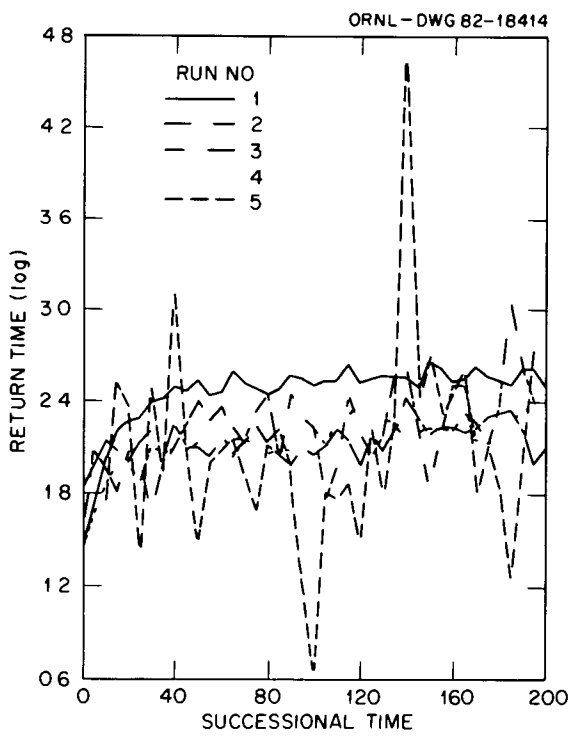

Fig 3 Plot of he logarithms of average return time for the food web as a function of successional time

where $T = \sum_i T_i$ T_i is the throughput of species i and $Q_i = T_i/T$ or the fraction of the total system throughput accounted for by species i Ascendency is a measure conditional on f_{ij} the probability of any biomass leaving species i directly going to species j and is defined as

$$A = T \sum_k \sum_j f_{kj} Q_k \ln\left\{ f_{kj} / \left[\sum_i f_{ij} Q_i \right] \right\}$$

To apply these measures of food web organization we must convert the Lotka Volterra equations at equilibrium into the appropriate flux representation In Fig 4 we have done this by assuming that all linear growth in autotrophs is input all linear loss in heterotrophs is respiration non linear losses due to trophic inefficiency are attributed to consumer respi ration

After each successful colonist development capacity ascendency and the ratio of ascen dency to development capacity were calculated The results appear in Figs 5-7 In some cases ascendency increased both in absolute terms and as a fraction of development capacity These runs 1 and 4 where $P_{prey} = 0\ 1$ indicating that the colonist is a relatively specialized predator or an autotroph These runs are also those where the difficulty of colo nization is low In other runs (2 3 and 5) ascendency is low or decreases with succession In these runs the colonists enter largely as polyphagous predators This results in extinctions of many of the autotrophs and a decline in development capacity and ascendency The fraction of development capacity attributable to ascendency while highly variable shows a slight decline with succession for these runs

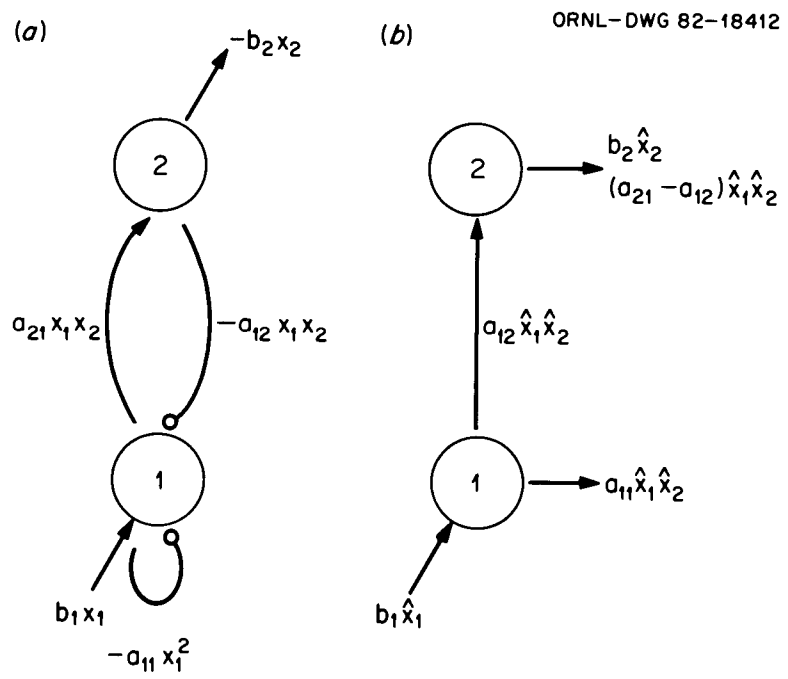

Fig 4 Conversion of food web from loop representation (a) to biomass flux repre sentation (b)

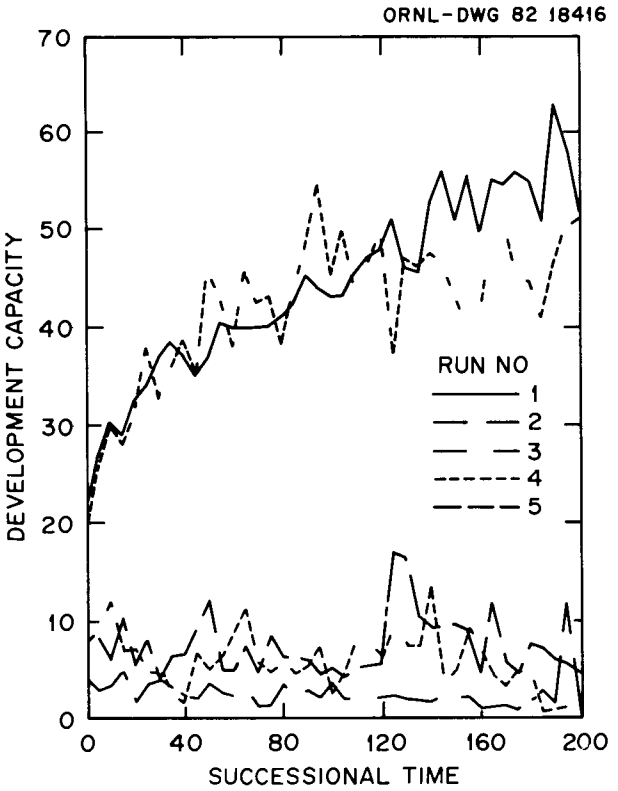

Fig 5 Development of capacity of food web with successional time

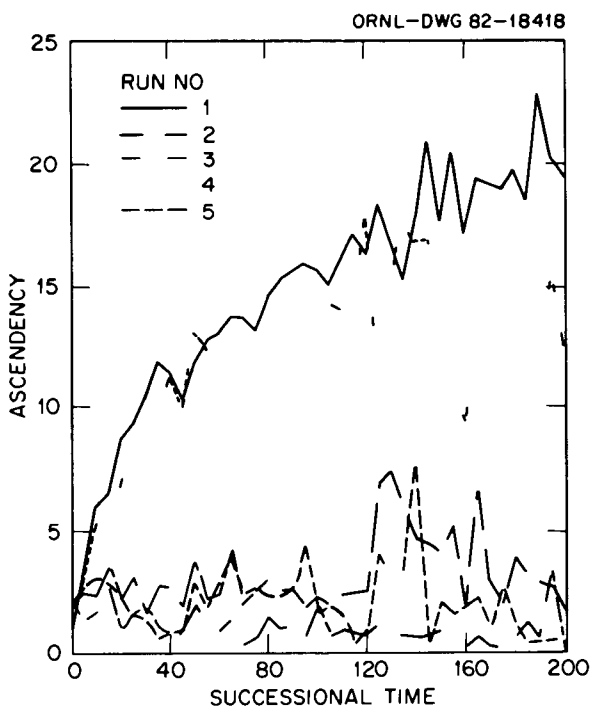

Fig 6 Ascendency of food web with successional time

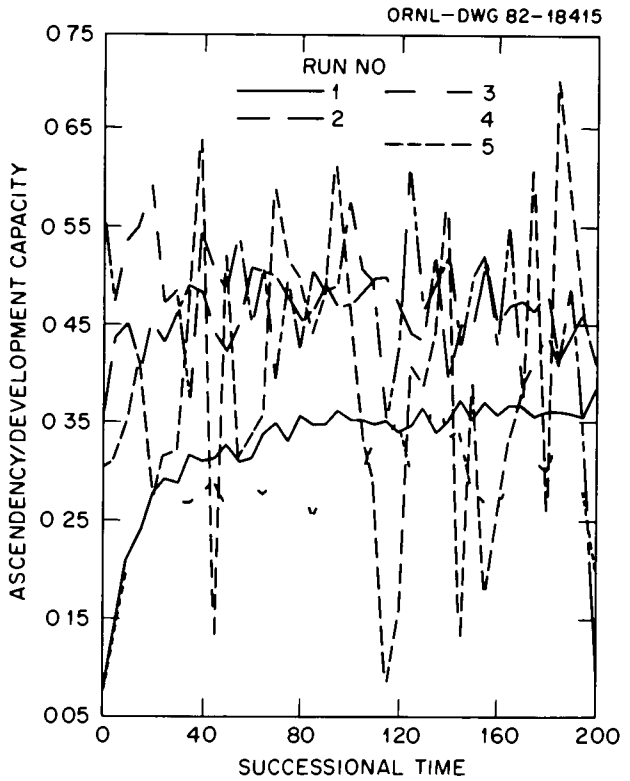

Fig 7 Proportion of development capacity accounted for by ascendency as a function of successional time

Conclusions

When model food web equations based on population dynamics are assembled according to a small number of ecologically plausible rules rich dynamic patterns occur Even though the number of species in a model food web assembly always reaches an equilibrium the turnover in species continues after equilibrium is reached However the rate of turnover declines with successional time The number of species and turnover rate depends on whether or not potential colonists are relatively monophagous or polyphagous The most structure as measured by development capacity and ascendency occurs in food web simulations where the colonists are relatively monophagous These are also the ones with highest species number and lowest difficulty of invasion

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REFERENCES

Cohen J E 1978 Food Webs and Niche Space Princeton University Press Princeton New Jersey

Lawton J H and S L Pinn 1978 Population dynamics and the length of food chains *Nature* 272 189-190

MacDonald N 1979 Simple aspects of food web complexity *J Theor Biol.* 80 577-588

Pimm S L 1979a Complexity and stability Another look at MacArthur s original hypothe sis *Oikos* 33 351-357

Pimm S L 1979b The structure of food webs *Theor Pop Biol.* 16 144-158

Pimm S L 1980a Food web design and the effect of species deletion *Oikos* 35 139-149

Pimm S L 1980b Properties of food webs *Ecology* 61 219-225

Pimm S L and J H Lawton 1977 The number of trophic levels in ecological communities *Nature* 268 329-331

Pimm S L and J H Lawton 1980 Are food webs compatmental? *J Anim. Ecol.* 49 879-898

Rejmanek M and P Stary 1979 Connectance in real biotic communities and critical values for stability of model systems *Nature* 280 311-312

Roberts A and K Tregonning 1980 The robustness of natural systems *Nature* 288 265-266

Robinson J V and W D Valentine 1979 The concepts of elasticity invulnerability and invadibility *J Theor Biol.* 81 91-104

Sugihara G 1982 Niche Hierarchy Structure Organization and Assembly in Naural Com munities PhD Dissertation Princeton University 1982

Tregonning K and A Roberts 1979 Complex systems which evolve towards homeostasis *Nature* 281 563-564

Ulanowicz R E 1980 An hypothesis on the development of natural communities *J Theor Biol.* 85 223-245

Yodzis P 1981 The structure of assembled communities *J Theor Biol.* 92 103-117

Biomass Stability and the Complexity of Grazer Dominated Food Webs

Anthony W King

Theoretical studies of the relationship between ecosystem complexity and stability usu ally conclude that complex systems are not as likely to be stable as simple systems Yet in one of the few empirical investigations of this problem McNaughton (1977) has concluded that increased complexity does stabilize certain ecosystem properties more precisely that a large mammalian grazer changed total green plant biomass less in more diverse grassland plots We have resolved this apparent contradiction between theory and empiricism by investigating in model grazing systems the relationship between complexity and the lack of change in plant biomass following herbivore removal which we call biomass stability

We established a set of structured food web models composed of an herbivore and n plant species We investigated 23 structures each with one herbivore species but with dif ferent numbers of plant species number of competitive interactions betwen plant species and the pattern of these interactions

The models were based on the familiar Lotka Volterra predator prey equations with biomass replacing the more commonly used densities

The equation parameters were determined by the biological details of the models Specific parameter values were selected at random from reasonable invervals [see Pimm 1979 and King and Pimm 1983] Briefly species at the base of a web were considered plants capable of increase in the absence of their herbivore and experiencing density dependent intra specific competition for non specified resources Inter specific competition between plants when appropriate to the simulation was usually less than intra specific competition implying some resource partitioning

In many grazing systems for example ungulates and grasses the per capita effect of the herbivore on the plant will likely be much greater than the converse Consequently we chose the magnitude of the parameters for the effect of the herbivore on the plant to be on aver age 10 times that for the effect of the plants on the herbivore

Now only those model simulations with a locally stable equilibrium involving species with positive biomasses were retained for further analysis From each of these models the herbivore was removed and the new equilibrium biomasses of the plants obtained Relative biomass stability was calculated from the proportional change in total plant biomass Clearly a small proportional change indicated biomass stability The details of this portion of our analysis are too lengthy to present here but are described elsewhere (King and Pimm 1983)

We explored the relationship between biomass stability and system complexity with three not entirely independent measures of complexity

1 Richness the number of species in the system We explored models with 2 3 4 5 6 8 and 12 species

2 The number of competitive interactions between plant species

3 Diversity like McNaughton we calculated diversity from the plant biomasses using the Shannon Weaver diversity index (H) which involves both a species richness component and an evenness component involving the species relative abundances

Our results can be enumerated as follows

(1) Species richness Figure 1a depicts the geometric means of the ratio of biomasses for models with different numbers of species and with no interactions between plant species An increase in the number of species from two to four was accompanied by an increase in biomass stability but as the number of species increased beyond four there was a decided reduction in biomass stability

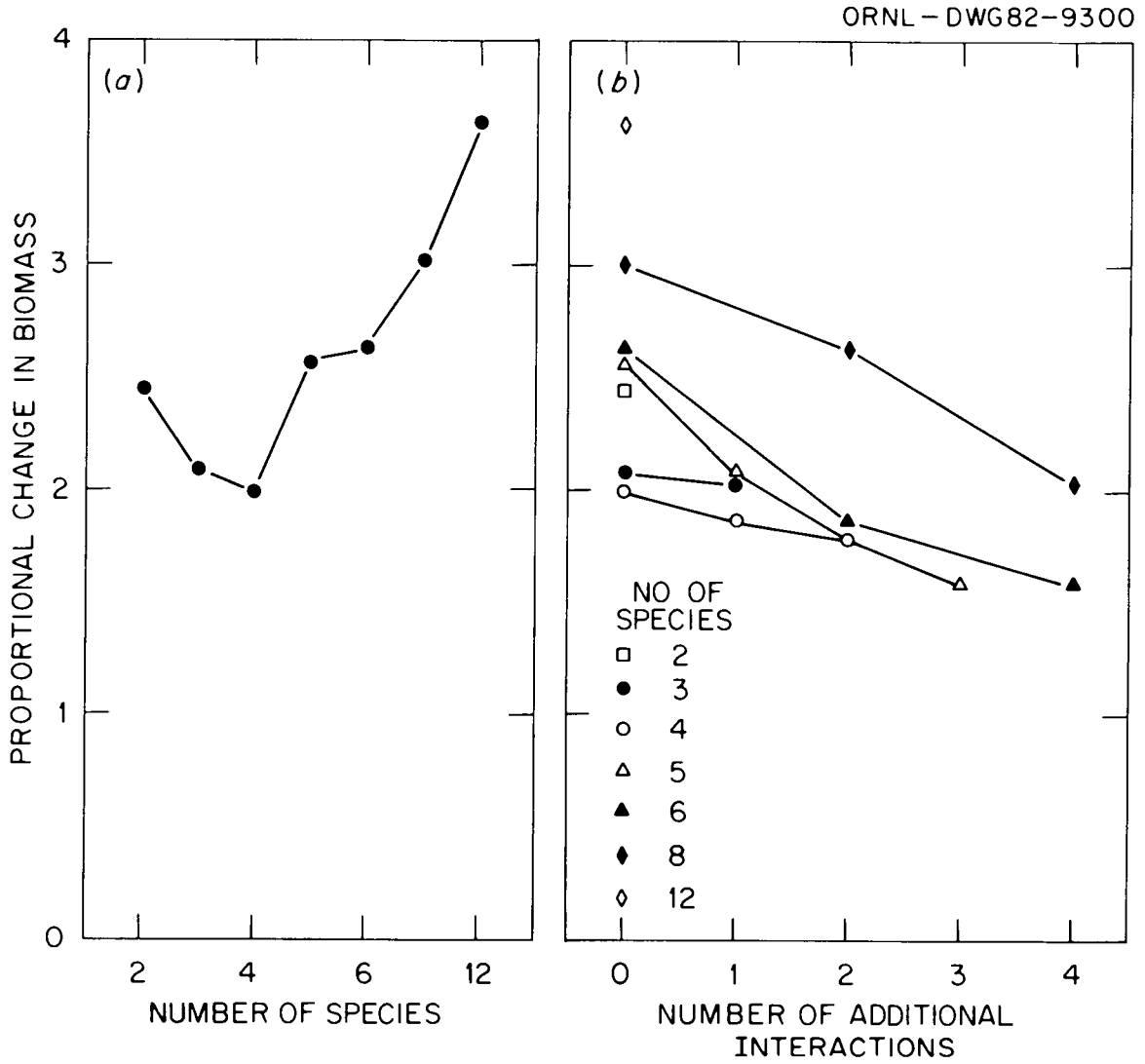


Fig 1 Geometric means of proportional changes in biomass (the ratio of total plant biomass without the herbivore divided by the total plant biomass with the herbivore) plotted against (a) the total number of species in the system (models without competitive interactions between the plant species only) and (b) the number of competitive interactions between the plant species

(2) Interaction between plant species Increased connectance (obtained by adding competitive interactions between plant species) yielded increased biomass stability (Fig 1b)

(3) Diversity and evenness The relationships between diversity evenness and biomass stability are not so simple as those discussed above In Figs 2a and b we plot the linear regression equations of the logarithms of the biomass ratios against the diversity of plant biomasses with (Fig 2a) and without (Fig 2b) the herbivore for each of the 23 food web structures analyzed For all but one the 46 regression lines greater diversity meant smaller changes in biomass The weakest relationships (and the only ones that were not significant at the 5% level) were between biomass stability and diversities in the presence of the herbivore when there were more than four plant species

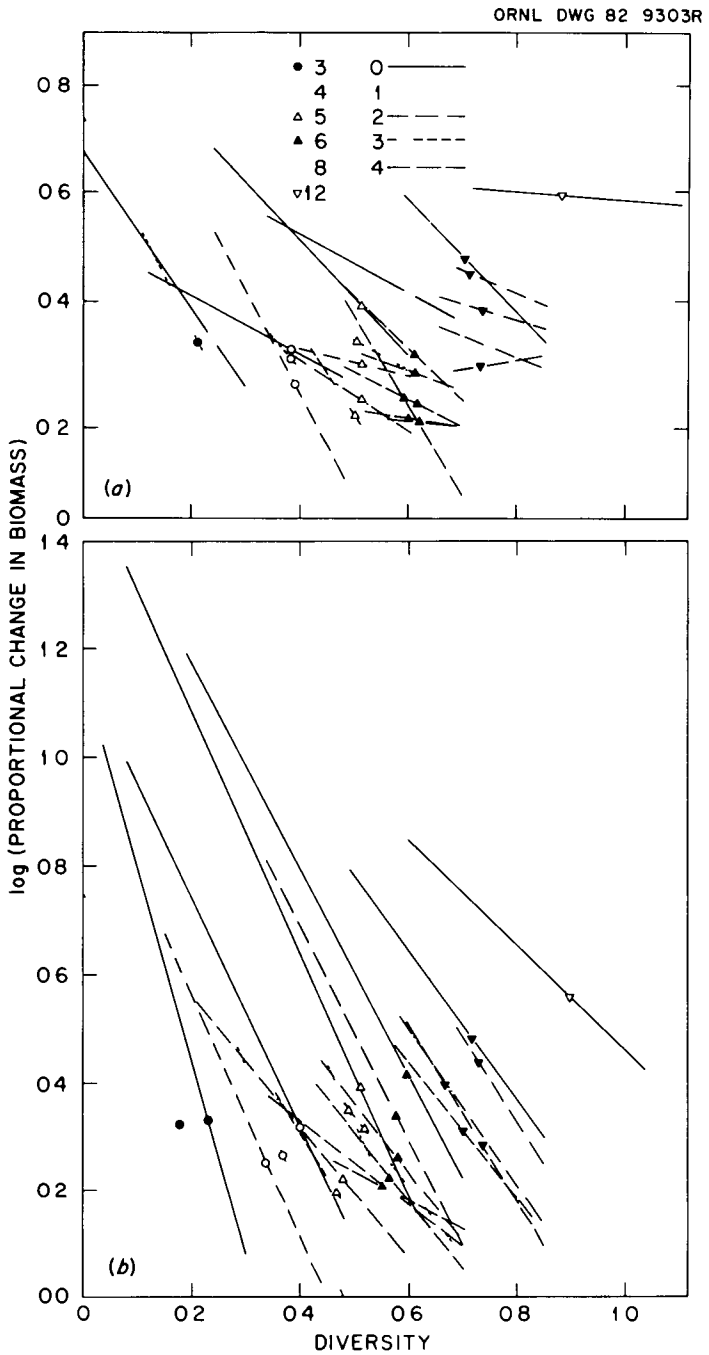


Fig 2 Regression lines of the logarithm of proportional changes in biomass for each of the 23 models analyzed against (a) the plant biomass diversity (H see text) with the herbivore and (b) without the herbivore Length of the lines represents 95% of the range of values observed in the simulations and the symbols are positioned at the mean diversity values for each regression Symbol type indicates the number of species in the models (including the herbivore) and line type indicates the number of competitive interactions between plant species Note that although the slopes are nearly always negative the positions of the symbols yield an overall positive correlation

Within each model the number of plant species is fixed thus these changes in biomass stability are affected by the evenness component of diversity alone Simply the more even the plant biomasses the greater the biomass stability

These results are clear the complications arise when we ask how biomass stability should be related to diversity over a wide range of systems Diversity has two components—species richness and evenness increases in the former cause greater changes in biomass increases in the latter exactly the opposite How should biomass stability vary with an index whose two components are related in diametrically opposite ways?

As noted above increases in richness cause greater changes in biomass And since there is a very strong positive correlation between richness and the Shannon Weaver diversity index over a wide range of systems the greater the diversity measured the greater the expected change in biomass This relationship overwhelms that for evenness and biomass stability Note the positive slope associated with the mean diversity values (Fig 2)

(4) Changes in diversity and evenness The greatest changes in biomass were associated with increases in evenness with the addition of herbivory (Fig 3) Biomasses changed less (the systems were more stable) when the addition of the herbivore caused a reduction in plant evenness Similarly when McNaughton found a decrease in diversity after the intro duction of an herbivore it was accompanied by a smaller change in biomass where diversity increased with grazing it was accompanied by the larger change in biomass (McNaughton 1977)

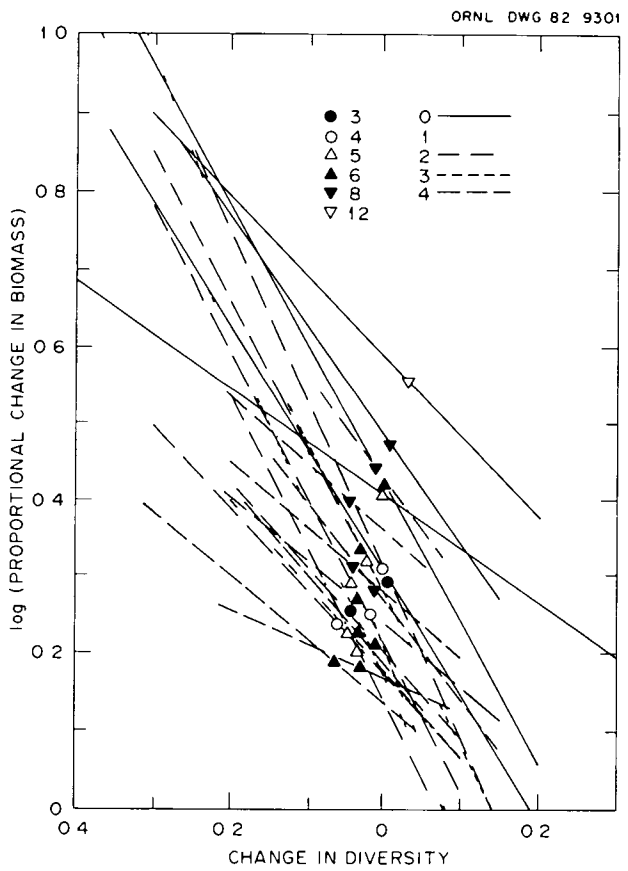


Fig 3 Regressions of the logarithm of proportional biomass change against the change in diversity (without the herbivore minus the herbivore) or each of the 23 models analyzed Lines and symbols as in Fig 3

As before the changes in diversity in Fig 3 reflect only changes in evenness within each model because within each model species richness is constant But these data do not produce the problems inherent in those of Fig 2 Because there is no relationship between the change in diversity and species richness the overall relationships between biomass change and diversity change follows the same trend as within models Unlike the data of Fig 2 the data in Fig 3 show no positive correlation of mean changes in biomass and mean changes in diversity

To summarize our results various facets of system complexity can enhance plant biomass stability in model grazing systems

1 Systems with relatively few plant species per herbivore are expected to be more biomass stable than systems with more (but also fewer) plants per herbivore

2 Systems with more competing species are more biomass stable than those with few if any interactions between plants

3 Increased evenness in plant abundances enhances biomass stability

4 With the removal of the herbivore increases in evenness are associated with smaller changes in biomass

In conclusion we note that McNaughton s experimental results can be demonstrated for at least some ranges of our model structure Yet our model systems are identical in both the equations and the parameters in those equations to previous studies which conclude that more complex systems are less likely to be stable than simple ones

There is no paradox here our study addresses a different question than previous theoretical studies However we feel that our results say something more than that one simply obtains different answers to different specific questions about complexity and stability

The question posed by this study differs in two fundamental aspects from previous theoretical studies First the property under investigation—total biomass—is different in kind from that approached by previous theoretical studies which focus on the presence of individual species Second and at least as importantly many theoretical studies cannot indicate whether among observed systems complex systems are more or less stable because the systems we observe in nature are by the usual definitions of stability unlikely to be anything other than stable These studies imply comparisons between existing communities and hypothetical ones In contrast our study suggests comparisons within existing communities that is whether plant community A is more or less biomass stable than plant community B in response to varying levels of herbivory

REFERENCES

McNaughton S J 1977 Diversity and stability of ecological communities a comment on the role of empiricism in ecology *Am. Nat* 111 515-525

King A W and S L Pimm 1982 Complexity diversity and stability a reconcilation of theoretical and empirical results (manuscript)

Pimm S L 1979 The structure of food webs *Theor Pop Biol.* 16 144-158

Invasibility in Lotka Volterra Interaction Webs

James A Drake

The contention that food web organization and stability are somehow related has provided a major theoretical and empirical focus for the study of food webs (May 1973 Pimm 1979 1980 Rejmánek and Stary 1979 Yodzis 1980 1981 McNaughton 1977 Hurd et al 1971 Hairston et al 1968 Gardner and Ashby 1970) For example Yodzis (1981) has shown that model stability is a rather good predictor of structure in real food webs finding that webs constructed to mimic nature are much more likely to be stable than randomly constructed webs Pimm (1980) has used model food web stability to successfully predict general patterns in real food webs One such prediction is that when a food web contains omnivores they should feed predominantly on adjacent trophic levels One of the most interesting problems in this area centers on how changes in food web size (number of species) and organization (pattern of interactions) resulting from successful invasion by new species alters web stability Also of interest are the characteristics of successful invaders and how if at all they change during food web assembly as complexity increases

In this study I will examine the assembly process in Lotka Volterra models addressing the following questions

(1) If we look only at those food web models which are stable is there a tendency toward increasing or decreasing stability as webs become more complex?
(2) Do species which successfully colonize complex webs differ in consistent ways from those which colonize simple webs?
(3) Are there characteristic differences between the stability effects of colonization by specialists and by generalist species?

The model

A relatively simple model capable of expressing the relationships encountered in food webs while retaining a degree of mathematical tractability is the general Lotka Volterra relationship of the form

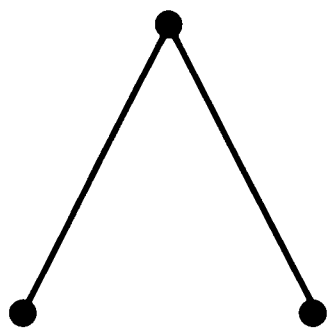
$$x_i = x_i(b_i + \sum_{j=1}^{m} a_{ij}x_j) \qquad i = 1\ 2 \quad m \tag{1}$$

where x_i is the abundance of species i b_i is the density independent component of the per capita rate of increase of species i and a_j is the per capita effect of species j on the per capita growth rate of species i The sign of b_i and a_j depend on whether species i and j are producers or consumers For example $b > 0$ if species i is a producer but $b_i < 0$ if species i is a consumer If species i and j do not interact then $a_{ij} = a_{ji} = 0$ Thus the pattern of connections in a food web is determined by which of the a_{ij} are zero which are positive and which are negative In the results to be reported species occupying the same trophic level are not allowed to interact directly though consumers which use some of the same prey populations do interact indirectly

As will be described below equilibria were located for various choices of a_{ij} The local stability of an equilibrium point was checked using Eispack matrix routines to compute the eigenvalues and corresponding eigenvectors of the stability matrix associated with (1) then determining whether the real part of every eigenvalue was negative If so the equilibrium is stable global stability was not considered

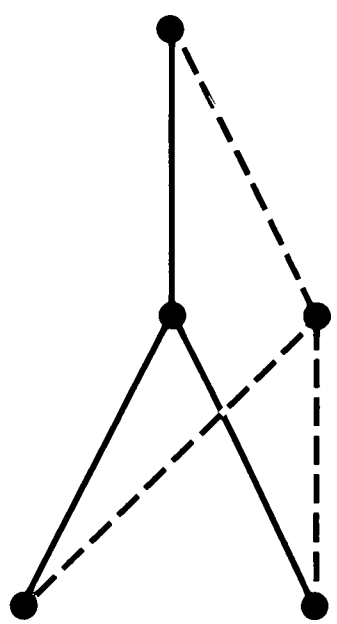
The assembly procedure

To examine characteristics of species assembly I add species to a 3 species base web and examine the local stability properties of both pre and post colonization webs (Fig 1) When a species is introduced to a web it must satisfy certain criteria if it is to remain First an introduced species must be energetically accommodated This precludes for example the possibility of adding a predator without a prey Second the newly introduced species must have a positive population size at equilibrium a condition known as feasibility (Roberts 1974) If an introduced species fails to satisfy any of these criteria it is removed



a

Fig 1a Three species base web consisting of two autotrophic species and one herbivorous species Producers are always self limiting (a_{ii} less than zero) while consumers are not (a_{ii} equal to zero)



b

Fig 1b Possible patterns of connection with an invading herbivore (connected with dashed lines) as it attempts to enter a four species web Six admissible patterns of connection are possible

from the web and another introduction attempted If all criteria are satisfied the new set of equilibrium sizes of pre colonization species are checked to determine whether any of these are now negative If so these species are removed before the new feasible equilibrium is examined for stability

Since each introduction is attempted numerous times using various patterns of connection and species characteristics I am able to determine how a particular introduction can effect food web stability This is done by fixing those elements in the interaction matrix (a_{ij}) which involve only pre colonization species while varying the effect of the interaction coefficients involving the newly introduced species For each pattern of connection the non zero interaction coefficients involving the newly introduced species are varied stepwise between 0 and 1 or 0 and 1 In this way it is possible to locate values of a_{ij} where the web undergoes a transition between stable and unstable states and I can determine the set of a_{ij} values which a successful invader can have The assembly process continues until I can find no further introductions which are successful at colonizing the web

Results and discussion

Since each introduction is attempted numerous times using various patterns of connection and species characteristics I am able to determine how a particular introduction can effect food web stability Usually varying a particular a_{ij} results in a significant change in food web stability characteristics Let us consider the following example A stable five species web consisting of three producers one herbivore and one predator is colonized by another herbivore Holding all interactions constant except the interaction between the predator and the new herbivore one sees an initial increase in stability as either a_{ij} or a_{ji} is increased from zero (Fig 2) Stability decreases rapidly after an initial increase as the effect of the predator on the new herbivore increases resulting in a transition from stability to instability However instability is never reached when the prey s effect on the predator is increased from zero to one although there is an overall decrease in stability

After all colonization attempts were concluded I examined each stable web comparing degrees of pre and post colonization stability I define the term relative stability (RS) as the ratio of the real parts of the dominant eigenvalues

$$RS = \frac{\mathrm{Re}(\lambda_{dom})}{\mathrm{Re}(\bar{\lambda}_{dom})} \tag{2}$$

where $\mathrm{Re}(\lambda_{dom})$ is the real part of the dominant eigenvalue of a specified web and $\mathrm{Re}(\bar{\lambda}_{dom})$ is the analogue for this web after being invaded by a colonist If the postcolonization web is exactly as stable as the precolonization web as measured by RS then RS will have a value of one However if the postcolonization web is less stable than the precolonization web then RS will have a value less than one

In nearly all cases each postcolonization web was less stable than the precolonization web (Fig 3) This resembles May s (1973) result (see conclusion) but goes beyond it since I find that even if only *stable* webs are examined there is an overall decline in stability with increasing complexity (number of species) That stability tends to decrease with increasing complexity does not preclude the possibility of successful invasions with increasing complexity but rather imposes constraints on species characteristics which must be satisfied if a colonist is to remain in a web

When characteristics of successful colonists are compared to those of unsuccessful colonists several patterns emerge If species are classified as either generalists (feed on all trophically appropriate populations) or specialists (feed on a subset of trophically appropriate

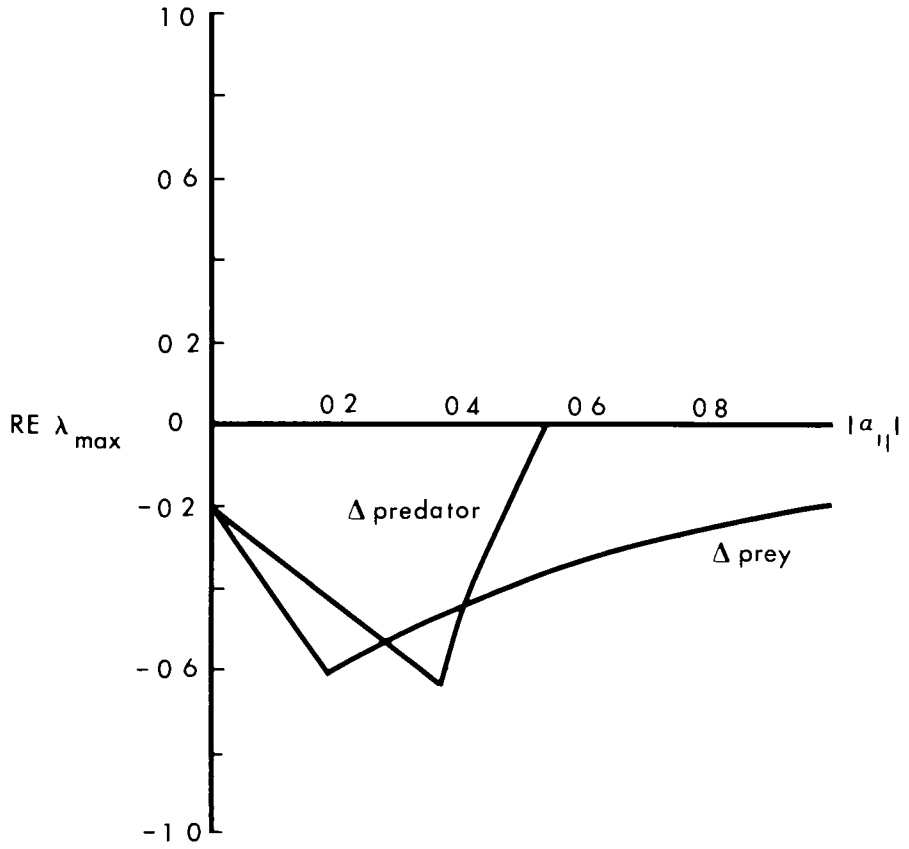


Fig 2 System response to changes in the magnitude of a single predator prey interaction The real part of the dominant eigenvalue Re(λ_{dom}) provides a way to monitor changes in the degree of stability When Re(λ_{dom}) is greater than zero the system is unstable If Re(λ_{dom}) is less than zero the system is stable and the farther below zero λ_{max} is the greater the degree of stability The Δ predator relationship is generated by holding all interactions constant while varying the effect (a_{ij} less than zero) of the predator on one of its prey Following an initial increase in stability system stability rapidly decreases to instability at an a_{ij} of approximately 0 55 The Δ prey relationship is generated by holding all interactions constant while varying the effect (a_{ji} greater than zero) of the prey on its predator A transition between stable and unstable states never occurs in this case

populations) then successful colonization of simple (less than six species) and complex webs (six or more species) differs significantly from specialists in colonizing simple webs while specialists tended to be more successful than generalists in colonizing complex webs (Fig 4)

Conclusions

A crucial test of the usefulness of such food web models is to show that decreasing sta bility is not simply a mathematical artifact of increasing complexity but rather a consequence of conditions which have a clear biological meaning and can thus guide our

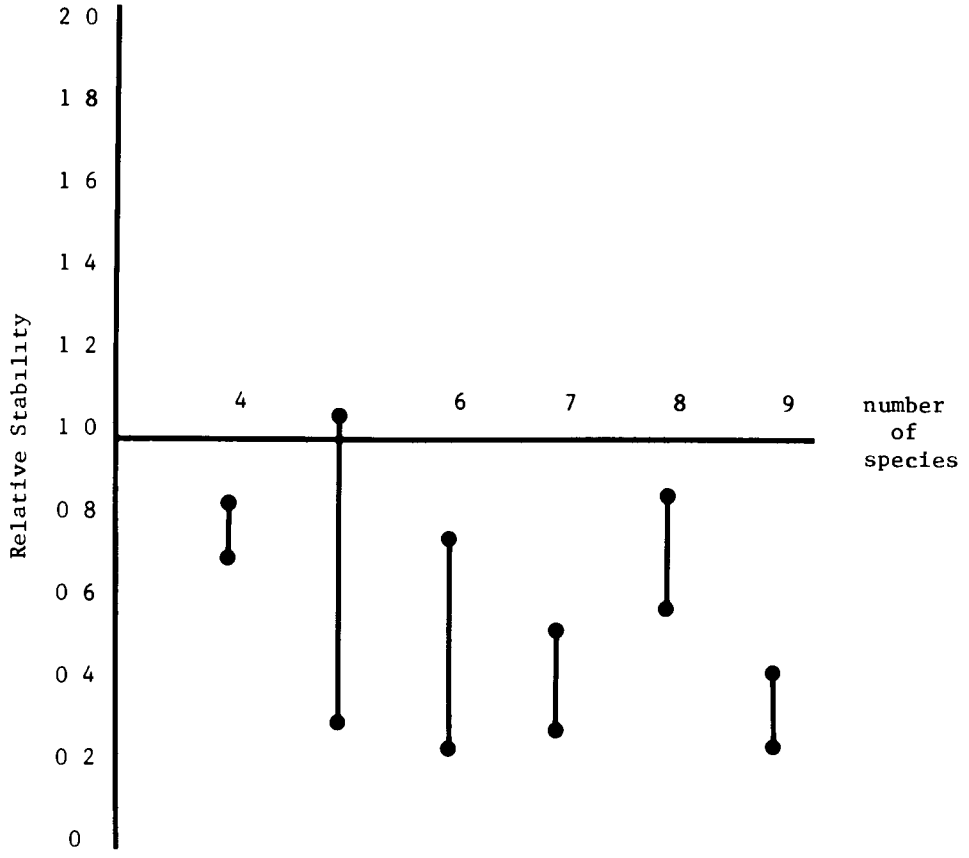


Fig 3 Relative stability defined as the ratio of the real parts of the dominant eigenvalue of post and pre colonization webs is examined with increasing web com plexity In most cases relative stability decreased with each successful invasion such that among stable webs addition of an invader tends to reduce system stability

intuition May (1973) showed that increasing complexity in randomly assembled communi ties leads to a rapid decline in system stability This result was extended by Pimm (1979) to models subject to reasonable biological constraints with a similar result I have found that any given food web is almost always more stable before a colonist is added than after a colo nist is added Hence even if only stable pre and post colonization webs are considered increased complexity reduces stability I have also shown that only a subset of all potential species introductions are successful in invading any given food web This result was obtained by classifying species as either generalists or specialists and food webs as either simple or complex Using these somwhat arbitrary divisions I find that generalists tend to be more successful than specialists at colonizing simple webs Conversely I find that specialists tend to be more successful than generalists in colonizing complex webs This result suggests that successful colonization is not random but rather that colonization is to an important degree regulated by properties of the existing food web and the invading species

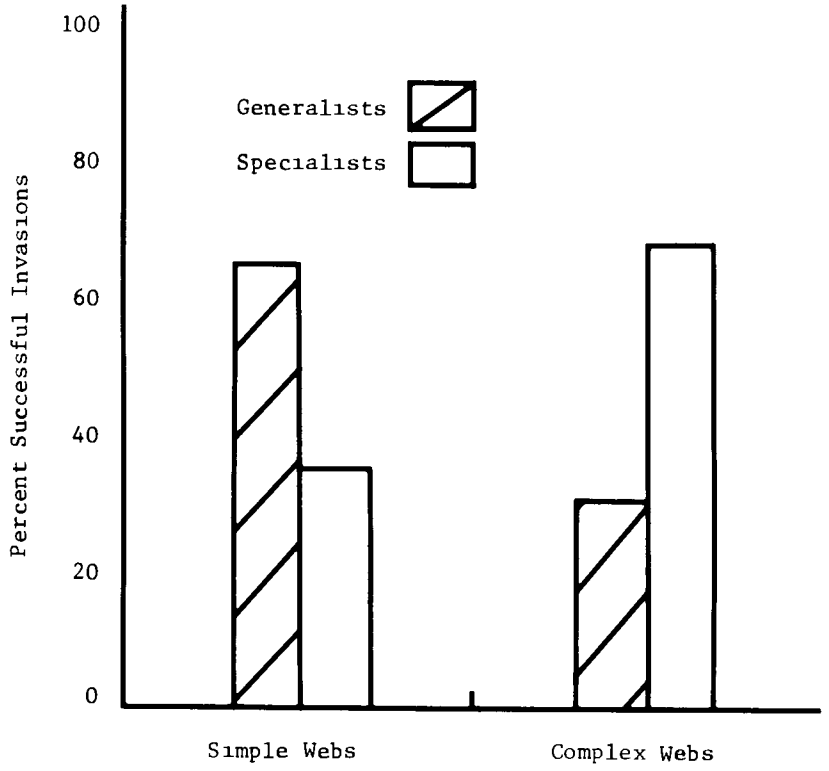


Fig 4 Differential colonization success as a function of trophic role and food web complexity In these simulations generalists (feeding on all possible prey populations) tended to be more successful than generalists in colonizing simple food webs (less than six species) Conversely specialists (feeding on any proper subset of prey populations) tended to be more successful than generalists in colonizing complex webs Differences are statistically significant at $p < 0\ 01$ using a nonparametric binomial test

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Appendix

The following procedure was used to determine if a colonizing species can increase when rare Let $(\hat{x}_1\ \hat{x}_2\ \ \hat{x}_n)$ denote the stable equilibrium point of the pre colonization food web consisting of species 1 2 n label the invading species n+1 The invader can increase when rare if the equilibrium $(\hat{x}_1\ \hat{x}_2\ \ \hat{x}_n\ 0)$ is unstable

To check the stability of ($\hat{x}_1$ $\hat{x}_2$ $\hat{x}_n$ 0) system (1) was linearized about this point and the eigenvalues of the resulting stability matrix were checked If the dominant eigenvalue has a positive real part the equilibrium is unstable and the invader can enter the food web

Once the eigenvalues have been determined for the pre colonization equilibrium point it is easy to determine those for ($\hat{x}_1$ $\hat{x}_2$ $\hat{x}_n$) say λ_1 λ_2 λ_n plus an additional eigenvalue λ_{n+1} given by

$$\lambda_{n+1} = b_{n+1} \sum_{j=1}^{n} a_{n+1,j} x_j \tag{3}$$

Thus hardly any additional labor is involved Since λ_1 λ_2 λ_n must have negative real parts the invader can enter the web provided λ_{n+1} is greater than zero

REFERENCES

Gardner M R and W R Ashby 1970 Connectance of large dynamic (cybernetic) systems critical values for stability *Nature* 228 784

Hairston N G J D Allen R K Colwell D J Futuyma J Howell M D Lubin J Mathias and J H Vandermeer 1968 The relationship between species diversity and stability an experimental approach with protoza and bacteria *Ecology* 49 1091 1101

Hurd L E M V Mellinger S L Wolf and S J McNaughton 1971 Stability and diver sity at three trophic levels in terrestrial successional ecosystems *Science* 173 1134 1136

May R M 1973 Stability and Complexity in Model Ecosystems Princeton University Press Princeton N J

McNaughton S J 1977 Diversity and stability of ecological communities a comment on the role of empiricism in ecology *Amer Natur* 111 515 525

Pimm S L 1979 The structure of food webs *Theor Pop Biol.* 16 144 158

Pimm S L 1980 Properties of food webs *Ecology* 61 219 225

Rejmanek M and P Stary 1979 Connectance in real biotic communities and critical values for stability of model systems *Nature* 280 311 312

Roberts A 1974 The stability of a feasible random ecosystem *Nature* 251 607 608

Yodzis P 1980 The connectance of real ecosystems *Nature* 284 544 545

Yodzis P 1981 The structure of assembled communities *J Theor Biol.* 92 103 117

Alternative Forms for Links in Trophic Webs

Peter A Abrams

Introduction

The diversity of types of interspecific interaction in nature is such that many questions about food webs cannot be answered without quantitative descriptions of the trophic links which make up the web The major component of any quantitative description of a trophic link is the functional response of the consumer involved in the link Many previous theoreti cal studies of trophic webs have explicitly assumed linear functional responses for all consu mers Other studies have simply studied community matrix representations of food webs without specifying the functional response The analysis presented below suggests that most such matrices are not consistent with many nonlinear functional responses Analysis of the interspecific interactions in systems with nonlinear functional responses reveals may poten tial interactions which have been neglected in most pevious food web studies

Type 2 and 3 functional responses

If a consumer species requires a finite amount of time to eat its prey and the number of predator prey encounters during search is a linear function of the density of each the func tional response will be type 2 If there are two prey types which can be hunted simultane ously the form of the consumer s functional response on prey type 1 will be

$$C_1N_1/(1 + t_1C_1N_1 + t_2C_2N_2)$$

where C_i is the per capita prey capture rate per unit of search time and t_i is the handling time and N_i is the population density of the prey type i An analogous expression may be written for the functional response on prey type 2 Clearly each prey has a beneficial effect on the rate of increase of the other prey type These effects arise because an increase in the population density of either prey reduces the amount of time which the predator spends searching for (as opposed to handling) both prey If the functional response is accel erating rather than decelerating and is a function of the population density of both prey each prey has a negative effect upon the rate of increase of the other Any sort of switching behavior will result in interactions between species which share a common predator and Chesson (1982 manuscript) has shown that positive or negative switching can arise as a result of between individual variation in populations in which the individuals do not switch Some direct interactions between species sharing predators should be present in most real world food webs

It should be stressed that these interactions are not analogous to the sort of indirect interactions discussed by Kerfoot in this symposium The effects discussed here do not require changes in the population densities of intermediate species and therefore occur on a much faster time scale Unlike traditional indirect effects " they require additional terms in matrix representations of interspecific interactions in food webs

Functional responses which result from adaptively variable foraging time

In a recent article (Abrams 1982) I suggested that functional responses in nature are often the product of functional response while foraging and the proportion of an animal s time which it spends foraging If the proportion of time spent foraging is adjusted in an

adaptive manner with changes in food density this can result in unusual functional response shapes for the given species The previous article did not discuss the effect that adaptive variation in foraging time by a prey has on its predator s functional response nor did it discuss functional responses on two or more prey types Both of these cases have implications for interactions in food webs

If a prey is not equally susceptible to predation while it (the prey) is foraging and while not foraging then the foraging strategy adopted by the prey will affect the predator s functional response This effect can most easily be illustrated with a model of a three species food chain in which the middle species has adaptively variable foraging time For simplicity I will assume that the prey is only available to the pedator while the prey is foraging Following Abrams (1982) I assume that the prey s per capita birth rate is an increasing concave downward function of energy consumed and that the per capita death rate is an increasing concave upward or linear function of time spent foraging Time spent foraging is adjusted to maximize individual fitness There are a number of plausible three species food chain models that fit these assumptions One example is the following

$$\text{Resource} \quad \frac{dR}{dt} = r_0 R\left(\frac{k - R}{k}\right) - C_0 NRT$$

$$\text{Prey} \quad \frac{dN}{dt} = r_1 N\left(\frac{C_0 RT}{Q + C_0 RT} - A_1\right) - C_1 NTP$$

$$\text{Predator} \quad \frac{dP}{dt} = r_1 N(C_1 NT - A_2)$$

$$\text{Optimum foraging time} \quad T_c = \frac{1}{C_0 R}\left(\sqrt{\frac{r_1 Q C_0 R}{C_1 P}} - Q\right)$$

The general features that emerge from three species food chain models of this sort are

(1) The predator has a self inhibition effect because higher predator density decreases the optimum amount of time which the prey should spend foraging

(2) The predator should have a positive effect on the per capita rate of increase of the prey s resource This arises because increases in predator population density always reduce the optimum fraction of time which the prey spends foraging

(3) The prey s resource population may have a positive or negative effect upon the predator depending upon whether increased resource densities favor increased or decreased foraging time If the birth as a function of energy curve is sufficiently saturated higher resource densities will favor lower foraging times If the birth function increases sufficiently rapidly at a given resource density then increasing that density will favor longer foraging times Abrams (1982) investigates some specific models

The magnitudes of the predator self inhibition and the effect between nonadjacent trophic levels can be determined by evaluating the partial derivatives of the per capita growth rates of each species with respect to the other populations at equilibrium densities This analysis is presented elsewhere (Abrams MS) There exists a large range of parameter values for which (1) the system has a stable equilibrium (2) the relative abundances of resource prey and predator are biologically realistic and (3) at least one of the effects between nonadjacent trophic levels is larger than the comparable effect between adjacent levels In the model described above changes in the population density of the predator gen

erally have a greater effect upon resource population growth rate than upon consumer population growth rate Large effects between nonadjacent trophic levels also occur in other models which make less extreme assumptions regarding the differential availability to predators of foraging and nonforaging consumers The above conclusions are not qualitatively changed if the predator as well as the prey has an adaptively variable foraging time

This type of analysis can be extended to food chains of four or more levels or food webs in which there are two or more species on a level In these cases if there is an intermediate optimum foraging time and if this time is adjusted to maximize fitness the following features emerge

(1) There will always be a (+ +) or ( ) interaction between two species on a given level which share a predator The first case arises when increases in total prey density decreases foraging time and the latter when foraging time is increased If the predators and the prey both have adaptively variable foraging times it is possible to have interactions between species which do not share a common predator For example if predator type 1 consumes prey types A and B and predator 2 consumes B and C then prey types A and C may interact as follows A change in the density of prey A changes the optimal foraging time of 1 which changes the optimal foraging time of B which alters the optimal foraging time of 2 which alters the optimal foraging time and per capita growth rate of C

(2) There should be interactions between species separated by any number of trophic levels as long as they can be connected in the food web through a chain of variable time foragers There should be positive effects on species which are an even number of trophic levels lower and negative effects on species which are an odd number of levels lower There can be + or effects on species at any number of trophic levels higher depending upon the quantitative details of the intervening species foraging strategies Together these upward and downward effects allow apparent cyclical predation loops of an odd number of links Of course one of the links is a non predatory (+) link In addition ( ) or (+ +) interactions may occur between species of widely separated trophic levels

III Implications and discussion

Very little is known about functional responses in the field or about the relative benefits and risks of foraging activity Although a number of cases of variation in foraging time in response to changed food or predator density have been observed there is very little quantitative information This makes it very difficult to make an informed assessment of the magnitudes of the effects discussed above It is possible to choose parameter values for the 3 species model presented above which do not a priori seem unreasonable and which result in level 1 level 3 effects being of the same order of magnitude as effects between adjacent levels It is likely that effects decrease in magnitude as the number of intervening species increases More literature searching and field work will be required before firm conclusions regarding magnitudes of effects can be drawn

Many of the same effects will occur if foraging effort or foraging location is varied rather than foraging time My biologist s intuition is that the conditions necessary for some effects between separated trophic levels are met very frequently

The implications that these effects have for stability analyses of food webs should be clear from the other contributions to this symposium which involve dynamical models If self regulation at higher trophic levels is as common as this analysis implies the argument for limitation of food chain length by population dynamics may not hold Nontrophic links between separated trophic levels may alter conclusions about the effect of omnivory on food chain stablity The potential for the types of interaction detailed here should be considered in future food web studies It may turn out that natural systems have a much higher connectance than has generaly been supposed

REFERENCE

Abrams P A 1982 Functional responses of optimal foragers *Amer Natur* 120 382 390

The Role of Symmetric Food Web Models in Explicating the Stability/Diversity Connection

Robert A Armstrong

Explicating the relationship between the stability of food webs and various aspects of their structure is a central problem in food web research Here I will focus on one particular aspect of this general problem the relation between the diversity of a food web and its sta bility

MacArthur (1955) made the first quantitative investigation of the relationship between the stability and diversity of food webs MacArthur s concept of diversity was related to the number of paths that might be followed by a packet of energy as it traverses a food web (Goodman 1975) A more diverse food web will have more paths and these paths will be more nearly equal with respect to the amount of energy flowing through them

MacArthur s concept of stability was defined by means of an example (MacArthur 1955 p 534) Suppose for some reason that one species has an abnormal abundance Then we shall say that the community is unstable if other species change markedly in abundance as a result of the first The less effect this abnormal abundance has on the other species the more stable the community

MacArthur then proceeded to argue that this type of stability should increase with diver sity The intuition behind this argument may be summarized as follows If a prey species which has but a single predator experiences an increase in numbers then all the excess energy in that species must pass through its single predator species markedly disrupting the population size of the predator species If on the other hand a given prey species has many predators then these extra energy conduits as it were can siphon off the excess energy while causing minimal disruption of the food web (see also Southwood and Way 1970)

More recent work by May (1973) and others have profoundly changed the nature and direction of research into the stability/diversity connection (for review see Armstrong 1982) Whereas MacArthur s (1955) notion of stability was related to the ability of a food web to continue functioning with little disruption in the face of a chronic disturbance May s (1973) notion of stability was the normal one used for dynamical systems a system is more sta ble the faster it returns to equilibrium following a temporary perturbation (see also Lewon tin 1969) And whereas MacArthur (1955) had considered only food webs in which the flow of energy from one species to the next is controlled by the concentration of energy in the species on the lower trophic level May (1973) allowed for the idea that predator species may exert considerable influence on the dynamics of prey predator interactions Using this defi nition of stability and its attendant mathematical structures May (1973) showed that the stability of randomly constructed model ecosystems tended to decrease with diversity

This new result so seemingly in contrast to MacArthur s occasioned a shift in view con cerning the relation of stability and diversity (McNaughton 1977) No longer was stability thought to devolve from diversity rather the view emerged that diverse ecosystems existed in spite of their tendency to be unstable This new view has occasioned an extended search for those special features of real food webs which would allow them to be both diverse and stable (May 1973 1979 Pimm 1982) While this search has produced several interesting results (for reviews see May 1979 and Pimm 1982) it has not yet produced the type of com pelling intuitive insight which would for example prompt field workers to undertake seri ous experimental investigations of the stability/diversity connection

Highly symmetric food web models (Armstrong 1982) may be useful in overcoming this problem Such models can be analyzed to a much deeper level than is possible with more general food web models This depth of analysis permits an intuitive understanding of model behavior the intuition thus gained can then be carried over to the study of less highly sym metric models or directly to field studies

I will present two such models Both have at their base a simple predator prey model of the form

$$\frac{dX}{dt} = F_1(X \quad R) = Xf(R)$$

$$\frac{dR}{dt} = F_2(X \quad R) = R[g(R) = Xh(R)] \tag{1}$$

Here X is predator species density R is prey species (resource) density and $g(R)$ is the per capita growth rate of the prey species in the absence of predation The function $h(R)$ is the per capita functional response of the predator species to prey density (Armstrong 1976) and $f(R)$ is the predator species growth rate which is also a function of prey density

The two examples I wish to discuss are constructed by taking systems of the general form (1) and attaching them to each other in a well defined and symmetric manner to form larger systems This attaching must be done carefully so that one is sure that any change in system behavior is due to the form of attachment (and hence the structure of the food web) rather than to any other cause Analysis of system stability near equilibrium then proceeds in the normal manner (May 1973 Armstrong 1982) involving determination of all eigen values and their associated eigenvectors The symmetric nature of the food web then allows relatively straightforward ecological interpetation of these results

The first example I present consists of two parallel predator prey systems which are crosslinked to form a single two predator two prey system in which each predator consumes both prey species The system is parameterized by p 0 5 $< p \leqslant 1$ which is the fraction of energy a given predator species receives from its preferred prey species An amount of energy $q = 1 \quad p$ flows up the crosslink from the nonpreferred prey (see Fig 1) As $p \rightarrow 0\,5$ the relative importance of the various energy pathways is equalized producing [sensu MacArthur (1955)] a more diverse system As $p \rightarrow 1$ diversity approaches a mini mum

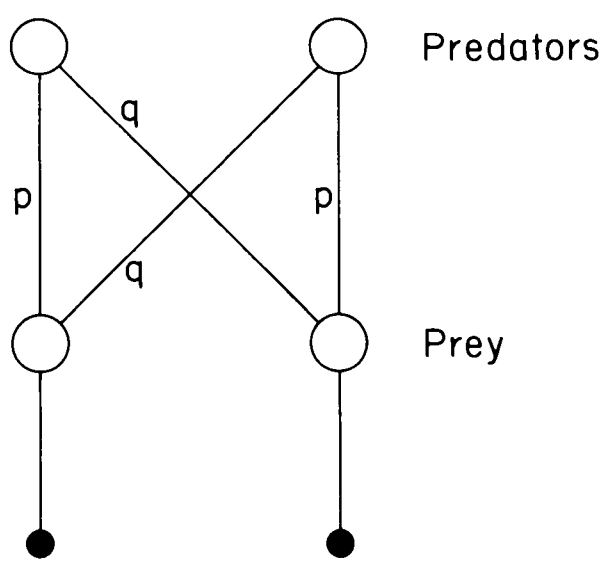

Fig 1

A detailed analysis of this system has been published elsewhere (Armstrong 1982) I will therefore not present further details of the construction of this model but will proceed directly to a summary of the results (i) There exist three identifiable modes of vibration of the model (ii) The first mode of vibration in which the densities of both predator species are equal and in which the densities of both prey species are equal so that the two linked systems vibrate in phase is unaffected by a change in p Thus in some sense the functional stability of this system as reflected in this ecosystem mode of vibration is not affected by the connectance p of the system (iii) The second mode of vibration of the system corresponds to a difference between the densities of the two predator species This mode of vibration is very sensitive to changes in p In fact as $p \rightarrow 0\,5$ the eigenvalue corresponding to this mode of vibration approaches zero This result is immediately interpretable in terms of normal ecological intuition as $p \rightarrow 0\,5$ the two predator species become indistinguishable generalists and any difference in their relative densities will die away very slowly (Miller 1969 May 1973 Armstrong 1982) (iv) The third mode of vibration corresponds to the difference in the densities of the two prey species As $p \rightarrow 0\,5$ this mode of vibration actually becomes *more* stable The interpretation of this result in terms of extra conduits equalizing productivity (and hence population size) among prey species is remarkably parallel to MacArthur s (1955) original intuition (Armstrong 1982)

The second example is based on a model of tropical forest structure proposed by Janzen (1970) Janzen proposed that each tree species may be limited by its own seed predator A simple model which captures the essence of this situation is shown in Fig 2 Here each of four prey (insect) species feeds on its own prey (tree) species while all tree species are limited by the same abiotic resource space This system can be assembled from the modules (1) by simply recognizing that the per capita growth rate of each prey species is a function not only of its own density but of the total density of all prey species We therefore write our model as

$$\frac{dX_i}{dt} = X_i f_i(R_i)$$

$$\frac{dR_i}{dt} = R_i[g_i(\sum_j R_j) \quad X_i h_i(R_i)] \tag{2}$$

for $i,j = 1 \quad n$ where n is the number of predator prey pairs present in the food web

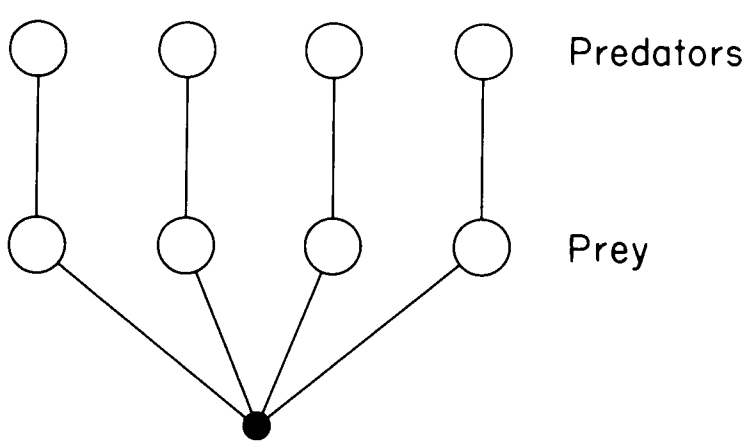

Fig 2

We now define two quantities $\sigma = R_t(\partial g_t/\partial R_t)$ and $\delta = X_t R_t(\partial h_t/\partial R_t)$ where the asterisks indicate that all quantities are defined at equilibrium It can then be shown that the real part of the eigenvalues corresponding to the ecosystem mode of vibration where all predator prey pairs oscillate in parallel is given by $(n\sigma \quad \delta)/2$ Likewise the real part of the eigenvalue associated with all other modes of motion of the system is given by $\delta/2$

Now the term σ is due to prey self limitation and generally is negative it therefore exerts a stabilizing influence on the system The term δ is due to the predator s functional response and can be positive or negative For a Holling Type II functional response δ is negative and therefore destabilizing a Type III response can be either stabilizing or desta bilizing (Armstrong 1976) It is this tension between the (usually) stabilizing influence of prey self limitation and the (often) destabilizing influence of the predator s functional response which determines whether the system will be stable or unstable near its equilib rium point (Armstrong 1976 May 1976)

It is therefore evident that the stabilizing influences of prey self limitation are all con centrated as it were in the ecosystem mode of vibration while all other modes of vibra tion of the system are bereft of this stabilizing influence In fact if the predator s functional response is destabilizing (δ <0) it is quite possible that ecosystem *function* will become ever more stable as the number of species pairs increases since $(n\sigma \quad \delta)/2$ will become ever more negative as n increases but that all species in the system will be experiencing more or less violent oscillations since all other modes of vibration will be unstable This dif ferentiation between stability of function versus stability of population sizes is an important intuitive contribution of the model this distinction has been discussed in an empirical con text by McNaughton (1977)

At several points in this synopsis I have stressed the fundamental importance of intuition formation as a goal of model building I believe this point is crucial The real dynamics of a Janzen system will be governed by equations too horrible to contemplate Yet the simple model (2) suggests that the functional stability of ecosystems may indeed increase with diversity even while species level stability is uncorrelated with diversity It is precisely this sort of intuition which can inspire more critical field studies into the stability/diversity connection and perhaps revive it from unwarranted disfavor in the con text of applied problems (see e g Goodman 1975) The Janzen model suggests for example that as species pairs are lost from an ecosystem the functioning of that ecosystem will become less stable Confirming or refuting such a statement may prove to be of considerable practical importance

Symmetric food web models because of their relatively simple structure are ideally suited to the task of intuition formation Their use as bases from which perturbations to more realistic food web models can be performed will greatly increase the intuitive content of food web research

REFERENCES

Armstrong R A 1976 The effects of predator functional response and prey productivity on predator prey stability a graphical approach *Ecology* 57 609 612

Armstrong R A 1982 The effects of connectivity on community stability *American Natur alist* 120 391 402

Goodman D 1975 The theory of diversity stability relationships in ecology Quarterly Review of Biology 50 237 266

Janzen D H 1970 Herbivores and the numer of tree species in tropical forests *American Naturalist* 104 501 528

Lewontin R C 1969 The meaning of stability p 13 23 *in* Diversity and Stability in Ecological Systems Brookhaven Symposia in Biology Number 22 National Technical Information Service Springfield Va

MacArthur R H 1955 Fluctuations of animal populations and a measure of community stability *Ecology* 35 533 536

McNaughton S J 1977 Diversity and stability in ecological communities a comment on the role of empiricism in ecology *American Naturalist* 111 515 525

May R M 1973 Stability and Complexity in Model Ecosystems Princeton University Press Princeton New Jersey

May R M 1976 Theoretical Ecology Sinauer Associates Sunderland Massachusetts

May R M 1979 The structure and dynamics of ecological communities p 385 407 *in* Population Dynamics R M Anderson B D Turner and L R Taylor *eds.* Blackwell Scientific Publications Oxford

Miller R S 1969 Competition and species diversity p 63 70 *in* Diversity and Stability in Ecological Systems Brookhaven Symposia in Biology Number 22 National Technical Information Service Springfield Va

Pimm S L 1982 Food Webs Methuen Inc New York

Southwood T R E and M J Way 1970 Ecological background to pest management p 6 29 *in* Concepts of Pest Management R L Rabb and F E Guthrie *eds* North Carolina State University Press Raleigh North Carolina

Time Delays and Food Web Stability Horizontal Food Chains

Len Nunney

Introduction

MacArthur (1955) argued that as the number of links in a food web is increased the effect of perturbations of one species upon the whole web might be expected to decrease The idea that increased complexity results in increased stability rapidly gained acceptance until the early 1970s when work on randomly structured food webs showed that at least in linear sytems increased complexity leads to decreased stability (see May 1973a)

Recent work has addressed the problem of analyzing more realistic food webs webs which include a trophic structure and/or non linear interactions (see for example DeAngelis 1975 Pimm 1979 Nunney 1980a) However one aspect of real ecological systems which has generally been neglected is the time delay between the birth of an organism and its reproductive maturity The analysis of time delayed systems is complex and here I wish to consider only one special case the effect of a number of predator or parasitoid species upon a single prey the life history of which can be divided into a number of developmental stages

Time as a resource dimension

Haigh and Maynard Smith (1972) made the important observation that two predators utilizing the same resource can coexist provided that they feed upon different life history stages of the prey May and Hassell (1981) demonstrated a similar effect using a difference model formulation of a two parasitoid one host system rather than the continuous time lagged form employed by the earlier workers

Can these results be extended to more than two predators? If so it suggests the idea of a horizontal food chain We usually represent energy shifts between trophic levels by vertical movement giving the usual vertical food chain (see Fig 1a) Here I wish to consider a system dominated by horizontal energy shifts that is energy shifting between the age classes of a prey (Fig 1b)

It is often considered that time delayed systems are always less stable than their non delayed counterparts however it can be shown that for moderate time delays (less than the natural period of the system) such lags tend to enhance stability (Nunney 1983) Furthermore the natural period of a predator prey system tends to be long when compared to that of the prey alone leading to the result that the addition of a predator can stabilize an unstable prey population (May 1973b)

The model

The model used is illustrated by Fig 1b The resource (or prey) species is assumed to have three life history stages of equal duration (T) For ease of discussion I shall refer to them as the egg larval and pupal stages There is also a reproductive adult stage Egg production is logistically regulated with regulation depending only upon adult numbers (negative production being considered as zero) The adults have a characteristic constant death rate (s) as do the larvae and pupae (u)

Each age class can be exploited by a single species of predator or parasitoid these two possible forms need not be distinguished because linear functional responses are used (see Nunney 1980b) For simplicity the attack rate of the first predator (feeding upon eggs) is defined by a that of the second by ab and that of the third and fourth by ab^2 and ab^3

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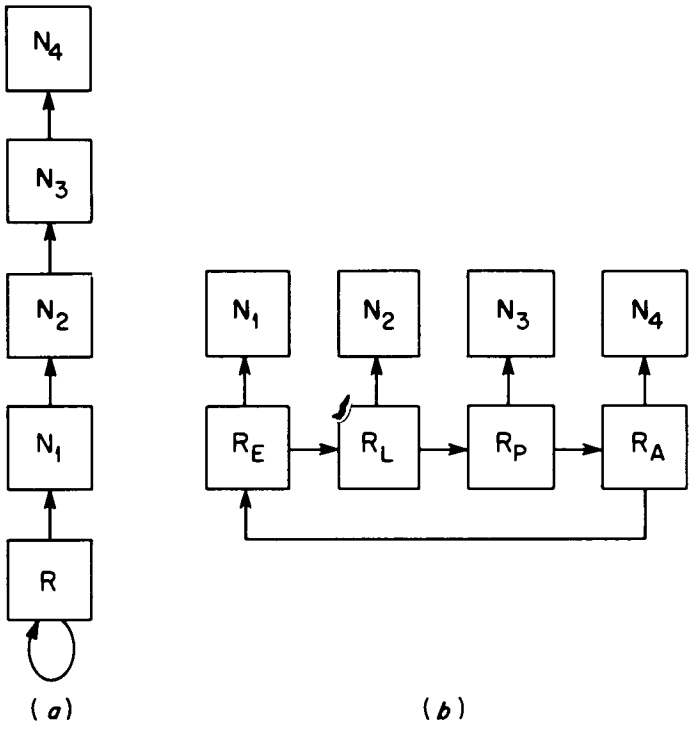

Fig 1 (a) a typical vertical food chain based upon the self regulating resource R (b) a horizontal food chain in which each of the four age classes of the resource can be exploited separately

Similarly the constant death rates are e ef ef^2 and ef^3 The conversion of predator intake into predator rate of change is fixed at c

Simulation of the model resulted in the following general conclusions

(i) Four predator species can coexist in a stable equilibrium on a single resource

(ii) Such coexistence can occur even though some predator combinations are unstable or cannot exist

(iii) If in the absence of predators the resource population oscillates then the addition of predators if successful will usually stabilize the dynamics

(iv) Predators which cannot invade at the hypothetical equilibrium of an oscillating prey population can often successfully invade due to their growth on the periodically high resource levels Following a shift in the age structure the whole system is then stabilized

An example illustrating these four points is summarized in Table 1

Discussion

Time delays are usually considered only with regard to their negative effect upon stabil ity Two points are apparent from simulations of the age structured model which suggest a shift of emphasis in our view of time lags in ecological systems The first is that age struc ture represents a resource dimension rarely considered in theoretical work The second is

Table 1 The behavior of a horizontal food chain

For simplicity only the numbers of prey in each class are given the predator numbers are omitted The results are from the model described in the text using the following values a = 0001 b = 1 17 c = 1 e = 05 f = 1 K = 10^4 r = 25 s = 05 u = 01 T = 10

Predators present	Age class			
	Egg	Larval	Pupal	Adult
0	3944	3754	3396	8037
		Predicted values-cycles of period ~90		
1		Unstable-predator lost		
2	6200	4274	2408	4555
3	6043	5778	3653	4090
4	5368	5133	4642	3122
1 2		Unstable-predator 2 then 1 lost		
1 3		Oscillations of large ampl -period >2500		
1 4	5000	4388	3969	3122
2 3		Unstable-predator 3 lost		
2 4	5368	4274	3013	3122
3 4	5368	5131	3653	3122
1 2 3		Oscillations of large ampl -period >2500		
1 2 4	5000	4274	3750	3122
1 3 4	5000	4370	3653	3122
2 3 4		Unstable-predator 3 lost		
1 2 3 4	5000	4273	3653	3122

that increased complexity lessens the chance of the highly oscillatory behavior often considered typical of time lagged systems If such a generality stands up to a more general investigation it may provide some insight into the question of whether or not simple ecosystems are more prone to oscillation

REFERENCES

DeAngelis D L 1975 Stability and connectance in food web models *Ecology* 56 238 243

Haigh J and Maynard Smith J 1972 Can there be more predators than prey? *Theor Pop Biol.* 3 290 299

MacArthur R M 1955 Fluctuations of animal populations and a measure of community stability *Ecology* 36 533 536

May R M 1973a Stability and Complexity in Model Ecosystems Princeton Univ Press

May R M 1973b Time delay versus stability in population models with two and three trophic levels *Ecology* 54 315 325

May R M and M P Hassell 1981 The dynamics of multiparasitoid host interactions *Amer Natur* 117 234 261

Nunney L 1980a The stability of complex model ecosystems *Amer Natur* 115 639 649

Nunney L 1980b The influence of the type 3 (sigmoid) functional response upon the stability of predator prey difference models *Theoret. Pop Biol.* 18 257 278

Nunney L 1983 Resource recovery time just how destabilizing is it? In Lecture Notes in Biomathematics Ed S Levin Pub Springer Verlag (In press)

Pimm S L 1979 The structure of food webs *Theoret. Pop Biol.* 16 144 158

Propagated Effects Along Food Chains Vaulting

W Charles Kerfoot

Introduction

Natural communities are complex assemblages of literally thousands of species set against a chemical physical background that both influences and is influenced by the living component In a lake for example complete enumeration of primary species in the pelagic zone would involve the listing of hundreds of bacteria scores of algae a dozen or more zoo plankters and a few pelagic fish One traditional approach to organizing this complexity has been to utilize dietary information to group species into food chains and webs While this procedure omits some important variables and greatly oversimplifies others (e g failure to incorporate spatial and temporal patterns Gilbert 1977 1980 difficulty in incorporating changing diets of life stages Pimm and Lawton 1977 1978 presumed fidelity of linkages Paine 1980) its power comes from its utility and versatility The topology of the food web serves as a type of biological road map tracing the avenues along which food travels through the community As such it is a descriptive tool This description can be broadened by assigning species to general (primary producers herbivores carnivores) or specific (various guilds e g sap feeders decomposers of cellulose) functional categories Likewise abundance data can be added to allow calculation of general trophic structure (e g Elton 1927) or material/energy flow rates incorporated to yield entire ecosystem dynamics (Lindeman 1942 DeAngelis et al 1975)

In nature communities are generally composed of far more species than can ever be managed by network analysis However recent investigations suggest that entire subunits of natural communities may depend upon a crucial few interactions for their support and thus may be organized into dependent sub blocks or tightly evolved units (Gilbert 1977 1980 for mutualists and parasitoid subgroups in tropical rain forests Paine 1980 for interaction modules in intertidal invertebrates) If the natural community is arranged into a few highly dependent subgroups with functional feedbacks this also has important implications for general stability arguments (Gardner and Ashby 1970 May 1973)

Concepts keystone predators and vaulting

A particularly strong example of propagated effects involves the Keystone Predator phenomenon and its associated repercussions By now there is substantial experimental evidence that in certain aquatic environments (rocky intertidal pelagic zone of freshwater ponds and lakes) the deletion of certain key predators can cause fundamental changes in community structure How generalizable this phenomenon is for environments other than intertidal or pelagic systems cannot be ascertained at this moment for although the dramatic results of a few early experiments have fostered follow up studies which have clarified interactions present in the original experiments they have not been tested for generality between various ecosystems Yet certain circumstances which lead to the importance of consumer control are evident in intertidal and lake ecosystems In both aquatic environments prey species are exposed to predators in an environment lacking the background structural heterogeneity (hiding places camouflage of plants) so characteristic of terrestrial environments Moreover in both environments either a single predator (*Pisaster* in the intertidal) or a guild of predators (planktivorous fishes in freshwater ponds) is able to regulate the density of a dominant competitor one which would otherwise monopolize or alter resources Under depression of the dominant competitor additional subordinate competitors

are able to enter the community and subsequently to serve as the foundation for the construction of subordinate food chains Removal of the keystone predator releases the competitive dominant it displaces the subordinate competitors and this change leads to collapse of the subordinate food web Finally in most cases important aspects of the actual dynamics hinge upon the various consumers ability to capture prey in particular there are important size cut offs or thresholds which limit the ability of grazers or carnivores to handle particular food items

As originally defined by Paine (1966 1969) the action of a keystone predator limits the abundance of a prey species which would otherwise monopolize resources in its trophic level This limitation allows competitively inferior species to penetrate the community and to increase in abundance with a resulting increase in community diversity In the words of Paine (1966) local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species The importance of Paine s statement is that it clearly illustrates how the original definition of the keystone predator phenomenon focused attention on the ability of a single species (i e the competitive dominant) to monopolize resources unless limited by predators (the keystone predator) That is the original definition of the keystone predator phenomenon focused on the primary competitive interacters and their limitation not upon the resulting construction of alternative food chains once resources were freed by predator limitation That the eventual influence of keystone predators went beyond opening up resources for inferior competitors to other more vertical components of diversity is clearly evident both in food web diagrams (Paine 1966 1974) as well as in subsequent discussions of intertidal community structure (Paine 1974) Recognition of this omission has prompted Paine (1980) to designate certain types of subordinate linkage hierarchies as modules i e blocks of co evolved species borrowing from the mutualistic parasitic constructs of Gilbert (1977 1980) Selection of this particular terminology seems unfortunate for the emphasis upon co evolved relationships obscures the general functional dependence of the entire set of subordinate food chains

Construction of alternative linkage networks involves a new and important concept one with both trophic and evolutionary implications We would propose applying the more general term vaulting to describe the dynamic process which leads to the formation of subordinate yet dependent linkage systems Derived from the term vault (an arched structure) the concept emphasizes the construction of subordinate food webs upon the base of subordinate competitors without necessarily implying close co evolutionary ties between the suite of subordinate resources and consumers Thus vertical elaboration of the food web may proceed through either of two ways Either a subordinate grazer may carry in a specific associated organism (parasite parasitoid or even attract consumers of the alternate competitor see Paine 1980 for an example of the latter) or the accumulative concentration of several subordinate grazers may furnish sufficient food to hoist a new subordinate predator into prominence (vaulting) In either case trophic diversity increases vertically as new links are added to the community In sum vaulting differs from keystone predation by emphasizing the creation and maintenance of novel and yet functionally dependent linkage networks It is similar to modules by its emphasis upon the network dynamics which tie together primary and subordinate food chains yet it is distinguished from this concept by its lack of reliance upon so called co evolved relationships

Does the concept of keystone predators apply elsewhere? In freshwater ponds and lakes space is not limiting and the pelagic environment is even more structurally simple than the intertidal Organisms are typically not in intimate contact unless mating or consuming and all are suspended in a fluid medium Given that the surrounding physical and chemical environments are suitable generally limitation comes from one of two sources either from below (nutrients or consumed particles) or from above (grazing predation) Ever since the

pioneering studies of Hrbacek (Hrbacek 1962 Hrbacek and Novotna Dvorakova 1965 Hrbacek et al 1961) and Brooks (Brooks and Dodson 1965 Brooks 1968 1969) the ability of certain large bodied grazers (*Daphnia* spp) to monopolize resources and yet to be especially susceptible to visually feeding fishes has emerged as a central theme Because fish differentially consume large bodied conspicuous grazers like *Daphnia* they in effect also act as keystone predators (Kerfoot 1975 1980 Neill 1975) This depression of *Daphnia* allows competitively inferior species (certain rotifers small cladocerans and copepods) to penetrate the community and to increase in abundance (see Fig 1) With the influx of small bodied and more fragile species subordinate linkage systems can also develop which support a variety of invertebrate predators (Dodson 1970 Kerfoot 1980 Zaret 1980) Because pelagic systems are so structurally simple and so dependent upon interconnected food chains these indirectly propagated effects (dependencies between a primary and subordinate food chain) would seem particularly important to whole community dynamics and yet provide a convenient way of summarizing structure without sacrificing the identity of the living components

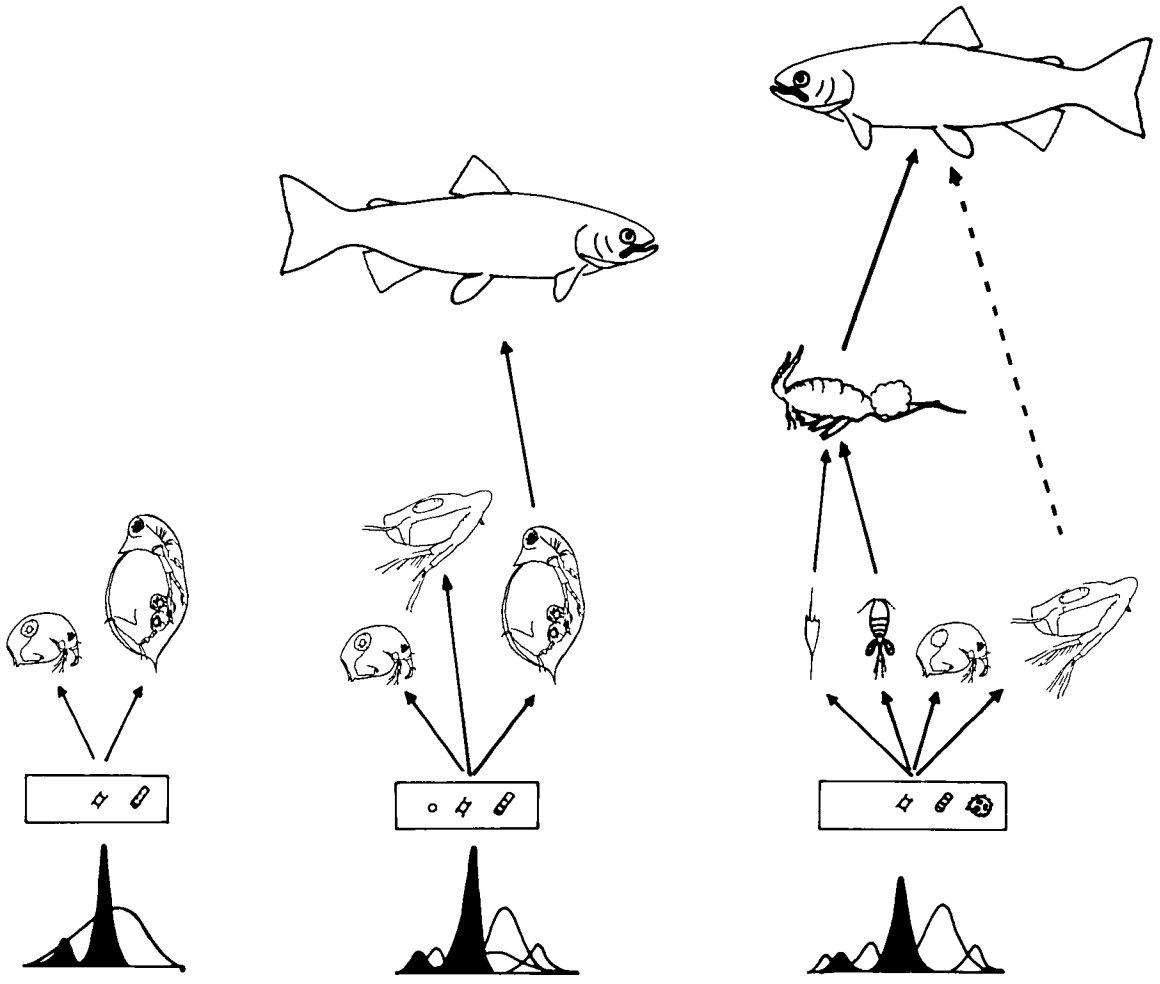

Fig 1 Diagrammatic representation of community changes following increase in fish predation Small bodied fragile zooplankton increase in abundance and diversity as phytoplankton become more abundant These small crustaceans and rotifers in turn serve to vault *Mesocyclops* into prominence Beneath the figure the frequency diagrams represent idealized size specific foraging curves for the various grazers When fish begin to feed upon *Mesocyclops* the alternate food chain is complete

The basic argument for dependent subordinate structure is built around three central points (1) the ability of *Daphnia* to monopolize resources (2) selective predation of fishes and the complementary bias of dependent invertebrate predators and (3) the overall dependent topology of the linkage network

REFERENCES

Brooks J L 1968 The effects of prey size selection by lake planktivores *Syst. Zool.* 17 272 291

Brooks J L 1969 Eutrophication and changes in the composition of zooplankton pp 236 255 In *Eutrophication Causes consequences correctives* Natl Acad Sci Publ 1700

Brooks J L and S I Dodson 1965 Predation body size and composition of plankton *Science* 150 28 35

DeAngelis D L R A Goldstein and R V O Neill 1975 A model for trophic interaction *Ecology* 56 881 892

Dodson S I 1970 Complementary feeding niches sustained by size selective predation *Limnol. Oceanogr* 15 131 137

Elton C 1927 *Animal ecology* Sidgewick and Jackson Ltd London

Gardner M R and W R Ashby 1970 Connectance of large dynamical (cybernetic) sys tems critical values for stability *Nature* 228 784

Gilbert L E 1977 The role of insect plant coevolution in the organization of ecosystems *Colloques Internationaux du C N R S* 265 399 413

Gilbert L E 1980 Food web organization and the conservation of neotropical diversity pp 11 33 in Soule M and B A Wilcox (eds) *Conservation Biology* Sinauer

Hrbacek J 1962 Species composition and the amount of zooplankton in relation to the fish stock *Rozpr Cesk. Akad. Ved Rapa Mat. Prir Yed* 72 1 116

Hrbacek J M Dvorakova M Korinek and L Prochazkova 1961 Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association *Verh. Int. Verein. Limnol.* 14 192 195

Hrbacek J and M Novotna Dvorakova 1965 Plankton of four backwaters related to their size and fish stock *Rozpr Cesk Akad. Yed Rada Mat. Prir Ved.* 75 3 10

Kerfoot W C 1975 The divergence of adjacent populations *Ecology* 56 1298 1313

Kerfoot W C (ed) 1980 *Evolution and Ecology of Zooplankton Communities* Univ Press New England 793 pp

Kerfoot W C W R DeMott and D L DeAngelis Submitted manus Cladoceran diets and grazer phytoplankton feedbacks *Ecology*

Lindeman R L 1942 The trophic dynamic aspect of ecology *Ecology* 23 399 418

May R M 1973 *Stability and complexity in model ecosystems* Princeton University Press Princeton N J 235 pp

Neill W E 1975 Experimental studies of microcrustacean competition community composi tion and efficiency of resource utilization *Ecology* 56 809 826

Paine R T 1966 Food web complexity and species diversity *Am. Nat.* 100 65 75

Paine R T 1969 A note on trophic complexity and community stability *Amer Nat.* 103 91 93

Paine R T 1974 Intertidal community structure experimental studies on the relationship between a dominant competitor and its principal predator *Oecologia* 15 93 120

Paine R T 1980 Food webs linkage interaction strength and community infrastructure *J Anim. Ecol.* 49 667 685

Pimm S L and J H Lawton 1977 Number of trophic levels in ecological communities *Nature* 268 329 331

Pimm S L and J H Lawton 1978 On feeding on more than one trophic level *Nature* 275 542 544

Zaret T M 1980 *Predation and Freshwater Communities* Yale Univ Press 187 pp

Loosely Structured Food Webs Composed by Density Vague Ecology Phytophagous Insects

Donald R Strong Jr

Insects on plants may exist in food webs with quite loose structure Interspecific competition between phytophages is relatively uncommon and where found is often apparently inconsequential to the structure of the community Parasitism and predation can be severe for phytophagous insects and high rates of mortality from natural enemies are not unusual for arthropods on plants However parasitism and predation are often not explicitly density dependent When it occurs density dependent mortality is often imposed by natural enemies over only a restricted range of densities Frequently natural enemies kill a greater fraction of phytophage populations at lower densities This inversely density dependent mortality can be destabilizing and may be involved in the escape of phytophages from natural enemies Independently of density relationships natural enemies can dramatically dominate large fractions of levels in phytophage food webs under some circumstances ants and birds are known to depress many species simultaneously when conditions are suitable

Host plant phenology chemistry and the mosaic of other plant species can greatly affect phytophage communities but particular effects are widely variable Some of the most dominating influences are from host plant phenology and seasonality Chemical effects in ecological time are mostly in terms of the nitrogen nutrition of the phytophage via the host plant Noxious secondary chemistry of the host plant less often has great influence on the phytophage community in ecological time The lack of influence of apparently noxious phytochemistry probably derives from the adaptation of insects of the particular chemical tactics of their host plants

Resource depletion by phytophages that leads to intraspecific competition can occur but is far from universal at this level other factors such as natural enemies patchiness in space and time of host plants and the weather suggest to me that phytophage food webs may often have system properties of donor control or at most only weakly reciprocal interactions between levels in the food web This means that quality and effective quantity of host plants directly influence phytophage populations and phytophages influence populations of natural enemies but reciprocal influences from natural enemies back to phytophages and phytophages back to plant populations are weaker indirect and not often demonstrably cybernetic

I propose that the key to understanding how phytophage food webs operate in nature lies in adopting empirically *operational* models of population dynamics These models describe dynamics that are tightly bounded only at very high densities (by orthodox density dependence) and at very low densities (by an Allee effect) The distinctive features of empirically operational population dynamics are stochasticity and density vagueness over intermediate densities within which populations exist most of the time Theories of density vague dynamics are not new but have been proposed independently by several ecologists who have addressed what real organisms actually do in nature as opposed to what elegant mathematics do in ideal equations (Milne 1957 Ehrlich et al 1972 Chesson 1978) The motivation for envelopist dynamics is frustration with the unrealistic nature of deterministic population models which relate all population behavior to a single parameter of population density

A review of published studies indicates that food web organization and population behavior is consistent with the above interpretation for phytophagous insects loose structure

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This contribution was originally scheduled but was not presented at the workshop Therefore it is not referred to in the concluding remarks by Robert May

intermittant and condition dependent interactions between species a lack of balanced reciprocity between levels in food webs and indeterministic population behavior especially at intermediate densities External factors such as opportunistic predators and the weather often have great influence in these communities and dominate the weaker Malthusian and other cybernetic factors

REFERENCES

Chesson P L 1978 Predator prey theory and variability *Annu. Rev Ecol. Syst.* 9 323 347

Ehrlich P R D E Breedlove P F Brussard and M A Sharp 1972 Weather and the regulation of subalpine populations *Ecology* 53 243 247

Milne A 1957 The natural control of insect populations *Can. Entomol.* 89 193 213

Habitat Selection and Trophic Strategy in a Protozoan Predator Prey System

Leo S Luckinbill

Many interesting and complex models exist of how predators optimally forage for their prey Most often these models deal with the more variable aspects of predator behavior which become optimized with respect to the type or frequency of various prey captured Besides the kind and frequency of prey captured other dimensions of these models have dealt with patchiness in prey populations having various dispersions or species composition and the corresponding predator behavior that would optimize choice within or among differ ent patches The study I report here deals with a somewhat simpler problem What guides a predator in determining whether a particular piece of environment is in fact a patch of prey habitat suitable for practicing predation?

This work began as an outgrowth of some previous research into the dynamics of predator prey interaction in microcosms Although the particular predator and prey popula tions studied had been widely analyzed in both experiments and models of predation it still seemed uncertain whether this particular predator actually hunted for its prey This ques tion evolved in an experimental context because it is an efficient highly specialized preda tor yet it clearly seemed to encounter its prey in a haphazard almost willy nilly fashion In view of this it seemed reasonable to ask whether the predator might have some behavior which would increase the chances of its encountering a prey

The predator and prey under study were respectively *Didinium nasutum* and *Paramecium* These organisms are both single celled protozoans and are often found together in fresh water ponds *Paramecium* is a bactivorous ciliate feeding primarily on bac teria and *D nasutum* is a predator that feeds on *Paramecium* or other ciliates

Didinium is itself a ciliate It is barrel shaped in appearance and is propelled through the water by two bands of cilia The front of the organism is flat and from this anterior end projects an elongated proboscis like attaching organ with which it secures its prey It swims in large open spirals with the attaching organ foreward like a lance and whenever anything is contacted it is probed for suitability with the attaching organ

A variety of ciliates serve as prey for *Didinium* They can range in size from very small starving *Colpidium* at about 50μ in size to the largest of the *Paramecium* species *P caudatum* at up to 300μ in size As a predator *D nasutum* is quite flexible also it can range in size from about 20μ under starvation conditions to about the size of a *Paramecium aurelia* 120μ or more (Fig 1)

Size variation in the predator however provides no real handicap to predation The attack on a large (250 μ) *Paramecium* by a small (50 μ) *Didinium* provides a spectacular display of predatory ability Since these small sized predators couldn t begin to swallow such a large prey whole they attack in rapid fire fashion tearing a piece from the prey each time and swimming in small tight circles which bring them back into repeated contact with the prey The more often they attack it the more placid *Paramecium* becomes A swarm of even minute *Didinium* will reduce a large *Paramecium* to half size in a matter of a few minutes while they become visibly larger and more active Eventually when one of them is large enough it attacks what remains of the *Paramecium* and swallows it whole

It has been shown that *Didinium* may need to eat approximately ten medium sized *Paramecia* over about six hours in order to divide On the other extreme it can take only 2 1/2—3 days to starve to death The smaller *D nasatum* gets as it starves the faster it swims At its smallest size there is almost nothing but the attaching organ and a small con densed nucleus left It is imperative for survival therefore that this predator make a cap ture at frequent intervals

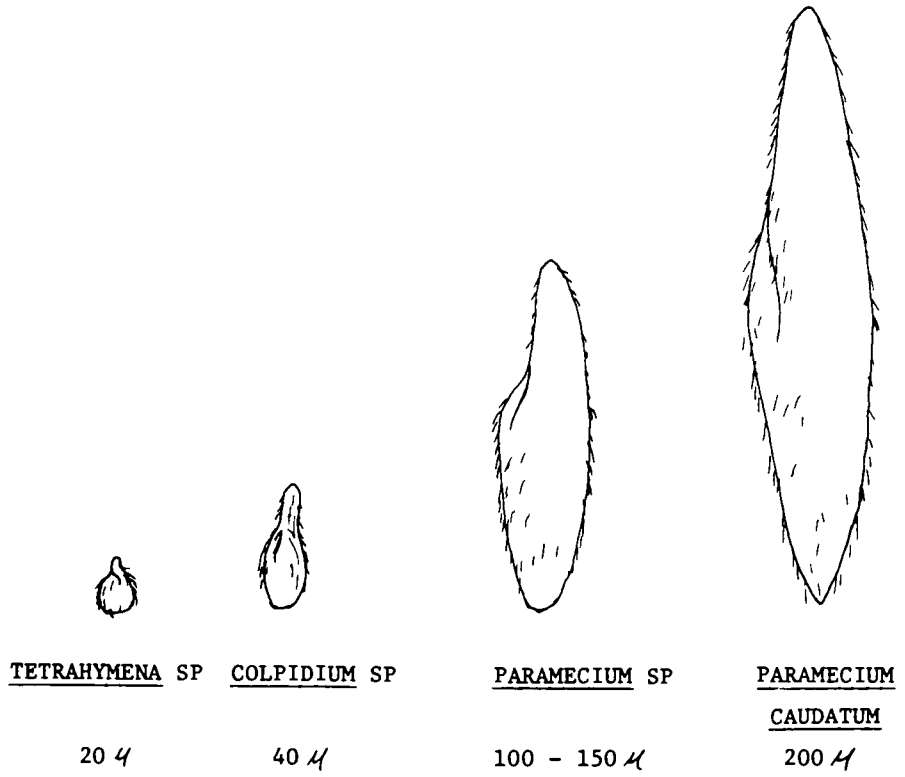

Fig 1

When seasonal or other conditions diminish bacterial food and the quality of *Paramecium* available declines *Didinium* can encyst It forms thick walled resistant cysts which remain viable for several months It emerges from these cysts in response to a flour ishing bacterial growth and immediately resumes predatory activity Although both encysted and excysted *Didinium* are frequently found in collections from nature the level of enrichment in laboratory experiments may prevent encystment there

These organisms then make an interesting if not useful means of studying predation and trophic dynamics They are often cultured for study using Cerophyl as a nutrient base for growing the prey s bacterial food Cerophyl is simply dried scotch grass from which a vitamin rich infusion is made that supports abundant bacterial growth The trophic struc ture of this microcosm is shown in Fig 2 and with possible changes in the species availa ble or quality of food is a good general representation of the natural food web these proto zoa are involved in

The question in this study was Does this predator depend for its success on totally ran dom encounters or does it track and search out its prey? One way to answer this question is to compare the spatial distribution of predators and prey in a microcosm If this predator hunts then the presence of a member of the prey species in a given quadrat should increase the likelihood of finding a predator there also To determine this I compared the dispersion in populations of *Paramecium* and *Didinium* in microcosms Equal numbers of predator and prey were introduced into 350 ml of fresh Cerophyl with a growing population of the bacte ria *Enterobactera aerogenes* at 27 C This culture was sampled in large rectangular pyrex baking pans (34 × 22 cm) that were mounted in a holder and covered with a pane of glass

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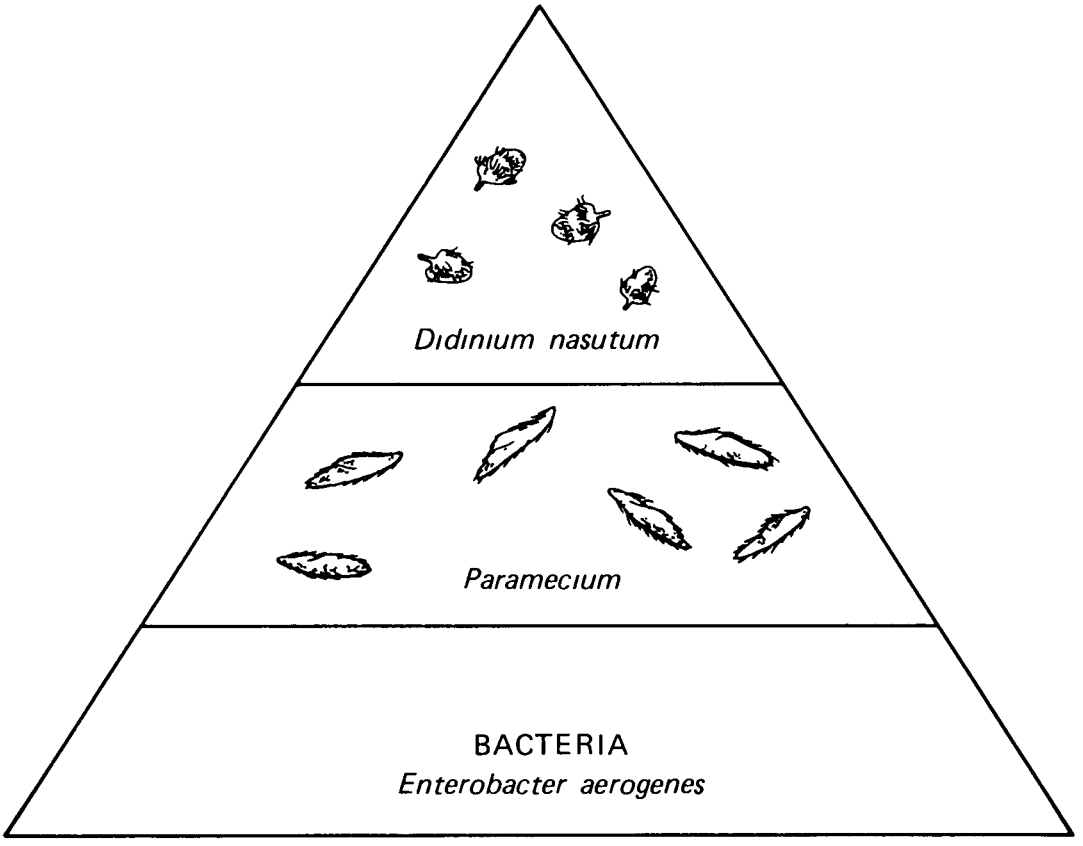


Fig 2

when not in use Samples consisted of visual counts in a microscope field of 1 0 cm diame ter taken in random order at uniformly spaced predetermined points in the pan In sam pling all the protozoa were counted and identified in the microscope field as the focus was moved from the surface to the bottom of the water column Thirty five such samples were taken in each of twelve replicate microcosms

Figure 3 shows the use of a method developed by Cole (1949) and later modified by Hurlburt (1969) for measuring the association of two species based on a presence or absence comparison As you can see the total number of samples is 420 and the comparison by Chi Square of the presence or absence of the prey with that of the predator shows that there is no significant association between the presence of the prey and presence of the predator in samples here The P value $95 < p < 99$ indicates that the calculated coefficient of association is not significantly different from two randomly interspersed noninteracting spe cies There is no evidence by this method of hunting behavior by *Didinium*

These results seem to agree with common observation Under close scrutiny the only time I have seen *Didinium* alter its behavior as a result of the presence of the prey appears to be when there has been actual or near physical contact as for example in a chance meeting of the two in swimming When contact of the prey is made *Didinium* becomes very agitated and attacks virtually anything it touches But unless there is actual physical contact or a very near miss the two can pass each other millimeters apart without the slightest appar ent recognition of the prey by the predator

CONTINGENCY TEST FOR ASSOCIATION				
		Paramecium tetraurelia		
		Present	Absent	Total
Didinium nasutum	Present	94	100	194
	Absent	108	118	226
	Total	202	218	420

Coefficient of association = 024
X^2 = 001 df = 1
95 < p < 99

Fig 3

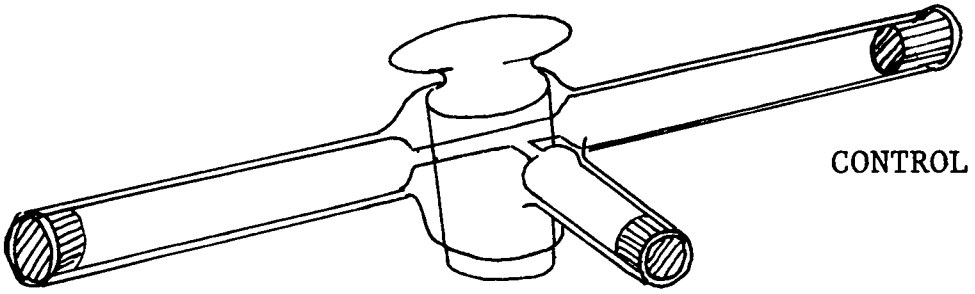
But one problem that might compromise these conclusions is that the confinement of predator and prey at high density in the rich media used here may perhaps prevent prey detection by the predator Perhaps the diffusive properties of this confined simulated envi ronment prevent the establishment of diffusion gradients that permit that predator to clearly distinguish the presence or absence of patches of prey

Despite the foregoing results it may still be possible therefore that *Didinium* has some sort of chemotactic attraction to *Paramecium* While not widely studied in these organisms chemotaxis is certainly well known generally among aquatic and marine oganisms If *Didinium* were chemotactically attracted for example to some respiratory or excretory metabolite of *Paramecium* then the effectiveness of its random search type hunting would be greatly increased A test for chemotaxis will more clearly determine whether hunting behavior exists

To test this we use a device alled a t maze (Van Houton et al 1975) which is simply a t shaped stop cock filled with medium into the middle arm of which has been introduced a population of predators (Fig 4) When the stop cock is opened *Didinium* has a choice of two alternate arms to which they can migrate The results of these experiments have been verified numerous times in Introductory Ecology classes at Wayne State and by Antipa *et al.* (1981)

Using this device the number of *Didinium* migrating to the arm of the maze having *Paramecium* or prey scent can be compared with the number migrating to the control arm having no prey Live *Paramecium* are insuitable for use in this particular comparison because they would rapidly swim out of the experimental arm as soon as the stop cock is opened Therefore a homogenate of live *Paramecium* was prepared for use instead by bursting cells under high speed centrifugation Thus the attractiveness of the cell walls and internal contents of a dense population of prey raised in Cerophyl were compared with that of a control arm having bacterized Cerophyl medium only Figure 5 shows the results of migration over a 30 min period in replicate samples of 200 *Didinium* each These results agree with the previous analysis of spatial distribution The expected number migrating was calculated by dividing the total number migrating by two Clearly no particular ability of this predator to chemically detect the presence of its prey is evident under these circumstances

The results of the preceding experiment clearly suggest that *Didinium* searches for its prey in a random manner but has no sensory or tracking capability geared to the particular



after Van Houten et al (1975) J Comp Physiol 104 211-223

Fig 4

CHEMOTACTIC PEFERENCE OF *D NASUTUM* FOR *PARAMECIUM*			
Test	Observed number migrating toward *Paramecium*	Expected $\left(\frac{\text{total migrating}}{2}\right)$	$\left(\frac{O-E}{E}\right)^2$
1	72	71	014
2	88	95 5	589
3	60	65	384
4	73	76 5	160
5	74	77 4	158
6	91	87 5	140
7	78	77	012
8	96	89	550
9	101	94 5	447
10	78	78	000
		Total	2 454

$X^2 = 2\,454$ df = 9 $98 < p < 99$

Fig 5

detection of *Paramecium* Encounters between predator and prey would seem to be highly physically deterministic—on the order of collisions between molecules of two gasses governed by temperature and pressure Such a simple model however seems somewhat incongruous when weighed against the fact that *D nasutum* is relatively successful as a common protozoan predator but is also conspicuously specific in its predation on ciliates

Despite the immensity of even small ponds and the apparent inability of those tiny creatures to track their prey they are nevertheless successful enough and achieve at least modest population sizes as shown in sampling studies Perhaps some method has evolved allowing *Didinium* to at least locate large general areas of prey concentration independently of the presence of prey itself

Aquatic pond habitats are in fact highly patchy Intensive sampling of ponds shows that local faunal patches undergo nearly continuous appearance and dissolution Patch formation typically begins with a local increase in productivity perhaps a leaf or say a piece of apple falls in The resident bacteria and fungus begin immediately to consume it Next the proto zoa including *Paramecium* and eventually also *Didinium* appear and commence feeding upon the bacteria So even though *Didinium* appears to be unable to directly detect the prey itself there seems to be some other way by which the predator locates these patches of prey

If this predator were chemotactically attracted to the producer or bacteria then even though it is unable to use the bacteria themselves in any way the degree of association with its ciliate prey would be increased by the fact that the prey are themselves attracted to growing bacterial populations and patchily distributed aggregating at sites of bacterial growth Instead of hunting prey specifically a good strategy for this predator might be to hunt its prey s objective on the next lowest or producer trophic level This would be effective if and only if finding a rich patch of bacteria increased the likelihood of also finding *Paramecium*

Are *Didinium* and *Paramecium* both chemotactically attracted to bacteria? In order to determine this the migration of *Paramecium* toward growing bacterial populations was measured first by comparing the number of *Paramecium* preferring bacterized as opposed to unbacterized medium The unbacterized medium was sterile and in the media used for com parison live bacteria or bacteria free filtrates from growing cultures worked equally well The bacterized medium was equally effective whether bacterial growth was slight (1 hour) or more extensive (24 hours)

One factor affecting this experiment in a nonspecific way was how clean and free from contaminating bacteria the *Paramecium* or *Didinium* were when introduced to the t maze for testing Cells taken from heavily bacterized freshly growing cultures tended more often to remain in the introduction arm of the T maze To introduce choice making therefore the *Paramecium* and *Didinium* were washed prior to experiments by allowing them to swim in sterile Cerophyl for up to one hour This treatment did not affect the direction or the out come of the choice made by potozoa in this experiment only the total numbers migrating out of the introduction arm

In this first comparison then 200 washed *Paramecium* were given a choice of migrating toward either unbacterized medium or filtered medium that had had the bacteria *aerogenes* growing in its arm Figure 6 shows the result of that test Clearly *Paramecium* is chemo tactically attracted to this bacteria ($p < 005$) A similar comparison was made for *D nasutum* and Fig 7 shows that it is also strongly attracted to the ($p < 005$) bacteria

The chemotactic attraction of *didinium* to the trophic level beneath its prey suggests a simple but effective predatory strategy capture of prey by *Didinium* may be by random contact but it finds local aggregations of prey through an attraction to the prey s food Furthermore these conclusions extend to the behavior of this predator on a seasonal cycle as well *D nasutum* is known to excyst in response to flourishing bacterial growth not the presence of its prey The fact that *Didinium* can in no way directly use the bacteria to which it is so clearly attracted points strongly to both the strategic capability of the sensory mechanism which evolution has provided this predator with and the high predictability of *Paramecium* in relation to that trophic resource

CHEMOTACTIC PREFERENCE OF *PARAMECIUM* FOR *ENTEROBACTER AEROGENES*			
Test	Observed number migrating toward *E aerogenes*	Expected $\left(\frac{\text{total migrating}}{2}\right)$	$\left(\frac{O-E}{E}\right)^2$
1	182	97 5	73 23
2	190	96	92 04
3	189	94 5	94 5
4	167	93 5	57 7
5	174	90 5	77 04
6	140	88 5	29 96
7	179	98 5	65 78
8	168	94 5	57 16
9	166	90 5	62 98
10	167	98	48 58
		Total	658 97

$X^2 = 658\ 97$ df = 9 $p < 005$

Fig 6

CHEMOTACTIC PREFERENCE OF *D NASUTUM* FOR *E AEROGENES*			
Test	Observed number migrating towards *E aerogenes*	Expected $\left(\frac{\text{total migrating}}{2}\right)$	$\left(\frac{O-E}{E}\right)^2$
1	142	94	25 51
2	129	90	16 9
3	157	84 5	62 20
4	137	78 5	43 59
5	140	79 5	46 04
6	170	96 5	55 98
7	177	93	75 87
8	133	90 5	19 95
9	124	86	16 79
10	121	88	12 37
		Total	375 2

$X^2 = 375\ 2$ df = 9 $p < 005$

Fig 7

REFERENCES

Antipa G A K Martin and M T Rintz 1983 A note on the possible ecological signifi cance of chemotaxis in certain ciliated protozoa *J Proto* 30 55 57

Hurlburt S H 1969 A coefficient of interspecific association *Ecology* 50 1 9

Van Houten J H Hansoma and C Kung 1975 Two quantitative assays for chemotaxis in *Paramecium. J Comp Physiol.* 104 211 223

Identifying the Structure of Cycling in Ecosystems

Robert E Ulanowicz

The observations that the pool of organic materials is finite and that the rates of their use by living organisms is very fast with respect to geological time gives rise to the notion that elements on the average pass repeatedly through the same populations i e one can identify cycles in the networks of transfers between species It is assumed that these cycles are the most important endogenous elements which determine the structure of an ecosys tem The purpose of this presentation is to achieve a systematic description of the cycles to be found in most networks of ecosystem flows

The discussion begins with the definition of a perfect simple cycle Such an entity con tains n elements called nodes (species trophic levels or other useful aggregations) which communicate with one another via directed channels of flow (arcs in network parlance) of energy or material A perfect cycle contains exactly n arcs and each node is the terminal point for a single arc and the initial point for exactly one other All n arcs have the same magnitude A perfect cycle is an abstraction—having no communication with the external universe it contravenes the second law of thermodynamics It is nonetheless a very useful abstraction for analyzing real networks

The perfect cycle is an enigma insofar as cause and effect within it are inextricably entwined Any flow considered as a cause can be traced around the cycle and seen to be its own effect and vice versa Behavior exhibited by the perfect cycle is said to be autonomous in the sense that one cannot attribute the events to an exogenous cause A strictly nonauto nomous system by contrast contains no cycles among its nodes It receives a set of inputs (causes) from outside the system and translates these into effects exported to the external world Any subset of a perfect cycle is seen to be strictly nonautonomous

Autonomous behavior in cycles underlies what is referred to elsewhere as holistic or emergent behavior of ecosystems In the normal analytic order one usually studies subsys tems of the overall ensemble and breaking away the subsystem usually entails cutting one or more directed cycles Whenever cycles are cut one can no longer observe the associated autonomous behavior Hence the truism that one cannot always infer the behavior of the whole from the behavior of its parts

If real networks are combinations of autonomous and nonautonomous elements (cycles and trees in network terminology) is it still possible to abstractly decompose any given graph into cycles and remnant straight through flows? If the cycles are indeed the structure determining elements of food webs then knowing their exact composition should assist one in understanding ecosystem dynamics and in qualitatively forecasting what the results of perturbations to specific flows might entail

The first task in the proposed decomposition is to identify and enumerate all simple cycles A simple directed cycle contains no repeated node The amount of time spent search ing for all simple cycles can increase exponentially as the number of nodes in the network—quickly outstripping the capacities of even the fastest modern computers For tunately efficient algorithms employing backtracking techniques which substantially reduce the required search time have been developed during the past few years Also ecological networks tend to be sparse in the number of connections thereby further reducing the search time The modified backtracking algorithm employed in this investigation searched a 21 compartment ecosystem network in less than a second of processor time

Given the pathway description of all cycles one is faced with the question of what quan tity of flow to assign to each circuit One way of choosing a value is to trace around every loop arc by arc to endeavor to find the most critical transfer in each cycle Criticality can be judged by any number of standards but for the sake of demonstration the most vulnerable arc will be assumed to be the one with the smallest magnitude of flow To separate the cycle

from the network one could simply subtract the values of the vulnerable arc from each flow in the cycle The problem with this approach is that in general the same arc may be the most vulnerable link in many other simple cycles If one has reason to distribute the value of the vulnerable arc over all cycles (say m in number) according to some criterion (for example to maximize ascendency) then the cycles can be removed accordingly In the absence of any preferred criterion it is reasonable to distribute the value of the vulnerable arc V equally among the cycles with the common vulnerable arc Thus the quantity V/m is subtracted from each link of each component cycle The common vulnerable arc is removed all the cycles in that group disappear from the residual network and no residual flow is forced negative To remove all cycles from the original network one starts by finding the smallest of all identifiable vulnerable arcs removes it reidentifies the next smallest vulner able arc and proceeds until there are no cycles in the remaining graph

This formula for removing cycled flow from a network has a particular advantage In the process one identifies groupings (nexuses) of cycles each of which is identified by a common vulnerable arc If any perturbation of the common vulnerable arc occurs it will affect the entire nexus of cycles In a sense the nexus associated with a vulnerable arc delimits the domain of immediate impact of the perturbation The collection of cycles into nexuses is a vivid way to portray the structure of cycling in the flow network

To demonstrate the technique the algorithm is applied to two networks of carbon flow in ecosystems belonging to practically identical salt marsh creeks near Crystal River Florida The single major difference between the two ecosystems is that one of them is chronically subjected to an average temperature elevation of about 6 C because of its proximity to a nuclear generating station It is a rare instance in which data is available for entire ecosys tem networks under both natural and perturbed conditions Both networks possess 17 com parable compartments (nodes)

Oddly enough the relative amount of carbon being cycled in the perturbed system is greater This despite the fact that one may identify 119 simple cycles in the unperturbed network as contrasted with only 46 in the heated ecosystem Even more striking is the change in the nexuses identified in both cases In the control system one may identify numerous large nexuses—one of 14 cycles another of 13 still another of 10 and three large collections of six cycles each In the disturbed creek network the nexus with the most constituent cycles consists of only four circuits Furthermore the large nexuses which failed to appear in the warm creek possessed longer cycles (i e ones with greater number of links and nodes) but smaller vulnerable arcs

The process of eutrophication is dramatically evident in the change in cycle structure The numerous longer (presumably slower) cycles have disappeared from the impacted sys tem The (trophically) shorter cycles remain but now cycle more intensely Should subse quent applications of this analysis to other situations yield similar pictures of the effects of perturbation then it may become possible to forecast *a priori* the weak spots in an unper turbed ecosystem In any event it seems clear that the method appears to be most sensitive to the smallest disturbances and could serve as a technique for diagnosing early signs of ecosystem response to stress

The method of cycle analysis is to be presented in detail in an upcoming issue of *Mathematical Biosciences*

Food Webs Biotic Control and Regulatory Problems

Simon A Levin

Introduction

Most of the considerable recent theoretical work on food web structure has had as its goals an understanding of how natural systems are organized in space and time and a determination of the properties and mechanisms which influence stability However other relevant theoretical questions exist especially those motivated by problems involving the regulation of toxic substances In these food web considerations are of profound importance but the fundamental questions have a different focus than those with which theoreticians traditionally have been concerned

In this paper I will address two basic categories of such problems

(i) those relating to the role of the web as a passive transmitter of materials and energy and

(ii) those dealing with the web as a propagator of effects these also involve consideration of the effects of perturbations on the maintenance of community stability

The trophic network as a passive transmitter

The food web may be viewed as a system of compartments (of variable size) among which materials and energy flow Compartments also exchange materials and energy with the abiotic environment and with other ecosystems When interest is centered on toxic substances a recognized problem is that of biomagnification consideration of it falls within the more general analysis of the fate and transport of toxic materials Some substances including mercury radionuclides and chlorinated hydrocarbons such as DDT are biomagnified substantially as they are transported to higher trophic levels (Gerould and Gloss 1981 Levin 1982) However many other compounds do not show such potential or at least not above a certain trophic level For example copper zinc and nickel near the infamous Sudbury smelter reach highest concentration in the periphyton and rooted macrophytes (Hutchinson et al 1976) To understand what accounts for these differences one must be concerned with processes

The major processes governing transport through the food web are depuration (elimination transformation and metabolization) uptake and adsorption and such physicochemical processes as chemical speciation and complexation with other compounds These can be incorporated into compartmental models as a means of estimating the probable distribution of toxic substances in the environment Such fate and transport models are assuming an increasingly important role in the regulatory process although description of food web transformations and non steady state analyses have not yet been sufficiently developed that models which deal with these aspects can be used reliably as part of a generic testing scheme However they represent an important area for theoretical investigation as do those which incorporate more realistic hydrodynamical and other physical transport processes Theoretical analysis can also help to elucidate the important factors governing biomagnification toxic distribution and residence times and to focus attention on those aspects which deserve the most serious attention

The trophic network as a propagator of effects

Under the Toxic Substances Control Act (TSCA) potential environmental effects must be evaluated for substances proposed for release and of course the need for such evaluation is of more general interest than within the limited framework of TSCA Too often this need is interpreted solely in terms of direct effects on individual species populations However there has been increasing recognition of the importance of examining both effects on ecosystem structure and function and indirect effects which are mediated by interspecific interactions Unfortunately the methodology for assessing such effects is not yet well developed (Levin 1982)

An ecological community may transmit the effects of xenobiotics to system components far removed in trophic status from those directly affected Examples include the cata strophic chain of events following the application of DDT to control mosquitoes in Borneo (see Ehrlich and Ehrlich 1970 Levin 1982) and the commonly observed rebound effects which result when natural enemies of target pest species are affected by pesticide applica tions (Pimentel 1971 Levin 1982) These are reinforced by the fundamental ecological studies of Paine (1966) and his followers examining the role of predation in maintaining the struc ture of natural communities In the transmission of indirect effects many factors assume importance including the strength and pattern of interspecific interactions and whether crucial linkage points are affected The key to understanding these is to understand the chains of control (rate limiting steps) of important processes and of species dynamics Criti cal (keystone) species (Paine 1966) or functional groups of species (Cummins and Klug 1979) must be identified and crucial linkages and mechanisms of control must be better understood When critical species can be identified they and the trophic pathways leading to them become natural objects of study by toxicologists concerned with the effects of toxic substances

To achieve the requisite understanding experimental work is essential but this experi mentation can be more intelligently designed and interpreted if it is carried out in concert with theoretical studies Thus such studies if addressed to the identification of critical spe cies groups of species or linkages can contribute substantially to improved environmental assessment Such theoretical work may be empirically motivated for example based on the examination of species distributions and relations along physical gradients or may consist of mathematical analyses of network properties sensitivity analysis graph theoretical methods or dynamical systems approaches which study the relationships between a system s structure and its capability to respond to stress (e g May 1974 Pimm 1980 Roberts and Tregonning 1980) A promising recent direction focuses on the compartmental structure of the food web (e g Paine 1980 Pimm and Lawton 1980) Such an approach is potentially amenable to the powerful methods of multivariate analysis and of graph theory and may be expected to contribute substantially to an improved understanding of commu nity organization

The current criteria for the identification of surrogate species for toxicological testing almost totally ignore aspects of food web structure With the advances which theoretical investigations such as those described in this paper may bring we can expect major improvements of schemes for testing the fate and effects of anthropogenic substances These improvements will include better criteria for the selection of test species as well as micro cosm and in situ direct testing of food web effects

REFERENCES

Cummins K W and M J Klug 1979 Feeding ecology of stream invertebrates *Annu. Rev Ecol. Syst* 10 147-172

Ehrlich P R and A H Ehrlich 1970 Population resources environment issues in human ecology W H Freeman & Co San Francisco

Gerould S and S Gloss 1981 Biotic mediation of contaminant distribution and effect in aquatic ecosystems Manuscript

Hutchinson T C A Fedorenko J Fitchko A Kuja J van Loon and J Lichwa 1976 Movement and compartmentation of nickel and copper in an aquatic ecosystem In J O Nriagu (ed) Proc 2nd Internat Symp Environmental Biochemistry Ann Arbor Sci Publ Ann Arbor Michigan

Levin S A (ed) 1982 New perspectives in ecotoxicology Ecosystems Research Center Cornell University Ithaca New York 125 pp Revised version in press Environmental Management

May R M 1974 Stability and Complexity in Model Ecosystems Monographs in Population Biology 6 Princeton Univ Press Princeton New Jersey

Paine R T 1966 Food web complexity and species diversity *Amer Natur* 100 65-76

Paine R T 1980 Food webs linkage interaction strength and community infrastructure *J Anim. Ecol.* 49 667-685

Pimentel D 1971 Ecological effects of pesticides on non target species Executive Office of the President Office of Science and Technology Washington D C 220 pp

Pimm S L 1980 Food web design and the effect of species deletion *Oikos* 35 139-149

Pimm S L and J H Lawton 1980 Are food webs divided into compartments? *J Anim. Ecol.* 49 879-898

Roberts A and K Tregonning 1980 The robustness of natural systems *Nature* 288 265-266

Food Web Structure Some Thoughts and Some Problems

Robert M May

What follows is a very brief summary of some thoughts about lines that future work might take A more discursive account of these thoughts along with reflections on the Workshop as a whole is presented elsewhere (May 1983)

A primary resource for any theorizing about food webs is of course a carefully compiled catalogue of known webs whose structure has been determined Several such catalogues have now been presented notably the 62 webs discussed by Briand As emphasized at the discussions at the Workshop however there are many respects in which these catalogues need to be improved these criticisms are much easier to raise than to answer First for most purposes one wants a community web embracing all linkages among the co occurring species it is necessary to avoid confusion with source webs (which trace the connections upward from a single resource species) or of sink webs (which trace the links downward from a single top predator) Second there are problems of consistent definition of the entities in the web many studies articulate individual species of predators at the upper levels but aggregate species at lower levels some systematic practice is to be desired In particular there remains an interesting possibility that different kinds of ecologists (for example terrestrial people versus marine people) might systematically follow different practices thus creating the impression that terrestrial webs differed from marine webs (when in fact the differences were cultural among the investigators) Third some studies include only those links between eaten and eater (the links along which energy or atoms flow up through the web) while others list links corresponding to direct competition or mutualism which kind of web the theorists want depends on the kind of analysis being undertaken Fourth and most important at what point does one decide links are too weak or too unusual to list? Clearly the flower child ecologist s perception that to pluck a flower is to disturb a star is too extreme but there is a real dilemma in deciding for example whether Paine s rocky intertidal communities should embrace the owls that eat the mice that occasionally eat the odd limpet Whether food webs should include all connections or only the significant ones and how significant is to be defined stands out as a major unsolved problem

I also think there is a need which would have been articulated more clearly had we had a slightly different cast of characters at the Workshop (systems ecologists) for a systematic compilation of food webs for which there is quantitative information about the magnitude of flows of energy or of nutrients (C P S N etc) along the lines of the synoptic collections presented by Briand and others As touched upon by Ulanowicz and others such quantitative information is necessary if one is to deal with interesting questions having to do with cycling in food webs and the like

Earlier in these proceedings Cohen has drawn attention to the desirability of having a systematic catalogue of information about the distribution of lengths of food chains in real food webs Other empirical questions which merit similar systematic investigation are

(i) Information about the average food chain length as a function of some objective measure of primary productivity in the food web where possible

(ii) Information about average food chain length for various kinds of endotherms and ectotherms (Pimm has presented some interesting statistics bearing on this question but a larger amount of information would be nice to have)

(iii) Pimm has raised and Yodzis questioned the possibility that real food webs contain fewer omnivores than would be expected were connections made at random I would like to see apodictic resolution of this question

(iv) Insofar as it is at all possible I would very much like to see information relating the distribution of lengths of food chains to the characteristic time scales (population doubling times) of the constituent species

Turning from empirical questions to more theoretical isues the following points seem to me to deserve more attention than they have so far received

(i) How are parasites—viruses bacteria protozoans helminths—to be included in food web studies? It is arguable that parasites are wholly or partly responsible for determining the magnitude and/or geographical distribution of many natural populations of plants and animals so that their inclusion in food webs is arguably often necessary if the structure is to be fully understood Not only are parasites usually totally neglected in food web studies but it is not clear to me exactly how to include them!

(ii) Southwood has introduced the notion of a tourist species (one that is only acciden tally or vagariously present yet can on occasion consume a significant fraction of available resources) How should such tourist species be included in studies of food web structure? Or as can be argued is this a non problem in that such species simply are usually taken account of in the ordinary manner of going about compiling food webs?

(iii) When decomposers are included in food web studies they are frequently treated as simply being another kind of consumer Properly included however decomposers are both consumer and resource recycling nutrient materials The proper accounting for decom posers when one is focusing on nutrient flows makes for the difference between an open and a closed system This is an important issue particularly when one is dealing with quan titative rather than qualitative studies of food web structure

(iv) Nunney Abrams and others touched upon the possibility that one cannot truly understand food web structure without getting into the details of interactions among spe cies including such things as time delays life history strategies and the direct and indirect effects of nonlinearities in interactions between species This is a very large topic but I believe it to be one that is central to the next generation of food web studies

(v) On a grander scale (but related to the questions raised below) it would be interesting to know how the currently denumerated 1 to 2 million species of plants and animals are apportioned among trophic levels Of course any such estimate would necessarily be very very rough

More broadly I believe there to be a set of big questions that are often overlooked in our pursuit of the more traditional detailed questions These include along with the ques tion of food web structure that was the concern of this Workshop such problems as what determines the total number of species (both locally and globally) what determines the rela tive abundance of species and how is the number of species of a given physical size deter mined (again both locally and globally) These large questions are intertwined and I think it may well be that ultimately one cannot understand the details of food web structure without understanding these other aspects of community organization Specifically for example Pimm s studies of the dynamics of food webs are keyed to the characteristic dou bling times of the slowest changing populations it follows that a tenfold speeding of meta bolic rates throughout the ecosystem may—other things being equal—enable food chains to lengthen while the overall dynamical stability remains unchanged Pimm s general line of analysis is rescued if the top predators in most food webs are relatively large vertebrates whose characteristic time scales for population change are all typically measured in years If this is so the fundamental question remains why it should be so It may be that the behavioral constraints on top predators force them to be large and thus long lived in which case we would have the remarkable situation that the behavioral ecology of individuals is intimately involved in explaining the gross structure of communities This is no more than one explicit example of how these large questions—food web structure and number of species—may interact There is considerable need both for more factual information about the empirical patterns pertaining to these questions and for fresh ideas about how the pat terns may arise

REFERENCE

May R M 1983 The structure of food webs *Nature* 301 566 568

APPENDIX

FOOD WEB WORKSHOP FONTANA VILLAGE INN, OCTOBER 25 27, 1982

PROGRAM

Monday October 25

9 00	9 45	Robert Paine	Intertidal food webs Does connectance describe their essence?
9 45	10 30	Joel Cohen	Recent progress and problems in food web theory
11 00	11 45	Frederic Briand	Biogeographic patterns in food web organization
11 45	12 30	George Sugihara	Holes in niche space A derived assembly rule and its relation to intervality
2 00	2 45	Mac Post	Dynamic patterns of randomly assembled food webs
2 45	3 30	Peter Yodzis	Community assembly energy flow and food web structure
4 00	4 45	Robert Armstrong	The role of symmetric food web models in explicating the stability/diversity connection
4 45	5 30	Stuart Pimm	The causes of food web structure Dynamics energy flow and natural history

Tuesday October 26

9 00	9 45	John Glasser	Variation in niche breadth with trophic position On the disparity between expected and observed species packing
9 45	10 30	Leo Luckinbill	Habitat selection and trophic stragegy in a protozoan predator prey system
11 00	11 45	Charles Kerfoot	Propagated effects along food chains Vaulting
11 45	12 30	Len Nunney	Time delays and food web stability Horizontal food chains
2 00	2 45	Simon Levin	Food webs biotic control and regulatory problems
2 45	3 30	Peter Abrams	Alternative forms for links in trophic webs
4 00	4 45	Harold Hastings	Stability of community interaction matrices
4 45	5 05	James Drake	Invasability in Lotka Volterra interaction webs

Wednesday October 27

9 00	9 30	Robert Ulanowicz	Identifying the structure of cycling in ecosystems
9 45	10 30	Anthony King	Biomass stability and the complexity of grazer dominated food webs
10 30	11 15	Robert May	Food web structure Some thoughts and some problems

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