A Cautionary Tale: The Goldilocks' Effect in Measuring

Ecological Complication in Food Webs[1]

By

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Abstract

The purpose of this paper is to apply the Goldilocks' Effect to an experimental marine plankton community to study the 'just right' level of food web complication using loop analysis. 'Just right' implies that (1) the food webs must be biologically reasonable, that is, could exist in nature, and that (2) the level of complication includes the sets or universes of all such food webs. The macro universe is the number of mathematically possible networks of N variables, but relatively few are biologically reasonable.   The micro universe represents all variables and links observed in a set of data fitted loop models and their combinations. It contains trillions of networks that can be summarized into Ecological Skeletons.   It is an overestimate since some networks are unstable and include matrix redundancies; it is an underestimate because there are inherent limitations on ecosystem observation in accurately capturing all variables and links in a real world food web. The meso universe is the micro universe corrected for these over and under estimations or the 'just right' measure of ecological complication.   To date, its exact size remains unknown, but loop analysis provides a way to approach a realistic estimation.   These results serve as a cautionary tale, however, that ecological complication is more expansive than is commonly understood. The Goldilocks' Effect has been previously used with food webs. Loop analysis, however, contributes new insights to these discussions, and a useful methodology for identifying biologically reasonable food webs, and several associated structural and functional measures.

Keywords:

Ecological Complication
Goldilocks' Effect
Loop Analysis
Biologically Reasonable Food Webs
Ecological Skeletons
Marine Plankton Community

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[1] Abbreviations used include: EC as ecological complication and ES(s) as ecological skeleton(s).

1.0 Introduction

1.1 The Goldilocks' Effect

Science often uses analogies such as the Goldilocks' Effect the refers to the cautionary tale about the dangers of children wandering off alone to strange places. Uninvited, Goldilocks entered the three bears' cottage (Southey, 1837) and made herself comfortable.   She used the timeworn method of 'trial and error' to select the warm porridge, the small chair, and the medium hard bed. Each one was 'just right' for her and they all belonged to baby bear. The bears were provoked with her intrusion, but she escaped unharmed. Finding the 'just right' level of ecological complication (EC) is not so easy, and Goldilocks' 'trial and error' method will not work for food webs. There are too many choices and alternative configurations.

The Goldilocks' Effect has proven to be a useful concept in many areas of science such as: cosmology, astrobiology, evolution, economics, psychology, medicine, and ecology among others.   For example, Davies (2006) asked why is the universe 'just right' for life and how did it become so bio friendly? A Goldilocks' planet, like Earth, is one that is located in a potentially habitable zone in outer space (Grebin, 2004; Lovett, 2012; Levin, 2005; Cirkovic, 2007). In ecology, the Goldilocks' Effect has also been employed. Optimal foraging models based upon a 'just right' prey size have been used to predict food web structure (Petchey et al., 2008; Berlow, et al. 2008). Food webs have been deemed useful in studying the dynamics of evolutionary open ended systems and how they overcome entropy in producing 'creative complexity'. To this end, Dorin and Korb (2010) hypothesized that there would be a Goldilocks' Effect in between low and high density networks. They proposed an information theoretic measure termed Shannon Web Complexity (SWC) to quantify web complexity for artificial life ecosystems that would faithfully exhibit the Goldilocks' Effect.

The Goldilocks' analogy has such broad scope and frequent application because it provides a way to match the 'just right' question/problem with the 'just right' answer/solution. 'Just right' does not necessarily mean the intermediate alternative, although it is the most common solution, but rather what is the best match such as Little Bear's small chair. When the levels between questions and answers are incommensurate, the outcome is rarely satisfactory. Many questions in science remain unanswered if not unexplored because of the mismatch of what we need to know with what we can know.   Usually what we 'need' to know involves a complex system, and in the real world, they are everywhere. As Weinberg (2001) concluded, science works on answering the questions that it can, and ignores those that it cannot, leaving us with an array of unanswered problems that are germane to our wellbeing. He also pointed out that because scientists has been so self congratulatory about their successes, there is a level of arrogance in believing science can answer all questions. It cannot. This mismatch has been particularly problematic in ecosystem management when ecologists fail to appreciate the level of EC operating in nature.

Given the current difficulties in defining and measuring complexity, here I focus upon EC, not as a surrogate or synonym for complexity, but as a concept that is useful in and of itself, and a necessary one if we are to understand and manage ecosystems critical to our survival. I use a qualitative network methodology, termed loop analysis, to measure complication and to

approach an estimate of the Goldilocks' 'just right' level of EC for some experimental marine ecosystems. While I believe these ecosystems are complex systems; I do not want to claim that I have captured a measure of complexity in this analysis.   Claims of measuring ecological complexity are frequently measures of EC (Lane, 2015; Lane, ms. In preparation).

1.2 Definition of Ecological Complication (EC)

For the purposes of this paper, I define EC to be similar to Weinberg's concept of middle number systems. Like Goldilocks' fictional world, Weinberg (2001) categorized the natural world into three types of systems: small (organized simplicity machines), medium (organized complexity systems), and large (unorganized complexity aggregates) based upon plotting randomness versus complexity (Weinberg, 2001; Weaver, 1948). Science has been successful in the evaluation of both small and large number systems, and useful methodologies have proliferated in these two areas (Weinberg, 2001). Small number systems, such as a swinging pendulum or a growing population, possess a small number of components with few interactions, which can be treated analytically by using a set of differential or difference equations. This approach, however, has limits. The Square Law of Computation warns how the amount of computation needed for a system of N variables increases as the square of N (Weinberg, 2001). We can push this boundary as our technology becomes more powerful, but computers being physical systems cannot have infinite computational power. Moore's Law, which correctly predicted that computing power would double every 18 to 24 months over the last five decades, is not expected to apply forever (Lloyd, 2000). Analytical capacity must eventually reach a limit.

In contrast, large number systems have many components and many interactions, such as a bottle of a mole of a gas whose 6.022×10^{23} molecules collide randomly with each other in a frenzy of disorder. For this system, the ideal gas laws could be formulated since mean values of temperature, pressure, and volume are sufficient descriptors.   These large number systems can be studied statistically when there are relatively small error terms (Weinberg, 2001). Medium number systems, which have intermediate numbers of components and interactions, have been neglected and poorly understood in science (Weinberg, 2001).   Food webs are subsumed in this intermediate category. There are too many species and interactions to be treated analytically, too few to ensure there are small error terms as well as insufficient randomness needed for the statistical methods to be valid. Davies (2006) pointed out that biological systems are in between the predictable rigid geometry of salt crystals forming in a solution and the chaotic behavior of gas in a bottle. The notion of the average organism in a lake or a forest is nonsensical as is the surety of small error terms. Scientific tools needed to study these food webs as medium number systems are scarce. Loop analysis is a useful tool for measuring many properties of middle number systems that can be considered to be aspects of EC.

Complication and complexity are not equivalent (Poli, 2013).   Complication can be measured; perhaps complexity cannot (Lane, 2015; Lane, ms. In preparation). Some authors have suggested that complexity resides in middle number systems (Weinberg, 2001).   For example, Parrott (2010) concluded that complex systems are in between highly ordered, predictable systems, and those that are highly disordered and random. "Complexity is neither

complete order nor complete disorder…Complexity always involves both order and disorder. Ecosystems show well defined regularities; but populations often fluctuate wildly" (Solé and Goodwin, 2000). This is perhaps another way of saying nature is a set of middle number systems. Whereas middle number systems can be viewed as complicated, Rosen (1987, 1991, and 2000) has challenged the notions that complexity arises from the number of parts and interactions in a system and that complex systems can be fully modelled. Until there is more resolution of this conceptual ambiguity, it appears prudent to refer to complication and not complexity in telling this cautionary tale.

Gregersen (2011) concluded that "complicated systems are large systems with distinct components whose aggregate behavior nonetheless (a) can be fully understood on the basis of the components of the systems, (b) can be compressed in algorithms, and thus (c) can be predicted. Examples are a Boing 747, crystals and other aggregates, or a system of rational choice agents." Loop analysis results do allow for Gregersen's points a, b, and c to be achieved, although his use of the term 'large' is problematic and undefined. Others have focussed upon how many interactions there are between pairs of components such as the standard measures of connectance and connectivity in food web models (Moore and de Ruiter, 2012). Whereas complication is not a surrogate measure of complexity, it can be useful for understanding how some complex systems function in the real world through enhanced understanding of the relationship of the parts to the whole; the roles of feedback, location of wasp and satellite variables; the degree of variable aggregation; the nature of link types; system response to its environmental perturbation, stability and resilience measures, identification of the operative pathways of effect, and potential universes of biologically reasonable network configurations, and Ecological Skeletons (ESs). All of these structural and functional aspects of complicated food webs can be explored with loop analysis.

2.0 Methods and Materials

2.1 Loop Analysis

Loop analysis is a qualitative form of network analysis that uses signed digraphs. Each variable can have a direct positive, negative or zero effect on another variable in the graph or network. A positive effect is diagrammed by a link ending in a small arrowhead attached to the variable that is helped and a negative effect is represented by a link ending in a small circle head attached to the variable that is harmed. Thus, each edge or link in the graph can have 3^2 or nine qualitative link types between every pair of variables including 'no link'. The methodology was created by Richard Levins (1973, 1975) and first used for aquatic ecosystems by Lane and Levins (1977). Loop analysis is inherently flexible in describing any systems of interacting variables in many disciplines; and it provides direct insight into the role of feedback in these systems. Each loop constitutes a feedback, which is defined as the effect of a variable on itself by way of intervening variables. When negative, feedback is stabilizing, and when positive, it is destabilizing. Even the presence of a few feedback loops can greatly increase levels of complication in ecosystems. The theory of loop analysis and more complete mathematical derivations and descriptions can be found in Wright and Lane (1986), and Puccia and Levins (1985).

Loop analysis facilitates the modelling of ecological systems.   Besides including all types of bivariate and univariate (self damping and self enhancement) link types, different types of variables can be used in a single loop model including biotic and abiotic ecosystem components as well as human variables. The methodology can also be used to help understand various environmental problems and make impact predictions. For example, Lane (1985) used loop analysis to make ecosystem level predictions for environmental impact analysis for oil development at Hibernia on the Grand Banks, Newfoundland in regard to sea bird populations, and for a large bridge constructed over the Northumberland Strait to Prince Edward Island, which could cause ice buildup and microclimatic changes that could impact a number of valuable commercial fisheries (Lane, 1998).

Unlike many descriptive food web methodologies, loop analysis employs a set of calculation equations for computing the changes in standing crops following a parameter input to the network [traditional community matrix] that portrays the interactions of N species using the following equation:

$$E_{ij} = \in P_{ij}^{(k)} \cdot F_{n-k} \{ \text{compl } P_{ij}^{(k)} \} / F_n,$$

where E_{ij} is the community effect of a parameter change to variable j on variable i; $P_{ij}^{(k)}$ is the algebraic product of links along a simple, open path k from variable j to variable i; k is the length of the path determined by counting its number of variables. $F_{n-k} \{\text{compl } P_{ij}^{(k)}\}$ is the feedback of order n-k variables that is essentially the determinant of the submatrix of the remaining variables not on the path. The sign of the complement is the sign of the determinant of this submatrix. F_n is the feedback for the total system represented by the determinant of the community matrix (level N). The feedback of any level k of the community matrix and its submatrices can be computed as:

$$F_k = (-1)^{m+1} \text{Loops}(m,k),$$

where m is the number of disjunct loops that total k variables. Disjunct loops have no variables in common whereas conjunct loops share at least one variable, and the latter are not used in the expansion of determinants or in loop analysis. Square matrices and loop analysis models from linear algebra are equivalent in this analysis when determinants are calculated with qualitative signs. The signed subproducts of the expansion of the determinant have a particular row and column represented only once each. Thus, the matrix elements in each subproduct constitute one or more disjunct loops.   To complete the calculations, the feedback of zero variables (F_0) is -1 and the value of a path of zero variables (P_0) is =1.

Loop analysis relaxes the need for measurement and quantification by giving more attention to food web structure and how it is influenced by environmental change (parameter input). Qualitative structure, as depicted from loop analysis, emerges from the fact that all variables are not connected to each other, and only pathways with valid complements operate in the overall network at a given time. This has important ecological ramifications in that variables that are not on a path of interest must be in motion among themselves for a particular path to operate. Thus, many potential paths in real world food webs essentially have zero effect and merely counting paths does not tell us which paths have effects and which ones

do not. Loop analysis also facilities the identification of where the environment is most strongly affecting a given food web, namely at the top, middle, or bottom of the food web. In addition, stability criteria further restrict when F_N is stable and this determines when calculations can proceed and when they cannot.

Loop diagrams can be created using only the investigator's intuition (Dambacher et al.; 2009) or by fitting data to directed changes in data sets as has been done here and in Lane (1986a,b; 2015). To date, most loop models have been purely hypothetical and theoretical, or loosely based upon their creators' intuition about a particular system. For example, Lane and Levins (1977) studied nutrient enrichment in model freshwater algal communities of 6-7 variables and showed that although limiting factors exist at the physiological level, the concept is less useful at the ecological level in a food web. They used the results of several decades of nutrient enrichment experiments, but without modelling a specific lake or plankton data set. In systems with 10 or more variables, it becomes difficult to compute loop diagrams by hand; and intuition becomes increasingly strained.

Lane (1986a) was the first investigator who used large scale data sets in fitting loop models to marine and freshwater ecosystems that had high taxonomic resolution by including hundreds of species in a single loop model for planktonic food webs in Delaware Bay. 'Fitting' loop models, a multistep process, is different from fitting quantitative parameters in computer simulation models (Lane, 1986b). First, species are divided via a qualitative correlation analysis into functional groups or loop variables. Second, the field data is organized into the same functional groups and graphed over time to identify qualitative trends of +, or 0 for each functional group from one sampling period to the next. Essentially, quantitative data are transformed into a qualitative format. Third, the loop models are constructed and adjusted until the best fit possible is achieved by matching the changes in standing crops predicted by the equations given above and the trends in the qualitative field data set. Because the effects of each parameter input is a function of the structure of the whole network, the operative pathways at a particular point in time are simultaneously affected by all of the feedbacks in the network. Thus, many potential configurations are impossible; many pathways are inoperative; and additional qualitative structural constraints are embedded in the loop models as they are created. The modeller then works iteratively to create the best fitting models. Successful prediction matches are usually 90-95% for a particular model.

Using loop analysis, a number of measures can be computed using specially designed algorithms to calculate various aspects of EC as similar to the 'organized complexity' of Weinberg's middle number systems. These measures include: enumeration of variables and links, operative pathways (1 to N), feedback levels (1 to N), network similarity coefficients, summary networks termed ESs, as well as universes or sets of various combinations of mathematically possible and/or biologically reasonable food webs. Each of these measures is explained in the next section.   Loop analysis also bridges the gap between structural and functional aspects of EC. Structure is analyzed by the various configurations of variables, links, and network subsystems, whereas function is studied through the temporal dynamics of parameter input, pathways of effect, variable change, and feedback relationships.

2.2 Marine Ecosystem Research Laboratory (MERL)Enrichment Experiment

The data for the present study come from a large nutrient enrichment press experiment involving nine shoreline tanks or mesocosms at the Marine Ecosystem Research Laboratory (MERL), Graduate School of Oceanography at the University of Rhode Island on Narragansett Bay.   The raw MERL data are routinely published and available to non MERL investigators as data reports (Frithsen, et al., 1985). There were three control tanks and six non replicated experimental tanks, 1.8 m in diameter and 5.5 m deep. The daily inorganic nutrient additions consisted of the basic ratio of 12.8 nitrogen to 1 phosphorus to 0.9 Si molecules in a geometric progression: 1X, 2X, 4X, 8X, 16X, and 32X. The experimental treatments were not replicated because the MERL scientists decided that a gradient of realistic sewage additions was more likely to produce experimental insight than one or two replicated treatments. In addition, mesocosms are inherently difficult to replicate. This gradient mirrored the sewage inputs known to occur along the Western Atlantic coastline in areas close to MERL with 1X being the normal level of nutrient enrichment for Narragansett Bay. The 1X and 2X treatments were labelled low, the 4X and 8X as medium, and the 16X and 32X as high nutrient enrichment tanks. The experiment was run for two years, but only the first year's data are analyzed here. The results focus upon the nutrient and plankton dynamics in the nine tanks over an annual cycle.

The mesocosms were well designed to simulate Narragansett Bay as closely as possible in terms of light regime, water column mixing, residence time, temperature, and benthic pelagic coupling. The bottom of each tank contained approximately 35 cm of sediment with a full benthic complement of species. Many benthic larvae are planktonic and interact with plankton species in the water column. Both phytoplankton and zooplankton species were identified to the smallest taxonomic unit possible and enumerated every three to four weeks giving 14 sampling dates for Year 1. Included in the analysis were 140 species/taxa of phytoplankton and 84 species/taxa of zooplankton and benthos. The MERL mesocosms and this particular experiment have been described in detail elsewhere (Oviatt, et al. 1986. 1989; and Kelly, et al 1985). The raw data for the total experiment are published in a two volume technical report compiled by Frithsen, et al. (1985), which is available at MERL.

3.0 Results and Discussion

3.1. Ecological Skeletons and Similarity

Loop models were constructed for the nine tanks over 14 sampling dates (T) for the first year of the experiment. This produced 13 loop models (T-1) per tank or a total of 117 models by fitting to the directed changes (+, -, or 0) in loop variables from one sampling date to the next. Ecological Skeletons (ESs) were calculated for each tank by summing up the most prevalent nodes (≥25%) and linkages (≥66.6%) as solid lines and less prevalent linkages (≥33.3-66.5%) as dotted lines for a set of loop models. These models were further summarized into three controls (39 models), and low, medium and high enrichment treatments (26 models each) as well as the overall composite ES for the total data set (117 models). This gave 14 ESs in total.

Figure 1 illustrates the composite ES for all tanks and sampling dates for the total set of 117 loop models. The key to all variables used in this paper is given in the legend to Table 1. The MERL plankton food web has three parallel food chains with some cross links essentially exhibiting a three tiered lattice structure. A_3 is a set of diatoms that are luxury consumers whereas A_1 diatoms are not luxury consuming. The central nutrient variable, N_1, is a ratio of bioavailable nitrogen over bioavailable phosphorus. All three nutrients (N_1=N/P, Si =silica and N_2 =organic N) are self damped since their input does not depend on their concentrations in the water column, but their uptake by algal species does. See Lane and Levins (1977) for a more detailed discussion of nutrient self damping. Algal variables can exhibit self damping when they self shade themselves and animals can be self damped when they are cannibalistic or when they suffer from major forms of mortality not represented by predators explicitly included in the models. Three major benthic larval forms (ML, P, and AL) act as predators on the diatoms (A_1), dinoflagellates, (A_2), and immature copepods (Z2). All of the animal variables are self damped. The numbers of variables and links included in the composite ES are summarized in Table 1. From work done to date in several ecosystems, the most common linkages are self damping loops, predator prey links of two variables one with the an arrowhead and one with the circle head, and one way linkages between two variables with either a single arrowhead or circle head. No self enhancing loops have been included in any of the hundreds of loop models completed on aquatic data sets to date. The number of empty elements in Table 1 clearly demonstrates the large amount of qualitative structure present in these food webs. Qualitative analysis tells us the most when each variable is not connected to every other one.

Figure 1.   Composite Ecological Skeleton (ES) of All Nine Tanks.   Key to variables is given in Table 1.

Table 1. Number of Most Frequent Variables and Links over All Tanks and Dates. Corresponding loop model showing composite ES given in Figure 1. The first column contains the number of times the variable appeared in the 117 loop diagrams. Numbers of self links are given down the main diagonal. The rest of the matrix shows number of loop diagrams in which there was a nonzero link between the pair of variables indicated by their respective column and row. Key to the variables: Si=silica, N_1=nitrogen/phosphorus ratio, N_2= organic nitrogen, A_1 =diatoms, A_2=dinoflagellates, A_3 =luxury consuming diatoms, Z_1=copepod adults group 1, Z_2= copepodites and nauplii, Z_3=copepod adults group 2, P=polychaete larvae, ML=mollusc larvae, and AL=anemone larvae.

| No.		Si	N_1	N_2	A_1	A_2	A_3	Z_1	Z_2	Z_3	P	ML	AL
116	Si	100			54		68						
117	N_1		100		63	49	44						
87	N_2			100		100							
103	A_1												
89	A_2								70				
109	A_3							65		78		79	42
101	Z_1							84	40				
114	Z_2								40	32	37		
95	Z_3									45			76
47	P										68		
70	ML											77	
57	AL												46

Figures 2-5 illustrate the ESs for each tank individually. No two of the individual diagrams making up these ESs or the ESs themselves are identical. The individual models can be likened to a set of chemical isomers that appear fleetingly in a chemical solution (Lane, 1986a). The compound only exists as a single isomer at one time, but does not exist in nature as the composite. Each of the loop models constructed here was unique, yet very similar to the others. A similarity matrix (not shown) was computed for the 14 ESs for the nine individual tanks, three controls, low, medium and high experimental tanks, and the composite ES for all tanks and sampling dates; this measure (S) gives values from 0.0 to 1.0 with 1.0 being the maximum similarity. S ranged from .78 to .88 for the 14 ESs with the more aggregated ESs exhibiting higher similarities (.86-.87) except for the high enrichment treatment (.82), which had the lowest similarity value because of the increased dominance of predatory benthic larvae in these tanks.

Figure 2.   Ecological Skeletons of Control Tanks (a) 00, (b) 05 and (c) 08. Key to variables is given in Table 1. The PC variable is a combination of polychaete (P) and cirriped or barnacle (C) larvae. C=cirriped larvae.
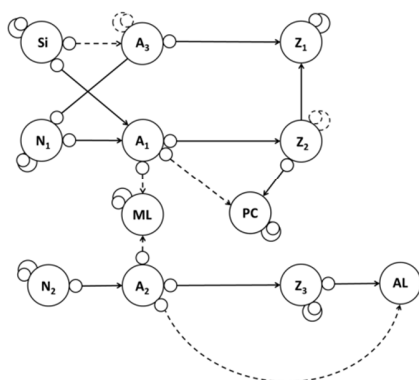
2.a.   2.b.
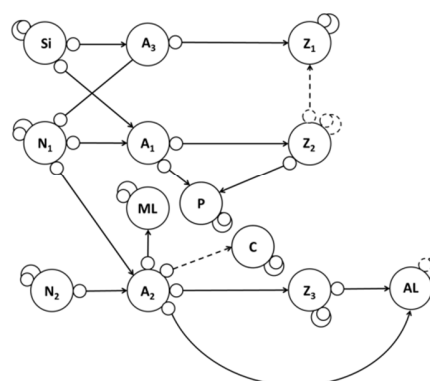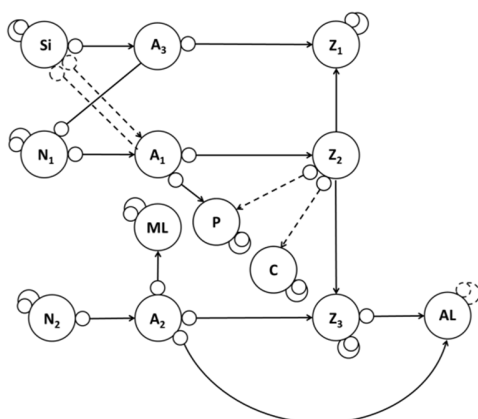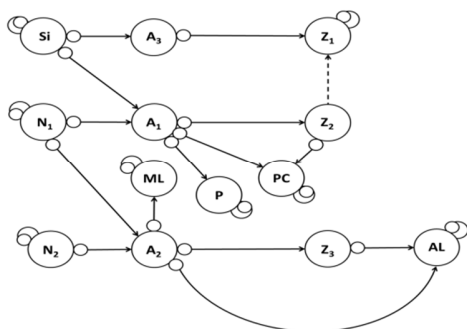

2.c.

Figure 3. Ecological Skeletons of Low Enrichment Experimental Tanks (a) 1X Tank 06 and (b) 2X Tank 09 . The PC variable is a combination of polychaete (P) and cirriped or barnacle (C) larvae.
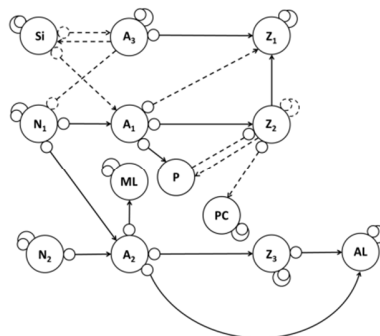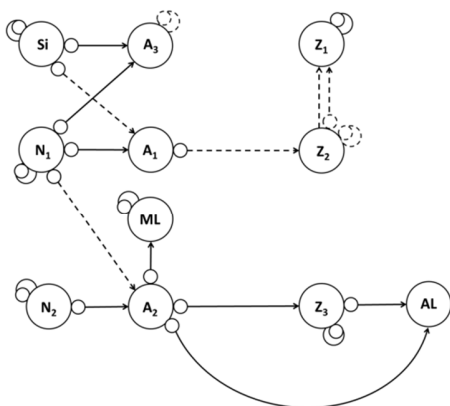
3a.

3.b.

Figure 4. Ecological Skeletons Medium Enrichment Experimental Tanks (a) 4X Tank 04 and (b) 8X Tank 01. Key to variables is given in Table 1.
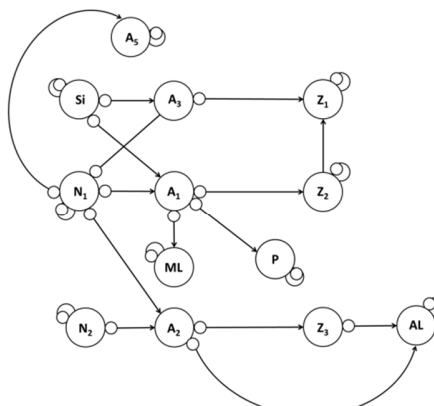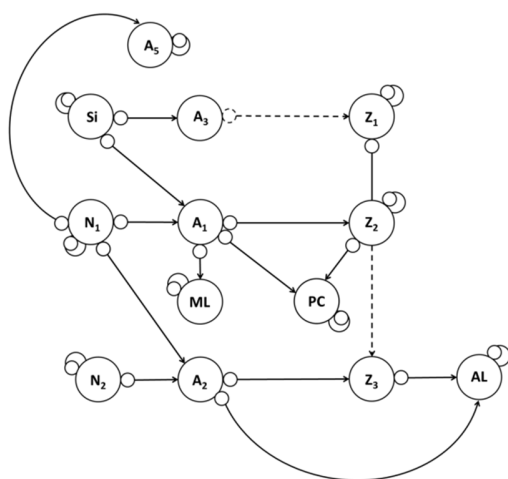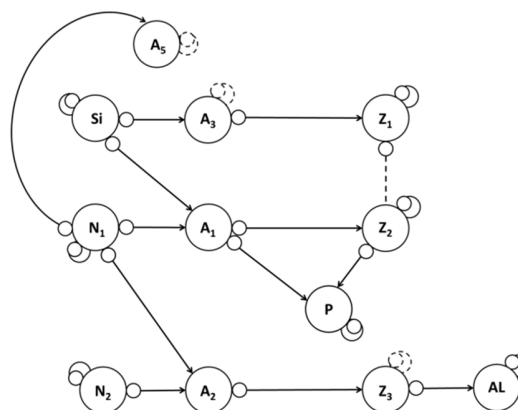
4.a.

4.b.

Figure 5. Ecological Skeletons High Enrichment Experimental Tanks (a) 16X Tank 02 and (b) 32X Tank 07. Key to variables is given in Table 1. The PC variable is a combination of polychaete (P) and cirriped (C) larvae.

5.a.

5.b.

When the links between two variables change frequently in one data set, they are termed, 'volatile links', and they often indicate the main sources of nonlinearity in their associated food webs. In the MERL tanks, a large source of link volatility is related to the myriad of relationships among the many species of calanoid and cyclopoid copepods (Z_1, Z_2, and Z_3). These animals have 12 life stages: 6 nauplii, 5 copepodite, and 1 adult. They change their feeding preferences as they grow and develop from consuming small plant and microbial foods, to small, and then larger animal prey. Older stages, especially adults, frequently prey on the young forms of their own or other species. Thus, the links among these zooplankton variables are highly variable and nonlinear; they are both one way and two way, and frequently reverse signs. There is also seasonal volatility between the two diatom variables and the silica pool. This link volatility gives the food webs a great capacity to respond to changing environmental conditions and parameter inputs, and ensures that the food webs are adaptive. The loop models show that the dominant feeding relationships are far more restrictive than the myriad of feeding links that are commonly included in food web models based upon two species feeding experiments in the field and laboratory. When a predator has a choice of consuming a particular prey species in an experiment or starving, they will consume that prey, but may rarely consume that prey in nature. Structural analysis of loop models also suggests that we need a much deeper understanding of EC before we can make informed arguments about relationships among diversity, complexity, and stability, etc. as well as create rules of construction for food webs.

3.2 Locations of Parameter Inputs

Table 2 contains a summary of the parameter inputs for all 117 individual models grouped as sets of models. The location of a parameter input identifies the first variable where the environment perturbs the food web. Parameter inputs in qualitative modelling are equivalent to driving forces or driving functions used in the quantitative models of systems ecology. Of all 117 parameter inputs (one per model), 56% entered one of the nutrient variables, 20% at one of the algal variables, and 25% at one of the zooplankton/benthic variables. These results demonstrate that even when we implement a treatment to an experimental system, in this case nutrient enrichment, the designed perturbation may not dominate other perturbations existing in the environment. There were even 12 instances of a negative nutrient parameter input even though nutrients were added continually throughout the year. For the MERL tanks, almost half of the parameter inputs entered at non nutrient variables. When loop models have been fitted to field data (Lane 1986a, 2015, and unpublished) approximately 85% of the parameter inputs enter at the nutrient and algal variables, and only 15% at the top levels of the trophic hierarchy, which indicates that trophic cascades might not be as prevalent as sometimes reported (Terbough and Estes, 2010). The higher percentage of parameter inputs entering at the predator variables in the MERL tanks probably reflect the intense benthic pelagic coupling that occurred in these confined ecosystems, and the relative success of the benthic larvae in outcompeting the pelagic invertebrate predators. The experiment began with several pelagic predators coexisting in the tanks, but they did not persist as the benthic forms became abundant. The benthic larvae are also effective vehicles in enhancing nutrient regeneration in the water column (Kelly et al, 1985) and this may confound the inorganic nutrient additions.

Table 2. Summary of Parameter Input Locations.

Model Set	M= # of Models	+N	-N	+A	-A	+Z	-Z
Control Tank (00)	13	4	1	3	1	3	0
Control Tank (05)	13	6	1	1	2	1	2
Control Tank (08)	13	6	2	1	0	2	2
Experimental Tank (06) 1X	13	8	0	1	3	1	0
Experimental Tank (09) 2X	13	3	2	2	1	2	3
Experimental Tank (04) 4X	13	7	0	2	1	3	1
Experimental Tank (01) 8X	13	6	1	1	0	3	1
Experimental Tank (02) 16X	13	7	3	1	0	1	1
Experimental Tank (07) 32X	13	6	1	2	1	2	1
Total	117	53	12	14	9	17	12
% of Total	100	56%		20%		25%	

3.3 Prediction Accuracy

Loop analysis calculations predict how all of the standing crops of organisms and concentrations of nutrients will change when the food web is perturbed by a parameter input. The predicted changes or community effects can then be compared to how the variables changed in the tanks. Prediction accuracy is summarized in Table 3. Of the 1146 predictions for individual loop variables of the 117 models, 114 were in error, or approximately one per loop model. The error values, however, include all zero values, that is, when there are zero changes in the data and yet, loop model variables are predicted to increase or decrease as well as zero loop model predictions when the data values increased or decreased. These discrepancies involving zero values are considered to be partial errors and are counted as 0.5 each. Errors involving zeros occurred because of the somewhat ad hoc method of computing directed changes, (Lane, 1986b). Consequently, many of the zero related cases may not be true errors. Of the 114 errors, only 12 did not involve zeros and were scored as clear errors at 1.0 each. This is approximately an overall error rate of 1%. Most inferential statistical methods permit a 5% error rate.

Table 3. Summary of Accuracy in Predicting Directed Changes.

Model Set	M=# of Models	# Predictions	# Right	# Wrong	# Sign Changes
Control Tank (00)	13	124	112.5	11.5	0
Control Tank (05)	13	123	100.0	14.0	1
Control Tank (08)	13	129	118.0	10.5	3
Experimental Tank (06) 1X	13	125	123.5	10.5	3
Experimental Tank (09) 2X	13	124	109.5	14.5	1
Experimental Tank (04) 4X	13	126	114.0	12.0	2
Experimental Tank (01) 8X	13	139	128.0	11.0	1
Experimental Tank (02) 16X	13	133	119.5	13.5	1
Experimental Tank (07) 32X	13	123	106.5	16.5	0
Total	117	1146	1032	114.0	12
% of Total		100%	90.1%	9.9%	1.0%

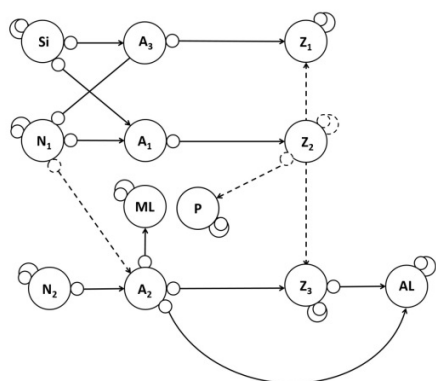### 3.4 Food Web Connectivity and Connectance

The "cohesiveness of a system is termed connectedness" (Allen and Starr, 1982). Measures of connectedness are given in Table 4 for the 14 ESs of the 117 individual tanks and treatments. ESs by treatment are given in Figure 6. Numbers of variables (nodes), links, and self damping loops are also listed. Connectivity is the number of links divided by the number of variables. This measure estimates the average number of links per node in the food web. Connectance is the proportion, usually expressed as a percentage, of the number of links in the system to the maximum number possible for a given graph representation. In the literature, several equations are used for connectivity and connectance because there are many different types of food webs that only include particular types of links out of the nine mathematically possible ones. Since loop models are signed digraphs, all nine link types are possible in the community matrix including self terms on the main diagonal. Thus, for a system of N variables there are N^2 possible links in loop analysis.

Table 4. Connectance and Connectivity Values for the 14 Ecological Skeletons as Shown in Figures 1 to 6. Key: M=number of models, V=number of variables, %SD=number of self damped variables, L=number of links, B=connectivity, and %C=connectance.

Model Set	M	V	%SD	L	B	%C
Control Tank (00)	13	12	75	37	3.1	25.7
Control Tank (05)	13	13	77	40	3.1	23.7
Control Tank (08)	13	13	62	38	2.9	22.5
Experimental Tank (06) 1X	13	13	77	42	3.2	24.9
Experimental Tank (09) 2X	13	13	62	37	2.8	21.9
Experimental Tank (04) 4X	13	11	73	32	2.9	26.5
Experimental Tank (01) 8X	13	12	67	32	2.7	22.2
Experimental Tank (02) 16X	13	13	69	37	2.9	21.9
Experimental Tank (07) 32X	13	12	83	34	2.8	23.6
All Controls	39	12	67	35	2.9	24.3
Experimental Tanks (1-2X)	26	13	69	36	2.8	21.3
Experimental Tanks (4-8X)	26	12	75	36	3.0	25.0
Experimental Tanks (16-32X)	26	14	79	41	2.9	20.9
All Tanks	117	12	75	34	2.8	23.6

Figure 6.   Summary of Ecological Skeletons by Treatment (a) Control, (b) Low Enrichment, (c) Medium Enrichment, and (d) High Enrichment.   Key to variables is given in Table 1. The PC variable is a combination of polychaete (P) and cirriped or barnacle (C) larvae.
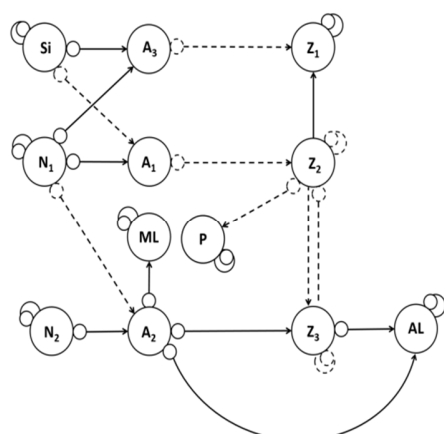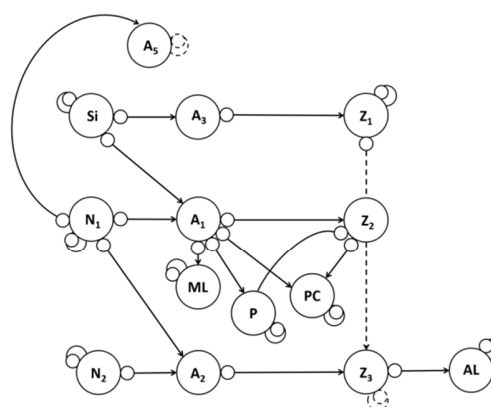
6.a.

6.b.
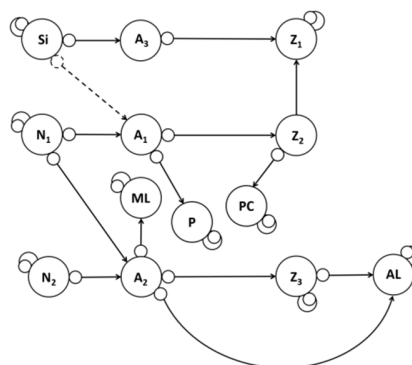
6.c.

6.d.

Connectivity measures in the MERL food webs were 2.8 for all tanks with a fairly small range of 2.7 to 3.1 for all ESs. Connectance values were 23.6% for all tanks with a range of 21.3% to 26.5% for all ESs. Gardner and Ashby (1970) reported that connectance values of 13% +/-2%, represents the boundary between almost certainly stable and almost certainly unstable networks. They worked with randomly generated networks that did not involve self terms.   In the last row of Table 4, tanks had on average 12 variables with 75% or 9 self damped variables. Given the connectance value of 23.6, if self damping is subtracted, then this gives a revised connectance value of 17.4%, which is fairly close to the upper bond of 15% in their calculations. The close proximity of plankton and benthos in these enclosed systems, may have also contributed to slightly higher connectivity and connectance values. The food webs for the MERL tanks are biologically reasonable whereas most of Gardner and Ashby's randomly generated models were not. In addition, all loop models were checked for stability before

predictions could be made, and their F_N vales were <0, thus satisfying a main stability criterion for loop analysis (Wright and Lane, 1986; Puccia and Levins, 1985). Thus, these loop models fall within Gardner and Ashby's 'almost certainly stable region'.

3.5 Operative Paths and Feedback Loops

Table 5 contains a summary of the number of all operative paths in each of the five ESs, summarized by treatment and path length. This latter value is the number of variables involved in each operative path from 1 to N, where N is the total number of variables in each food web. The five ESs for the controls, low, medium and high enrichment treatments, and all tanks contained 462, 274, 404, 424, and 294 operating paths respectively. Rarely did the tanks have paths longer than 9-10 variables. Loop analysis is useful in that it can delineate operative versus non operative paths; the majority are non operative. For a pathway to be operative, it must have a minimum of one valid complement composed of the variables not on the path that are configured in a set of disjunct loops. This means that the non path variables must be in motion in their respective feedback loops.

Table 5. Summary of Operative Paths by Enrichment Treatment and Variable Number, where the maximum N=14 for all Ecological Skeletons (ESs). X indicates the number of variables were present, but not in an operative path. * indicates that the corresponding number of variables was not present in the particular ES.

Variable Number	Controls	Low Enrichment	Medium Enrichment	High Enrichment	All Tanks
1	12	13	12	14	12
2	27	27	27	30	25
3	49	47	49	59	43
4	62	46	62	81	48
5	79	48	74	84	54
6	87	42	71	72	49
7	70	26	52	45	35
8	51	15	39	23	22
9	22	8	16	12	6
10	3	2	2	4	*
11	*	*	*	*	*
12	*	*	*	*	*
13	X	*	X	*	*
14	X	X	X	*	*
Total	462	274	404	424	294

Table 6 lists the number of feedback loops at each level (L_N), per number of variables (N) in a loop, for the same combinations of ESs, and summarizes the loops as total ($\sum$), positive and negative. Each loop diagram can contain positive and negative feedback loops at a variety of levels from zero to N such that level 0 (L_0) has no variables; L_1 has one variable so this level includes all the self loops; L_2 contains two variables and includes all the standard two-species biological interactions such as competition, predation, and mutualism; up to L_N where all the variables of a network are included in one or more large loop(s). L_1 were all negative self damping terms, and most of the L_2 loops were predator prey interactions. Since the predator receives a positive effect from consuming a prey (+), while the prey is harmed (-), the algebraic product of these L_2 loops is (+) x (-) = (-) or negative. The majority of the loops were short negative ones that are maximally stable. Long loops are less stable than short ones, and positive loops are less stable than negative ones (Levins, 1973; 1975). Table 6 illustrates that most loops in the ESs were negative and short involving L_1 and L_2. On average, there was approximately one loop of L_3 and less than 1 loop for all loops L>3 in the individual models. For the ESs, there were more loops of longer lengths because of the composite nature of these models. Short negative loops have to be abundant enough to balance any longer positive or negative feedback in loop models if they are to be stable. Tables 5 and 6 begin to address EC in loop diagrams directly and to illustrate how many pathways and feedback loops are involved in the functioning of the MERL food webs.

Table 6. Summary of Feedback Lo9ops by Enrichment Treatment and Number of Variables Where L_1 = 1 variable, L_2 =- 2 variables, etc. The maximum level of L_x=14 for all ESs. X indicates that the corresponding variable level was not present in a particular ES.

Variable Level (L_x)	Controls			Low Enrichment			Medium Enrichment			High Enrichment			All Tanks		
	$\sum$	+	-	$\sum$	+	-	$\sum$	+	-	$\sum$	+	-	$\sum$	+	-
1	8	0	8	9	0	9	9	0	9	11	0	11	9	0	9
2	12	0	12	13	0	13	13	0	13	14	0	14	11	0	11
3	2	1	1	2	1	1	2	1	1	3	2	1	2	1	1
4	1	1	0	0	0	0	2	2	0	1	1	0	1	1	0
5	3	3	0	1	1	0	2	2	0	1	0	1	2	2	0
6	1	1	0	0	0	0	0	0	0	2	2	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	X	X	X	0	0	0	X	X	X	0	0	0	0	0	0
14	X	X	X	X	X	X	X	X	X	0	0	0	0	0	0
Total	27	6	21	25	2	23	28	5	23	32	5	27	25	4	21

3.6 Macro and Micro Universes

Table 7 gives more insight into EC with the calculation of micro and macro universes based upon the numbers of variables and links in the 14 ESs. Loop models portray an intermediate number of components and links commensurate with Weinberg's notion of middle number systems. The macro universe is the simple, but unwieldy set of all mathematically possible networks for N variables. It is calculated as 3^{N*N} where N is the number of variables in a loop model. For example, a 20 variable loop model has 3^{N*N} or 7.06 x 10^{190} mathematically possible configurations, but most are not biologically reasonable and impractical to tackle directly. This universe also includes large numbers of unstable and unconnected networks as well as those whose matrix representations have linear dependencies, that is, identical rows or reordered row and column permutations making non unique matrices. All investigators working on food webs have similar macro universe calculations to consider for every value of N.

Loop analysis, however, enables the identification of much smaller set of biologically reasonable networks or micro universes that are useful for studying the middle number system level of complication. Micro universes are calculated as (K * M) * (L * N) where K equals the number of types of links (1-9) for each pair of variables times M which is the number of two node links times the product of L, the two types of self links found in MERL loop models, zero or minus, times N, the number of one node self loops. This calculation assumes that all variables and links are independent of each other. If we had better rules of construction for food webs, it is possible some further restrictions could reduce the size of this micro universe. The values of the micro universes ranged from 1.4 x 10^{10} to 5.9 x 10^{13}. The micro universes were extremely small compared to their corresponding macro universes as shown by the E values (Table 6).

Any tool that can get us closer to the set of biologically reasonable networks has to be given serious consideration. Lawlor (1978) calculated that for a 40 variable system there are 10^{764} networks with +, -, or 0 interactions. Even if 10^{500} were biologically reasonable, they would be so sparse that random searching would not find them. He also computed that for a 10 variable system "there is a 95% expectation of never encountering an ecological system in 10 years while generating random systems at the continuous rate of 1 million per second". He further estimated there is less than one chance in a google of constructing an ecosystem with a random number generator. He concluded that we should be concentrating on real ecosystems or at least those that are biologically reasonable, and that random generation of networks should be abandoned. Loop analysis gives us a way to identify the biologically reasonable networks and discard the rest. Given the numerous degrees of variable aggregation and observed link diversity between pairs of interacting variables, however, there is still a large number of biologically reasonable food webs that are relevant to the concept of EC.

Table 7. Macro Universe and Micro Universe Calculations for Nine MERL Tanks and All Tanks Together. Key: M=number of models per tank(s), V = total number of variables, $\bar{V}$ = mean number of variables per set of networks, L = number of links per set of networks that are nonzero, MA_V = macro universe calculated over all variables per set of networks, $MA\bar{V}$ = macro universe calculated over the mean number of variables per set of networks, MI = micro universe calculated over all link alterations per set of networks, MI* = standard micro universe calculated as (MI/M), E = MI/ $MA\bar{V}$ which is a measure of the relative size of MI. 1X to 32X indicates the level of enrichment. Tank number is given in parentheses in the first column labelled 'Network Set'.

Model Set	M	V	$\bar{V}$	L	MA_V	$MA\bar{V}$	MI	MI*	E
Control Tank (00)	13	21	11.2	245	2.6×10^{210}	7.1×10^{59}	1.2×10^{13}	9.2×10^{11}	1.7 x 10-47
Control Tank (05)	13	19	9.8	229	1.7×10^{172}	6.6×10^{45}	5.8×10^{12}	4.5×10^{11}	8.8 x 10-34
Control Tank (08)	13	17	10.9	229	1.7×10^{137}	4.9×10^{56}	3.3×10^{12}	2.5×10^{11}	6.7 x 10-45
Experimental Tank (06) 1X	13	19	9.1	239	1.7×10^{172}	3.2×10^{39}	2.9×10^{12}	2.2×10^{11}	6.9 x 10-28
Experimental Tank (09) 2X	13	18	10.7	231	3.8×10^{154}	4.2×10^{54}	2.6×10^{12}	2.0×10^{11}	6.2 x 10-43
Experimental Tank (04) 4X	13	20	10.8	235	7.0×10^{190}	4.5×10^{55}	2.6×10^{11}	2.0×10^{10}	5.8 x 10-45
Experimental Tank (01) 8X	13	19	10.6	237	1.7×10^{172}	4.1×10^{53}	5.9×10^{13}	4.5×10^{12}	1.4 x 10-40
Experimental Tank (02) 16X	13	19	11.2	245	1.7×10^{172}	7.1×10^{59}	8.3×10^{13}	6.4×10^{12}	1.2 x 10-46
Experimental Tank (07) 32X	13	19	10.3	235	1.7×10^{172}	4.1×10^{50}	1.4×10^{10}	1.1×10^{9}	3.4 x 10-41
All Controls	39	22	12.1	703	8.4×10^{230}	4.6×10^{69}	1.3×10^{19}	1.0×10^{18}	2.8 x 10-51
Experimental Tanks (1X-2X)	26	21	13.3	470	2.6×10^{210}	2.8×10^{84}	1.1×10^{17}	8.4×10^{16}	9.3 x 10-60
Experimental Tanks (4X-8X)	26	20	12.6	472	7.0×10^{190}	7.3×10^{75}	6.8×10^{16}	5.2×10^{15}	3.9 x 10-68
Experimental Tanks (16X-32X)	26	20	14.7	480	7.0×10^{190}	1.1×10^{103}	3.0×10^{19}	2.3×10^{18}	2.7 x 10-84
All Tanks	117	22	10.5	1925	8.4×10^{230}	4.5×10^{55}	8.3×10^{28}	7.1×10^{26}	1.8 x 10-27

Micro universe calculations are also sensitive to the number of networks producing them. The micro universes presented here do not provide all of the information that is needed because they are empirically fitted to a set of data directed changes, which are limited by observational effort. For example, there were only 14 sampling dates for each tank giving 13 directed change models per tank. It is unknown what was happening in the tanks at other times when they were not sampled. It is possible that not all variables and links were identified. Each new variable or link multiplies up the number of networks in the micro universe. Thus, the micro universes are underestimates on biological or empirical grounds, but overestimates mathematically especially given stability requirements. Increased sampling and data collection

can improve the underestimates, but never entirely eliminate them because we could never know if all variables and links had been captured. This is a common problem for all investigators measuring food web interactions in the field and laboratory. Theoretically, universes of food webs could be generated individually and tested for stability with a powerful computer. What we would really like to know is the meso universe or the total number of biologically reasonable and mathematically stable networks for a given level of variable aggregation and connectedness. This is unknown at present, and we do not know if the meso universe will eventually be smaller or larger than the initial micro universe values calculated here, but knowing the micro universe is a necessary step to determining the meso universe.

This study provides several measures of EC using loop analysis. First, the level of variable aggregation is about 1 to 10 for the number of functional groups used as loop variables to the original number of taxonomic units identified. This level of aggregation is directly related to EC. Second, from this and other loop modeling results, a minimum of 8-10 loop models are needed to prepare an ES, and ESs have been similar in their three tiered lattice structures across all marine environments studied to date. Third, link type and loop frequencies have been fairly constant over several marine ecosystems (field and laboratory). Fourth, the levels of connectivity and connectance have also been similar with the exception that the MERL tanks have more connected food webs than many field communities because of strong pelagic benthic coupling. Fifth, the micro universes are also of similar magnitudes for different environments. It is these features and measures taken together that constitute a 'just right' level of EC for marine plankton communities. This level is manageable with today's computers, at least barely so, but there is much more complication occurring in nature than is usually acknowledged. It is also clear that simple descriptive food web models, on a species by species basis, with one type of link, no self damping, randomly generated , not biologically reasonable, without functional understanding of the feedback relationships and operating pathways, or combinations of these features, are probably not going to provide much insight into the 'just right' level of EC.

There is still a considerable amount of work to do in regard in applying loop analysis in similar food web applications. First, it would be useful to have a way to determine if the loop models pictured here are the best that could be produced and are they the only ones that yield the associated levels of prediction accuracy. This has been called the 'uniqueness problem' (Lane 1986a). Second, if variables and links are not independent of each other as the micro universes have been calculated, then it would be possible to reduce the size of these sets of food webs substantially, which would be convenient. Third, the exact size and composition of both the micro and the meso universe need to be better measured in so far as possible, both empirically and theoretically. Fourth, it is possible that a realistic set of rules of construction could follow from this work and be useful. Fifth, the community of microorganisms and the community of large fish and other predators need to be analyzed using these methods so that a more complete understanding of complete marine food webs could be realized.

4.0 Conclusions: A Cautionary Tale

How should ecologists determine the 'just right' level of EC? The 'trial and error' approaches favored by Goldilocks are not going to work, although many have opted for this method by using a few species in the field or laboratory and attempting to extrapolate iteratively to the whole while obliterating the key links with other ecosystem components as if they were optional. They are not. Constructing small intuitive networks is also problematic given that there are large numbers of these systems in the micro universe. Others have reduced systems to the type of matter constituting their components. A list of chemical ingredients is not helpful for understanding whole food web properties like EC.   We need good simplification, but without the pitfalls of arbitrary bottom up extrapolation or top down destructive reduction. Loop analysis is a useful tool for simplifying middle number systems at the 'just right' level of EC. The technique can also measure a large number of aspects not only of system structure, but also function. Do the 117 models described here give a complete description of MERLs ecosystems: of course not, but they do improve understanding of EC in a biologically reasonable and realistic way that is useful. All ecologists working with food webs, deal with similar amounts of EC.

Why does understanding the 'just right' level of EC matter? Futurists predict that our species will suffer increasing levels of existential risk in the coming decades (Bostrom, 2002, 2013; Martin, 2006) from a variety of planetary hazards and extraterrestrial disasters not least of which is the largely human-induced destruction of our only habitat through the cumulative effects of biodiversity loss, climate change, pollution, eutrophication, acidification, habitat fragmentation, etc. Some have concluded that it is an open question whether the human species will successfully transit the 21st Century, or perhaps the 22nd (Bostrom, 2002, 2013).

Consider just one of these existential risks: biodiversity loss. The Earth is presently undergoing the sixth mass extinction. Weinberg (2001) concluded that "science is the study of those things that can be reduced to the study of other things. Science, in other words, is essentially reductionist." Ecologists have been too blasé while muddling along with reductionism. A reductionist strategy of saving one species at a time is at best inadequate, and at the worst, harmful. There continues to be many extinctions of anonymous species never named and never mourned.   It is difficult to save what is not even comprehended.   We do not even know how much biodiversity is needed for our own survival, but clearly we will not survive alone.

Goldsmith (2002) asked "what happened to ecology?" and then observed how convenient it has been to wed reductionism with neoclassical economics. How well the individualistic concept of community structure, advanced by Henry Gleason (1917, 1926) almost a century ago, has served our socioeconomic interests throughout the 20th Century to the present. If ecosystems are only random assemblages of species each seeking their 'just right' set of conditions for survival and reproduction, than plowing down a little more forest to make another subdivision or highway is not a felony crime, only a small misdemeanor like a speeding ticket. When there is nothing special about a particular natural community and we believe it can be reproduced elsewhere when the same set of environmental conditions are present, then the overall damage is less consequential; and we can permit ourselves to be complacent about

ecological destruction. But if ecosystems have emergent properties arising from their complexity at a whole system level, then destroying them capriciously as we have in the last centuries is a much higher risk activity, and perhaps, the ultimate existential risk. Whereas the measures of EC for marine food webs given here are not equivalent to complexity per se, they do give us more insight into how these food webs work.

We need to manage ecosystems holistically on an urgent basis. We need to understand ecosystem structure and function at the appropriate level of complication, not a compromised and reduced level that although expedient, is inadequate. Key to this understanding is identifying the 'just right' level of complication that shapes ecosystem integrity and food web dynamics while ensuring a sufficient basis for biodiversity to flourish. The results presented here also constitute a cautionary tale not just for ecologists, but for everyone. Although Goldilocks unwittingly placed herself in danger in searching for her 'just right' level of comfort, her story had a happy ending.   We have even more at stake, and a happy ending is anything but assured (Bostrom, 2002, 2013).

5.0 Acknowledgments

6.0 References

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