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ARTIFACTS OR ATTRIBUTES? EFFECTS OF RESOLUTION ON THE LITTLE ROCK LAKE FOOD WEB[1]

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Abstract. A detailed and relatively evenly resolved food web of Little Rock Lake, Wisconsin, was constructed to evaluate the sensitivity of food-web patterns to the level of detail (degree of resolution) in food-web data. This study presents definitions (e.g., ecosystem food webs) and methods for constructing and reducing the resolution of food webs to provide relatively pragmatic and rigorous touchstones for consistency in future food-web studies. This analysis suggests that food-web patterns such as the scale-invariant links-per-species ratio, short chain lengths, and limited number of trophic levels are constrained by the resolution of food-web data rather than by ecological factors. Patterns less sensitive to changes in resolution such as directed connectance (the proportion of observed directed links to all possible directed links) may be robust food-web attributes.

The food web of Little Rock Lake appears to be the first highly and evenly resolved food web of a large natural ecosystem originally documented for the purpose of examining quantitative food-web patterns. This ecosystem food web contains roughly twice as many species as the largest web to date. It also may provide the most credible portrait available of the detailed trophic structure of a whole ecosystem. The 93-trophic-species web of Little Rock Lake differs from previously published trophic-species webs by having more links per species ($L/S = 11$), longer chain lengths (average: ≥ 10, maximum: ≥ 16), species at higher trophic levels (maximum: = 12), higher fractions of intermediate species, and smaller fractions of top species and links to top species.

The sensitivity of quantitative food-web patterns to changes in resolution was examined in several series of trophically aggregated Little Rock Lake webs. Each of the series starts with a highly and relatively evenly resolved web with 182 consumer, producer, and decomposer taxa and ends with low-resolution webs with 9 aggregates of taxa. Taxa were aggregated based on the proportion of predators and prey shared by the taxa. Different series of webs were generated using different criteria for linking aggregates to evaluate the sensitivity of food-web patterns to linkage criteria.

The sensitivity analysis revealed that several, but not all, quantitative food-web patterns are very sensitive to systematic aggregation of the web. Sensitive patterns include number of links per species, linkage complexity, the distributions of chain lengths and species among trophic levels, and the proportions of top species and links to top species. Less-sensitive patterns include connectance, the ratio of predators to prey, the proportions of intermediate and basal species, and the proportions of links that are between intermediate and basal species. Directed connectance is the only pattern examined that is both very robust to trophic aggregation and generally comparable to other community webs. Quantitative food-web patterns in published community webs are generally similar to highly aggregated Little Rock Lake webs (versions with 9–40 aggregates). These findings suggest that previously described community food webs are severely aggregated versions of more elaborate webs similar to that of Little Rock Lake.

Key words: aggregation; community food web; connectance; ecosystem food web; food chains; food webs; linkage criteria; Little Rock Lake; quantitative food-web patterns; resolution; trophic levels; Wisconsin.

INTRODUCTION

Quantitative patterns in food webs have been the subject of controversy for several years. To some ecologists the patterns are considered remarkable regularities in ecosystem structure (e.g., May, 1983*a*, Briand and Cohen 1984, Holling 1986). To others the patterns do not deserve interpretation (Paine 1983). Critics of the data argue that "artistic convenience" (Paine 1988), "the workings of the human mind" (May 1988), and cultural differences among sub-disciplines of ecology (e.g., terrestrial vs. aquatic ecologists, May 1983*a*) may be responsible for certain patterns. Interpreters with more confidence in the data argue that ecological phenomena such as environmental variability (Briand

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1983*a*), dynamics (Pimm 1982), energetics (Yodzis 1981, 1984), and ecosystem type (Briand 1983*b*, 1985, Briand and Cohen 1987) constrain food-web structure. Here I argue that most published food-web patterns appear to be artifacts of poorly resolved data. Still, quantitative food-web study is warranted by the possibility that more directly and objectively compiled, evenly resolved data may point toward robust food-web attributes. The discovery of such attributes may lead to new insights (Cohen 1989*a*) and predictive power in ecology (Martinez 1988, Peters 1988).

Conclusions from food-web analyses have been much discussed (DeAngelis et al. 1983, May 1983*a*, Strong 1988, Lawton 1989, Roughgarden et al. 1989) and structural food-web studies represent an active area of theoretical ecology. An attractive aspect of this work is the capability to compare quantitatively whole communities and ecosystems (Cohen 1989*a*). Such comparisons may delineate constraints and similarities in all ecosystems (Cohen 1978, Pimm 1982, Sugihara 1983, Briand and Cohen 1984, Cohen and Briand 1984, Cohen and Newman 1985, Cohen et al. 1985) and also in certain types of ecosystems (Briand 1983*a, b*, 1985, Briand and Cohen 1987). Several excellent papers summarizing food-web controversies have been published recently (Strong 1988, Lawton 1989).

Most food-web patterns are based on analyses of poorly resolved webs (Paine 1988, Lawton 1989), with an average of ≈20 species or less (e.g., Rejmánek and Starý 1979, Pimm 1982, Cohen and Briand 1987, Sugihara et al. 1989). This analysis complements the others by thoroughly documenting and examining a highly resolved and relatively complete web (relative to previously reported webs) to indicate likely strengths and weaknesses of the previous data and analyses. To do this, I systematically aggregated the food web of Little Rock Lake to investigate resolution-related problems with several statistics commonly used to describe and theorize about food webs. My purpose was to illuminate which food-web patterns may represent meaningful attributes of ecosystems and which patterns are likely to be artifacts of the coarse resolution of present data (Martinez 1988, *in press*, Sugihara et al. 1989). Given the scale-related difficulties with food-web data (May 1983*a, b*, Paine 1983, 1988, Cohen and Newman 1988), patterns very sensitive to changes in resolution are less likely to be fertile ground for discussion and theory. A recent study (Sugihara et al. 1989) using aggregation algorithms practically identical to those developed for this and earlier work (Martinez 1988) concludes that several patterns are relatively unaffected by varying data resolution. Substantially different conclusions are reached here and elsewhere (Martinez 1988, *in press*).

One serious problem with describing webs is deciding how many and which groups of organisms should be included for the web to meaningfully represent a community's trophic structure. Another problem is deciding how much trophic interaction warrants designating a link between two groups of organisms. The latter problem, which may be the most difficult, includes the question of which criteria should be used to measure strength of interaction. Absolute and relative quantities of trophic flow in terms of energy and individuals are possibilities (Odum 1971, Baird and Ulanowicz 1989). The degree of trophically mediated community-level effects of removing a species is another possible criterion (Paine 1980), as is the degree of selectivity and preference for prey by predators (Lawlor 1980). This analysis addresses the importance of these problems by varying the number of species and the criteria for linking species.

Several authors (e.g., Auerbach 1984, Paine 1988) informally discuss some of these difficulties. This monograph reports the results of the first formal analysis of food-web statistics (Martinez 1988) that directly addresses several common criticisms of connectance-based food-web studies (May 1983*a, b*, Paine 1983, 1988, Auerbach 1984, Peters 1988, Lawton 1989). To my knowledge, the food web analyzed here is the first to be originally collected to equitably describe all trophic interactions of all trophic groups (consumers, producers, decomposers) in a natural ecosystem (Martinez 1988). By "equitable" I mean that a large amount of effort went into including all species and their trophic relations irrespective of each species' trophic group. Additionally, spatial and temporal scale and criteria for designating linkages are explicitly defined, and the data are not confounded by "artistic convenience" (Paine 1988) because no diagram has been drawn of the web.

METHODS

Data collection and description

Little Rock Lake is a small (area: 18 ha, maximum depth: 10.3 m, average depth: 3.5 m), two-basin, mesotrophic lake in northern Wisconsin. In 1984 the lake's two basins were separated to conduct a 6-yr experimental acidification of the north basin as part of the United Stated National Acid Precipitation Assessment Program (Brezonik et al. 1986, Watras and Frost 1989). There were 15 investigators studying the effects of acidification on the lake. Several investigations within Little Rock Lake concern trophic interactions, energy flows, population ecology, and community ecology.

The first step in data collection was to assemble the most complete list of taxa in Little Rock Lake that was available. Then the field ecologists mentioned below designated the diets and predators of the taxa on which they specialized. Only organisms that spend virtually all the specified life stage at or below the lake's surface are included in the web (Appendix I). Taxa are given the most precise taxonomic label provided by the collaborating investigator. A link is assigned between taxon "A" and taxon "B" whenever an investigator believes that "A" is likely to eat "B" during a typical year. This criterion was explicitly stated throughout construction of the web. Different criteria probably would result in different links being designated.

Most vertebrates and zooplankton are resolved to the species level. Some vertebrate and zooplankton biological species are divided further into functionally different "trophic taxa." For example, yellow perch is separated into a taxon called young-of-year and a taxon called year-plus because the life-history stages have different sets of predators and prey. Fish eggs are considered a taxon that includes the eggs of all fishes. Additionally, there are many species of juvenile zooplankton that are grouped into a taxon. For example, several juvenile copepod species are in the taxon called nauplii. Many taxa of phytoplankton and benthic species are resolved only to genera and sometimes only to family. All organisms in a taxon are assumed to have identical sets of predators and prey for this analysis.

To describe the Little Rock Lake food web, I consulted investigators of Little Rock Lake. In the spring of 1985 I met with P. Garrison (Wisconsin Department of Natural Resources–Madison), T. Kratz (Northern Lakes Long Term Ecological Research Site, University of Wisconsin–Madison), J. J. Magnuson (Center for Limnology, University of Wisconsin–Madison), M. Sierszen (Center for Limnology, University of Wisconsin–Madison), and K. Webster (Wisconsin Department of Natural Resources–Madison). The food web documented in that meeting was refined further by inclusion of fish gut content data from W. A. Swenson and M. S. Kruse (University of Wisconsin–Superior, see Swenson et al. 1986), literature searches, and further consultation.

J. J. Magnuson (*personal communication*), W. A. Swenson (Swenson et al. 1986), and M. S. Kruse (*personal communication*) were primary sources of fish diet information. M. Sierszen (*personal communication*) provided pelagic zooplankton species designations as well as predation and diet information. Sierszen's dissertation topic includes the selective grazing by Little Rock Lake zooplankton (Sierszen 1988). K. Webster and P. Garrison (*personal communication*) provided benthic invertebrate species and diet designations. K. Webster and M. Butler of North Dakota State University (*personal communication*) provided benthic insect species, predation, and diet information. P. Garrison (*personal communication*) provided benthic crustacean information. K. Watras (Wisconsin Department of Natural Resources and Center for Limnology–Madison, *personal communication*) provided the phytoplankton data.

These definitions and procedures produced a food web of 182 taxa (Appendix II), most of which are genera of phytoplankton and benthic invertebrates (Appendix I). Field ecologists designated the prey and predators for 174 of the 182 taxa from their first-hand knowledge and familiarity with the literature concerning feeding habits and natural history. Additional consultation (P. Garrison, *personal communication*) and literature research for six benthic crustaceans were required before their diets could be designated. Their diets were designated as consisting of certain benthic diatoms, a filamentous algae, and fine organic matter, because these crustaceans were known to have scraping mouth parts and to be restricted to certain areas within Little Rock Lake.

Consultation with other field ecologists further refined the data. For instance, divers who located largemouth bass nests also observed yellow perch and largemouth bass raiding the nests of other fish and eating the young-of-year. Yellow perch were observed frequently sucking up benthic material and spitting out detritus (M. S. Kruse, *personal communication*). Gut content data demonstrated that yellow perch eat many benthic macroinvertebrates that were not originally designated prey of yellow perch. These feeding relationships were added to the food web. Another example of data used to refine the food web comes from field workers studying freshwater sponges in Little Rock Lake; they often observed Neuropteran sponge flies feeding on the sponges. Such rare or energetically minor relationships seem to be those most vulnerable to the data filtering that occurs before publication of most food-web data. Ignoring such rare and specialized feeding relationships would systematically distort food-web data.

Completeness of data

Because it is unlikely that any food-web data set will specify all organisms and their interactions, it is important to indicate the completeness of the species list on which a food web is based. With this information, the representative nature of the food web can be more clearly evaluated.

In the summer of 1986, I updated the Little Rock Lake list of taxa with additions and corrections. Inaccurate taxonomic labels in the 1985 list were corrected, but adding the new taxa to the food web was left as a future exercise. Due to the frequent sampling of Little Rock lake during 1985 and 1986, the taxa added to the list in 1986 mostly include rare, previously unidentified taxa. An exception is the macrophyte taxa. They were not included in the 1985 food web because an investigator familiar with the trophic relationships of Little Rock Lake macrophytes was not available. Yet, it appears that many trophic relations concerning the macrophytes involve the epiphytic filamentous algae that were included in the web.

Table 1 shows that the food web defined in 1985 and used in this analysis includes 70% of Little Rock Lake taxa identified in 1986. Most species in Little Rock Lake are probably benthic organisms such as micrometazoans and other microbes (Strayer 1986). Unfortunately these species are included in each year's list under the severely aggregated taxon called fine or-

TABLE 1. Comparison between the lists of taxa assembled in 1985 and in 1986.

Aggregate	Number of taxa identified 1985	1986
Fish	11	16
Zooplankton	47	66
Benthic macroinvertebrates	62	65
Fine organic matter	1	1
Algae	61	95
Macrophytes	0	17
Total	182	260

ganic matter. This complex group of organisms has been found to include >300 species in a small temperate lake in New Hampshire (Strayer 1985, 1986, Strayer and Likens 1986). Fine organic matter is considered a nonpredatory taxon that is the food source of all taxa that eat benthic organisms other than macroinvertebrates and listed crustaceans. Judging by the 1986 list, the food web includes most Little Rock Lake fishes, zooplankton, macroinvertebrate, and algae taxa. Though 30% of the taxa in the 1986 list were not included in the web, few of these additional taxa appear to have sets of predators and prey that differ significantly from those of taxa already in the web. This suggests that inclusion of the new taxa would primarily change the amount of trophic redundance in the web, but not significantly change the web's structure.

Definitions

Taxon is used here to refer to the finest level of taxonomic definition in the appendices and can be an arbitrary group of organisms (e.g., fine organic matter), a life-history stage of related organisms, a species, a genus, or a family. *Cluster* refers to one or more taxa that share some predators and/or prey. *Trophic species* refer to clusters containing all taxa with the exact same set of predators and prey (Briand and Cohen 1984). Taxa, clusters, and trophic species specify different aggregation levels of the more general term, *species*. *Top species* have prey but no predators while *basal species* have predators but no prey (Briand and Cohen 1984). *Intermediate species* have both prey and predators (Briand and Cohen 1984). The sum of top and intermediate species divided by the sum of intermediate and basal species is the *predator/prey* ratio. *Webs* refer to both community food webs (Cohen 1978) and Little Rock Lake ecosystem webs at various levels of resolution.

Food chains are directional paths of trophic energy or, equivalently, sequences of links that start with basal species, such as producers or fine organic matter, and end with consumer organisms. *Links* are trophic interactions directed from prey to predator. Chain length is measured by the number of links in the sequence from producers or fine organic matter to a consumer. A web's *average chain length* is the average number of links in every chain connecting all consumers to basal species. The difference between this average chain length and the more conventional mean length of chains to top species (Briand and Cohen 1987, Sugihara et al. 1989) is discussed later (see *Discussion: Chain length*). *Loops* are food chains that include the same species twice.

Methods of aggregation

To aggregate the taxa in the raw food web (Appendix II), the taxa are hierarchically clustered based on the amount of trophic overlap between taxa. A trophic overlap similarity index (I) between every pair of taxa is calculated using an algorithm defined by Jaccard (1908):

$$I = c/(a+b+c)$$

where c = number of predators and prey common to the two taxa, a = number of predators and prey unique to one taxon, and b = number of predators and prey unique to the other taxon. When the two taxa have the same set of predators and prey, $I = 1$. When the two taxa have no common predators or common prey, $I = 0$.

An agglomerative, hierarchical, cluster analysis (SPSS 1988) used the similarity indices (I) as a proximity measure to sequentially group the most similar taxa into clusters. Initially all taxa were considered separate clusters. Then the procedure grouped trophically equivalent (Sugihara 1983) clusters into trophic species (Briand and Cohen 1984), i.e., clusters containing similarity indices equal to 1.0. The web in which all trophically equivalent taxa were clustered into trophic species is called the trophic-species web. After all trophically equivalent taxa were clustered into trophic species, clusters with the largest average of similarity indices between cluster members were grouped.

The average-linkage method (not to be confused with the "average-linkage criterion"—see *Methods: Methods of assigning linkages*, below) was used to calculate the similarity of clusters. This method measures the similarity between two clusters as the average of similarity indices between every member within the first cluster and every member within the second cluster. This average of the similarity indices is called the "coefficient of similarity" (SPSS 1988).

From the sequential clustering results, several series of sequentially aggregated food webs with progressively fewer species were generated. I wrote a computer program that uses the clustering sequence to create food webs with the same number of species (clusters of taxa) as exists at each stage of the cluster analysis. At each stage, two clusters were combined into a new cluster. Links were assigned between the new cluster formed at each stage and all other clusters based on the predators and prey of the new cluster's members.

Methods of assigning linkages

Several linkage criteria were employed to assign links between clusters. Employing the minimum-linkage criterion creates minimally connected webs. The maximum-linkage criterion creates maximally connected webs. Intermediate criteria span the middle ground, thereby allowing an analysis of the sensitivity of food-web statistics to linkage criteria. These linkage criteria span about the largest possible range of connectedness during systematic food-web aggregation.

To generate minimum-linkage webs, the minimum-linkage criterion requires every member within a cluster to be linked to every member of another cluster in order for the clusters to be linked. To generate maximum-linkage webs, the maximum-linkage criterion requires only that at least one member within a cluster be linked to at least one member of the other cluster in order for the clusters to be linked. Aggregated webs were also generated using the average-linkage criterion. This criterion requires that there be at least half the number of links between two clusters as are required by the minimum-linkage criteria in order for the clusters to be linked. Intermediate criteria halfway between minimum and average and halfway between average and maximum were also employed to create aggregated webs. These intermediate criteria, respectively, require at least 25% and 75% of the number of links between two clusters as are required by the minimum-linkage criteria.

Methods of calculating "species"

The term "species" as used in food-web studies usually refers to a group of organisms with generally or exactly similar sets of predators and prey. *Species,* as used in this analysis, refers to the clusters within each version of the Little Rock Lake web. The number of species is the same as the number of clusters at each stage of aggregation. When used to compare statistics from other food-web studies, species also refers to species as used in those studies.

Following convention (Cohen 1978, Briand 1983*a*), trophically disconnected species, i.e., species with neither predators nor prey, were excluded from calculations of food-web statistics. This exclusion simplifies gathering food webs from studies that list many organisms but only describe the trophic habits of a few. Disconnected species are also excluded from the original food web with 182 taxa (e.g., aquatic macrophytes). Sometimes several clusters with few links are trophically disconnected by the aggregation procedure. This happens when fewer members of a cluster than the linkage criterion requires share any predator or prey.

Connectedness calculations

Connectedness is a general term describing the degree to which components of a system are affected by each other (Allen and Starr 1982). Three aspects of connectedness have been described: *connectance* refers to the proportion of all possible interactions within a system that are realized (Gardner and Ashby 1970); *connectivity* refers to the number of interactions per component of a system (Levins 1974, Allen and Starr 1982); *interaction strength* (Paine 1980) refers to the intensity rather than the quantity of interactions. If either connectance, connectivity, or interaction strength increases while the others remain constant, connectedness increases (Allen and Starr 1982). Only connectance and connectivity statistics are directly examined in this study. Investigations of interaction strength require data different from those collected here (Paine 1980).

Within food-web studies there are two prevalent connectance statistics: interactive connectance and upper connectance. "Interactive connectance" (Briand 1983*a*), also called "lower connectance" (Yodzis 1980), refers to the proportion of all possible undirected, interspecific, trophic interactions that are realized. "Upper connectance" (Yodzis 1980) refers to the proportion of all possible interspecific trophic interactions plus competitive interactions. These competitive interactions are assumed to exist between predators that share at least one prey. Besides these two connectance statistics, I have calculated a third, called "directed connectance," described below. Connectivity has two associated statistics used in the literature: links per species (Briand and Cohen 1984), and linkage complexity (Briand 1985) or $S \cdot C$ (S·Connectance, May 1972, 1974).

To calculate *interactive connectance,* I took the square, directed food-web matrix in which non-zero elements (a_{ij}) indicate that the species referred to by the column number (j) preys upon the species referred to by the row number (i), and made the matrix symmetrical by setting the corresponding a_{ij}s equal to the non-zero a_{ji}s. This removes the information describing the feeding direction from the directed food-web matrix. Then the diagonal elements were set to zero to eliminate interactions representing cannibalism from the calculation. The new total number of non-zero a_{ij}s (A_i) was then used to calculate interactive connectance with the following algorithm:

$$\text{Interactive Connectance} = A_i/[\text{species}(\text{species} - 1)].$$

This algorithm for calculating interactive connectance avoids the common mistake of double-counting "mutual predation links" (species A preys on species B and species B preys on species A, Polis 1991) and "cannibalism links" that may occur when the conventional interactive connectance algorithm (links/[{species(species − 1)}/2], Paine 1988, Cohen and Newman 1988) is used. Such mutual predation loops and cannibalism are common in the Little Rock Lake webs and in several other directly documented webs (Sprules and Bowerman 1988, Warren 1989, Winemiller 1990, Polis 1991).

Upper connectance (Yodzis 1980, Briand 1983*a*, 1985) measures interspecific food-web complexity, which includes competitive interactions. It is calculated by assigning non-zero values to elements (a_{ij}) representing competitive interactions between predator "j" and predator "i" if they share any prey to the interactive connectance matrix. Upper connectance also excludes diagonal elements to maintain its interspecific focus. The new number of non-zero elements (A_u) is used to calculate upper connectance as follows:

$$\text{Upper Connectance} = A_u/[\text{species}(\text{species} - 1)].$$

Directed connectance is the proportion of documented directed links out of the maximum number of possible directed links in the food web, including cannibalism and mutual predation. Diagonal elements represent the existence of cannibalism within a species. Cannibalism is an important aspect of food-web structure (Polis 1981, Sprules and Bowerman 1988) which, in the interest of consistency and realism, I have decided not to ignore. Accordingly I use the following algorithm:

$$\text{Directed Connectance} = \text{links}/(\text{species})^2.$$

The number of trophic links divided by the number of species in a web is the links per species ratio. Links per species designates the average number of predators of each species. The average number of predators per species equals the average number of prey per species. Upper connectance multiplied by the number of species is referred to as linkage complexity and $S \cdot C$ (Briand 1985). Linkage complexity multiplied by 2 describes the average number of undirected trophic and competitive interactions per species in a web.

Chain calculations

A chain is a sequence of links that starts at a basal species and ends with a consumer species. All possible chains to all consumer species were calculated. Chains were calculated using two different algorithms to examine the effect of loop-forming species on chain lengths. One algorithm excludes chains through any organisms that prey on organisms later in the chain sequence. The other algorithm includes chains through organisms that prey on later organisms but excludes chains that include the same organism twice. An example of the first algorithm is: when chains to yellow perch are calculated, even though perch eat leeches, chains from basal species through leeches are excluded because leeches eat perch. The second algorithm includes chains that go through leeches to yellow perch, but not chains that go leeches-largemouth bass-leeches and then to yellow perch. Use of the second algorithm results in longer chain lengths only if there are loops in the web.

Using the first algorithm, each cluster within the average-linkage webs with 9–137 species is assigned a trophic level equal to the closest integer to the species' average chain length plus one. Using the second algorithm, each cluster within the minimum-linkage webs with 9–57 species is similarly assigned to a trophic level. Limited mainframe computer time prevented larger webs from being analyzed for chain lengths and trophic levels. A species' average chain length is the average number of links in all possible paths leading to the species from basal species. Therefore, species with no prey are assigned to the first trophic level.

Top, intermediate, and basal cluster and link calculations

Webs generated using the average, minimum, and maximum linkage criteria were analyzed for proportions of top, intermediate, and basal species (Briand and Cohen 1984). The same webs were analyzed for links between intermediate and top species (I-T links), basal and top species (B-T links), intermediate and intermediate (I-I links) species, and basal and intermediate (B-I links) species (Cohen and Briand 1984).

RESULTS

This section summarizes the results by first giving an overview of the clustering results and then describing the behavior of quantitative patterns in aggregated webs generated with different linkage criteria. Each criterion employed generates a series of webs having the same number of species as the number of clusters at each stage in the clustering sequence. Each series starts with the 182-species raw food web and ends with a highly aggregated web with 9 species. Close to the middle of these series is the trophic-species web. Trophic-species webs are conventionally considered a standard of comparison. The stages of aggregation between the raw food web and trophic-species web are described to illustrate effects of varying amounts of trophic redundance in webs.

All taxa with identical sets of predators and prey were clustered into trophic species in the first 89 stages of the cluster procedure (Fig. 1). These 89 stages reduced the 182 taxa in the original data to 93 trophic species. Trophically equivalent algae (basal species) were clustered in the first 53 stages, leaving 129 clusters or species. Trophically equivalent invertebrate taxa were clustered in the following 36 stages. None of the fish taxa were trophically equivalent. After all clusters with a coefficient of similarity of 0.100 or higher were aggregated, only nine clusters remained. The step-by-step sequence of cluster formation is described in my thesis (Martinez 1988), with the dendrogram describing the trophic similarity of the taxa.

I have followed the convention of graphically representing quantitative food-web patterns on the y axis vs. the number of species on the x axis except in Fig. 1 and the three-dimensional-surface graphs. The conventional left-to-right increase in number of species is also maintained, even though the aggregation sequence starts with many species and ends with few.

Connectedness results

The interactive connectance (which excludes competitive links, cannibalism, and mutual predation) of

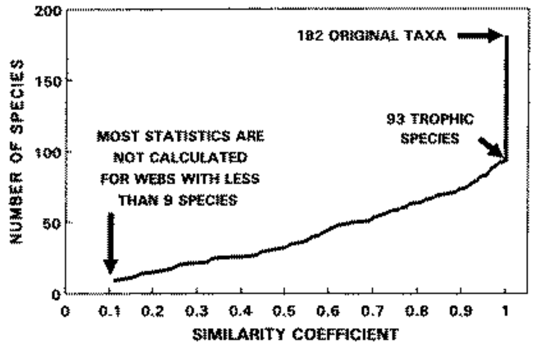

FIG. 1. The number of "species" delineated as a function of the minimum similarity coefficient among taxa within clusters (see *Methods: Definitions*) in the Little Rock Lake (Wisconsin) food web. As less trophic overlap is required for taxa to be within a cluster, fewer clusters or "species" are used to describe the web. Trophically equivalent taxa are aggregated into trophic species in the vertical portion of the curve at the 1.00 similarity coefficient.

aggregated webs initially increases during the clustering sequence, as trophically redundant algae (basal species) are lumped (Fig. 2a). Once all trophically equivalent taxa are lumped into 93 trophic species, interactive connectance is 0.220. Until this point, aggregated food webs with the same number of species and generated using different linkage criteria are equally connected. Different linkage criteria do not generate differently connected webs in this area because all the members of each cluster have identical predators and prey. To the left of the trophic species web, the connectedness of webs generated with different linkage criteria diverges.

The surface in Fig. 3a is abstracted from Fig. 2a to quantify the sensitivity of interactive connectance to aggregation and linkage criteria. The x axis of Fig. 2a is replaced in Fig. 3a by the similarity coefficients corresponding to the webs with 9 to 93 species. Remember that the similarity coefficients describe the minimum trophic overlap of members within a cluster (Fig. 1). This graphic replacement emphasis resolution between species, which might be generalized to other webs more persuasively than the number of species. In addition to the results from maximum-, average-, and minimum-linkage criteria, results from the intermediate criteria halfway between maximum and average, and between average and minimum, are included in Fig. 3a.

The variation of directed connectance is similar to, but less extreme than, the variation of interactive connectance (Figs. 2a and 3a). For all linkage criteria, directed connectance (Figs. 2b and 3b) remains within 10% of its value (0.120) within the trophic-species web in all webs aggregated to similarity coefficients within the range of 1.00 to 0.86 (Fig. 3b). In the maximum-linkage webs, directed connectance remains within 10% of 0.12 over the large interval between similarity coefficients 1.00 and 0.32. Overall, directed connectance remains within 10% of its value within the trophic species web over 48% of the area, including all linkage criteria and similarity coefficients between 1.00 and 0.10. Because there is a relatively large area of the surface (Fig. 3b) where directed connectance remains within 10% of 0.120, one can be fairly confident that

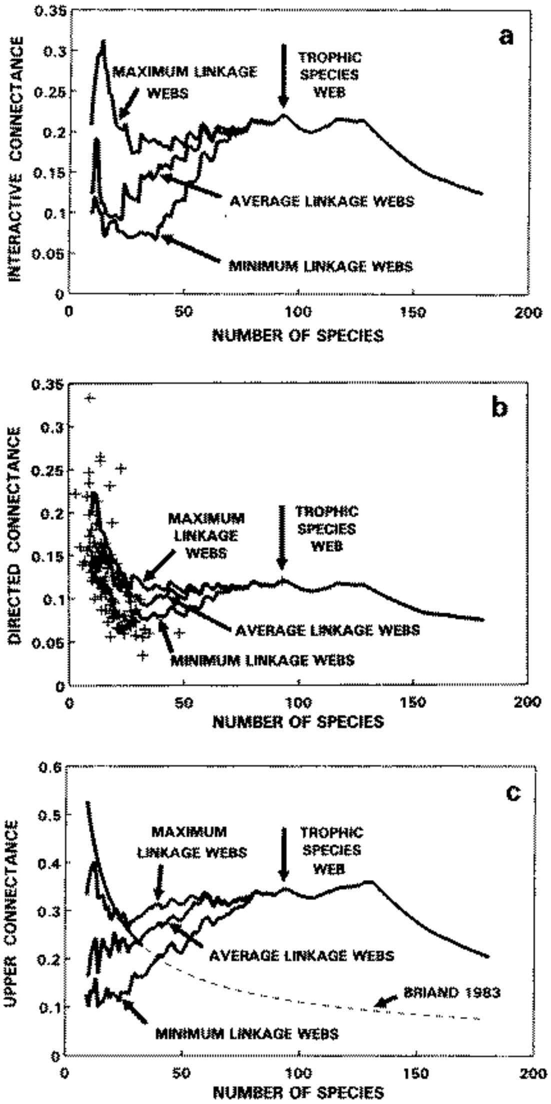

FIG. 2. Interactive (a), directed (b), and upper (c) connectance of aggregated webs, with 9 to 182 species, generated using the maximum-, average-, and minimum-linkage criteria. Trophic species are disaggregated into a set of trophically redundant species to the right of the trophic-species web. Trophic species are aggregated into trophically similar species to the left of the trophic-species web. These latter areas of these graphs are shown in more detail in Fig. 3. Other data points (+) in (b) show Briand and Cohen's (1987) 113 trophic species webs for comparison. The behavior of upper connectance (c) is compared with Briand's (1983) regression derived from 40 food webs in the literature; the dashed line represents Briand's regression extrapolated to webs with more species than in Briand's data.

the directed connectance of Little Rock Lake is between 0.10 and 0.15.

Upper connectance (Figs. 2c and 3c) is over triple the value of directed connectance and, along with interactive connectance, is about half as robust as directed connectance. Upper connectance and interactive connectance have generally similar patterns of variation during aggregation (Fig. 2a and c). Upper connectance stays within 10% of its value in the trophic-species web (0.390) over 25% of the area, including webs generated by all linkage criteria aggregated to similarity coefficients from 1.00 to 0.10 (Fig. 3c). This area and the comparable area of interactive connectance (Fig. 3a) is about half the area over which directed connectance stays robust during decreasing resolution (Fig. 3b).

The ratio of links per species increases and decreases before it equals 11 in the trophic-species web (Fig. 4a). After this point in the more aggregated webs, the links-per-species ratio decreases fairly consistently. Note that number of links per species varies over a wide range, from <1 to >14, with virtually no significant areas where the ratio remains within a narrow range. Linkage criteria affect links per species much less than does aggregation.

Linkage complexity varies more severely than, but analogously to, links per species before and after the trophic-species web. In other words, linkage complexity varies the most of any connectedness measure (Fig. 4b). Linkage complexity equals 36.3 in the trophically equivalent web, and varies between 54 and 1 among the webs analyzed. Similar to links per species, linkage criteria affect linkage complexity much less than does the degree of aggregation.

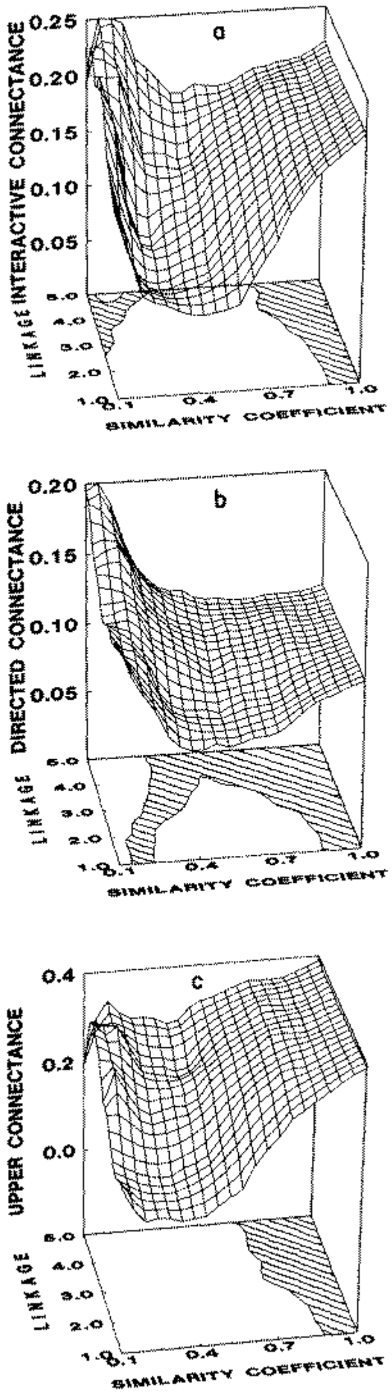

FIG. 3. Surface used for quantifying the robustness of interactive (a), directed (b) and upper (c) connectance. These surfaces reveal the sensitivity of connectance to the level of disaggregation determined by the similarity coefficient and linkage criteria employed to generate aggregated webs (1 to 5 = minimum- to maximum-linkage criteria). The hatched areas below the contour surfaces indicate where connectance remains within 10% of the connectance values in the trophic-species web—0.220 in (a), 0.120 in (b), 0.390 in (c); the hatched area covers 25% of the total possible area in (a), 48% in (b), and 25% in (c).

Food chain results

Chain distributions excluding chains containing loop-forming species were calculated for average linkage webs with 9 to 137 species (Fig. 5a). Chain distributions including chains containing loop-forming species were calculated for average linkage webs with 9 to 57 species (Fig. 5b). When loop-forming species are excluded from chain length calculations, maximal chain lengths of 11 are observed in webs with >72 species (Fig. 5a). When loop-forming species are included in chain length calculations, a maximal chain length of 17 is observed in the maximum linkage web with 53 species (Fig. 6a). The difference between average chain lengths including and excluding loop-forming species can be seen in Fig. 6b. The algorithm including loop-forming species calculates longer average (Fig. 6b) and maximal chain lengths (Figs. 6a and 5b vs. Fig. 5a). This difference illustrates both the effects of including loop-forming species in food chain calculations and that Little Rock Lake contains many loops such as mutual predation.

When chains containing loop-forming species are excluded, average chain lengths of webs with 9 to 93

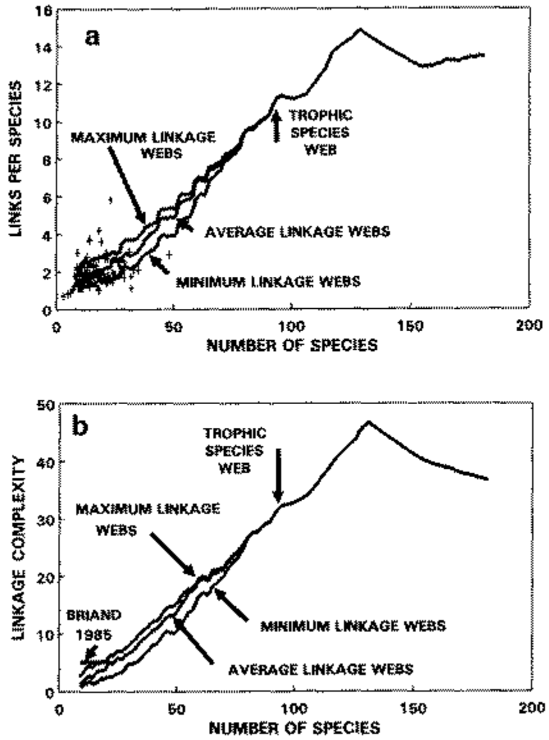

FIG. 4. The variation of links per species (L/S, a) and linkage complexity ($S \cdot C$, b) in aggregated webs with 9 to 181 species, generated using the maximum-, average-, and minimum-linkage criteria (lines). Links per species includes links representing cannibalism. Other points (+) in (a) show Briand and Cohen's (1987) 113 webs for comparison. In (b) Briand's (1985) average linkage complexity for 12 lake webs with 9 to 22 species is shown for comparison.

species vary from about 1 to 7 (Fig. 6c). Chain lengths become approximately normally distributed as the number of functionally different species increases (i.e., from 9 to 93 species, Fig. 5a). Average chain lengths increase much less in webs with increasing trophic redundance (93 to 137 species, Fig. 6c) compared to webs with increasing numbers of trophically distinct species (9 to 93 species, Fig. 6c). There is a much larger variance of average chain lengths between webs of different size than between minimally and maximally connected webs of the same size (Fig. 6b and c). When chains with loop-forming species are included, average chain lengths can vary between <2 and >10 in webs with fewer than 60 species (Fig. 6b). In the same webs, maximum chain length varies from 2 to 17 (Fig. 6a).

Like the distribution of chain lengths (Fig. 5a), the distribution of species among trophic levels is very sensitive to trophic aggregation beyond the trophic-species web (93 to 9 species, Fig. 7a), yet relatively insensitive to aggregation before the trophic-species web (137 to 93 species, Fig. 7a). Fig. 7a shows that, within webs analyzed with the first chain-length algorithm, the second trophic level consistently contains the most species, except in the coarsest webs with fewer than 12 species. The first and third levels are the next most populous levels, except in webs larger than ≈80 species, where a bimodal distribution is consistently observed. In these webs with >80 species the number of species at trophic level 5 gains over the number in trophic level 3. Overall, more species at higher trophic levels are observed in the less aggregated webs. Species at trophic levels 7 and 8 are observed in webs with >50 species. Several species at trophic level 9 are observed in webs with >90 species (Fig. 7a).

Similar, but more extreme, trends result from analyzing chains in average linkage webs including loop-forming species (Fig. 7b). The bimodal distribution of species among trophic levels is attained in webs with 23 species. Species at trophic levels 4 to 12 are observed in average linkage webs with 9 to 57 species, respectively.

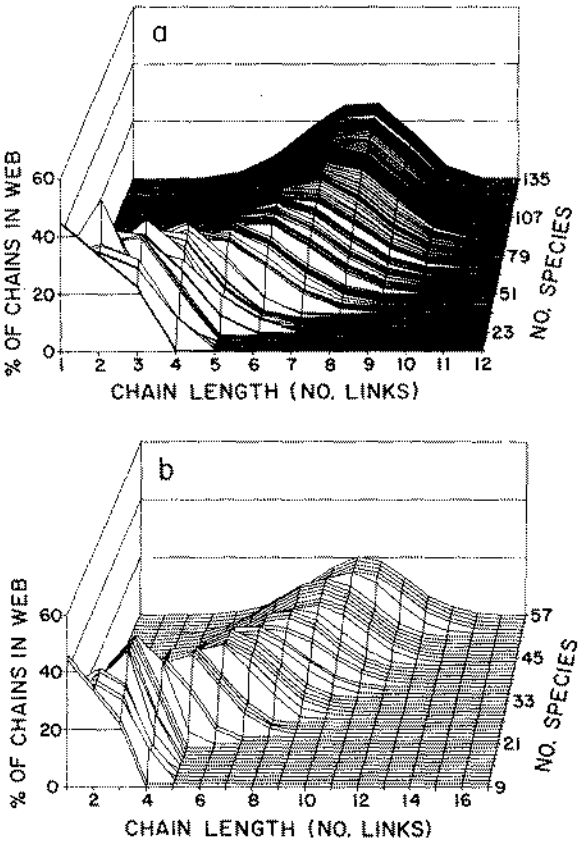

FIG. 5. Proportional distributions of chain lengths as a function of the number of species in average-linkage webs. In (a) chain lengths were calculated excluding chains with loop-forming species. Fig. 8a shows, for example, that ≈25% of all the chains in the 93-trophic-species web of Little Rock Lake are 7 links long and ≈45% of the chains in the 9-species web are of length 1. In (b) chain lengths were calculated including chains with loop-forming species. Note that maximum chain lengths of 15 are observed in (b) vs. the chains of length 10 in similarly sized webs observed in (a).

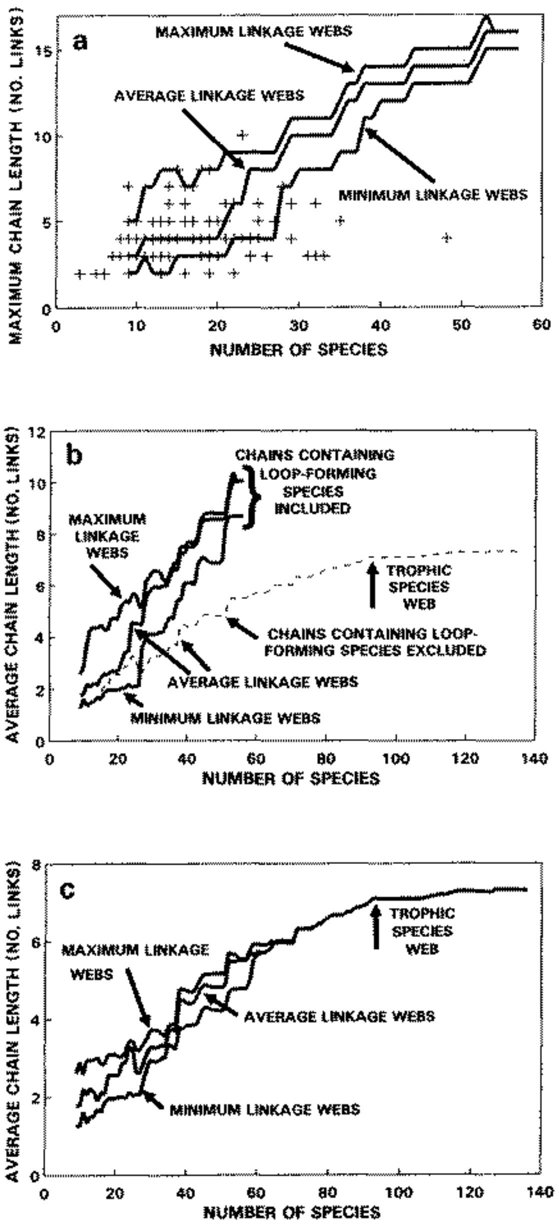

FIG. 6. (a) Maximum chain lengths observed in Little Rock Lake (Wisconsin) webs with 9 to 57 species. These chain lengths were analyzed including chains with loop-forming species. The maximum chain lengths observed in Briand and Cohen's (1987) 113 webs are shown (+) for comparison. (b) Comparison of average chain lengths analyzed using two different algorithms. Average-linkage webs with 9 to 137 species were analyzed excluding chains with loop-forming species (- - -). Webs with 9 to 57 species were analyzed including chains with loop-forming species (——). (c) Comparison of average chain lengths of maximum-, average-, and minimum-connectance webs from Little Rock Lake (Wisconsin) with 9 to 137 species. These chain lengths were calculated excluding chains with loop-forming species.

Proportions of top, intermediate, and basal species

In the trophic-species web of Little Rock Lake, the proportions of top, intermediate, and basal species equal 0.01, 0.86, and 0.13, respectively. The ratio of predators to prey is 0.88. These proportions, excepting that of top species, are relatively robust, and do not change much until the web is aggregated to <50 species (Figs. 8 and 9). The highest proportions of top and basal species are observed in webs with <35 species. The ranges of these proportions are affected by linkage criteria as well as by the number of species in the web.

The proportions of top species in webs generated using the maximum-, average- and minimum-linkage criteria are summarized in Fig. 8a. These proportions vary between 0.00 in the maximum-linkage webs with 9 to 24 species and 0.18 in the minimum-linkage web

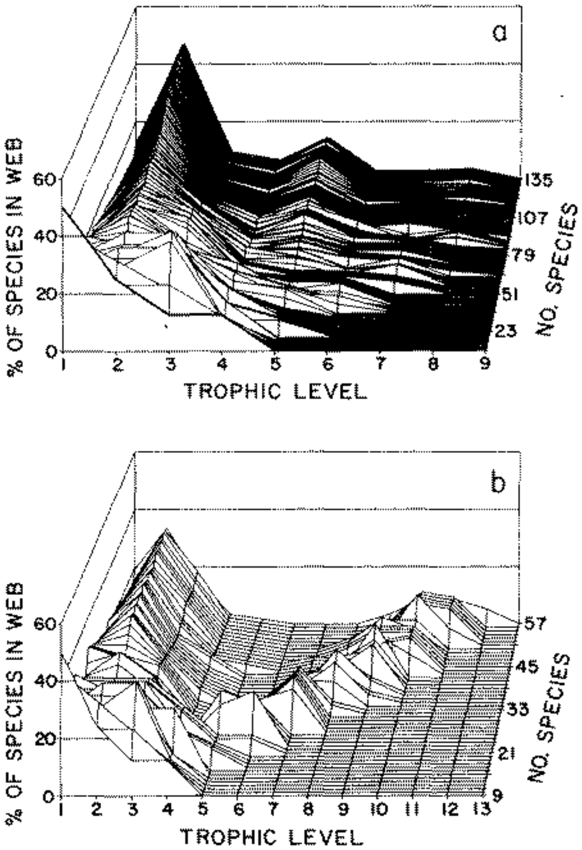

FIG. 7. Proportional distributions of species among trophic levels within average-linkage webs. Trophic levels in (a) were analyzed employing the chain length algorithm that excludes loop-forming species. This graph shows, for example, that the proportions of species at trophic level 2 vary between 25% in the smallest web to <50% in the largest web. The distribution of species among trophic levels does not vary much in webs with >93 species. In (b), trophic levels were analyzed employing the chain length algorithm that includes loop-forming species. Both graphs (a) and (b) show that larger webs have species at higher trophic levels.

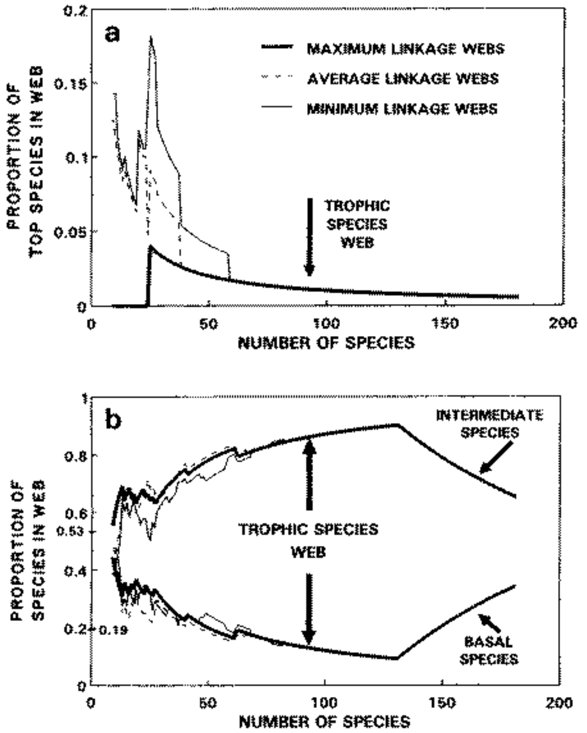

FIG. 8. Proportions of top species (a) and intermediate and basal species (b) in aggregated webs generated using the minimum-, average-, and maximum-linkage criteria. The key in (a) also applies to (b). In the 93-trophic-species web, 0.86 and 0.13 of the species are intermediate and basal species, respectively. For comparison, the "scale-invariant" proportions of 0.29 top species, 0.53 intermediate species, and 0.19 basal species in 62 community webs have been reported (Briand and Cohen 1984).

with 25 species. Most webs have only one top species, a filter-feeding bivalve (Appendix I: species 112) with no reported predators (Appendix II). In the webs with <25 species, the bivalve is lumped with three filter-feeding sponges (Appendix I: species 119–121, Martinez 1988), which are preyed upon by Neuropteran sponge flies and the chironomid *Stenochironomus* (Appendix II). Since three of the four members of this cluster have the same predators, the cluster is an intermediate species in the average- and maximum-linkage webs and a top species in the minimum-linkage web. This effect of the minimum-linkage criterion eliminating predation links of a newly formed aggregate causes the minimum-linkage webs to possess the largest proportions of top species. The proportions of top species above 0.01 are an artifact of the linkage criteria and aggregation procedure rather than an observed property of the Little Rock Lake food web.

Fig. 8b summarizes the proportions of intermediate species in aggregated webs, which vary from 0.90 to 0.38. The high variability of this proportion in highly aggregated webs reflects the high variability of the proportion of top species in the same webs (Fig. 8a). Fig. 8b also summarizes the variation of the proportions of basal species in all the webs generated by the maximum, average, and minimum linkage criteria. The proportion of basal species initially declines from 0.34 in the raw food web to 0.09 when all the algae are aggregated into trophic species and intermediate and top taxa are not yet aggregated into trophic species. Once all taxa are aggregated into trophic species, 0.13 of the species are basal species. This proportion rises to 0.50 in most aggregated webs. Aggregating beyond the trophic-species stage generally increases the proportion of basal species.

Fig. 9 shows that the ratio of predators to prey increases from 0.66 in the raw food web to a maximum of 0.92 as the phytoplankton are aggregated. As trophically higher organisms are then clustered, this ratio then declines to 0.88 in the trophic-species web. Fig. 10 demonstrates that the predators to prey ratio [(top + intermediate species)/(intermediate + basal species)] stays remarkably robust to decreasing resolution, especially beyond the trophic-species web. Indeed, the 68% of the area in which predators/prey retains its trophic-species value suggests that predators/prey is the most robust pattern examined. This robustness is largely due to the fact that the proportions of top and basal species both increase with aggregation. This complementary change of these distinct portions of the numerator and denominator of predators/prey allows this ratio to retain its trophic-species value over a wide range of differently resolved data.

Proportions of links

Fig. 11a describes the effects of aggregation on the proportions of links to top species [intermediate-top (I-T) links plus basal-top (B-T) links]. There are no I-T links and only one B-T link in the trophic-species web, accounting for 0.001 of the links. This one link exists between the one top species in the web, the freshwater bivalve, and the fine organic matter it filter feeds upon.

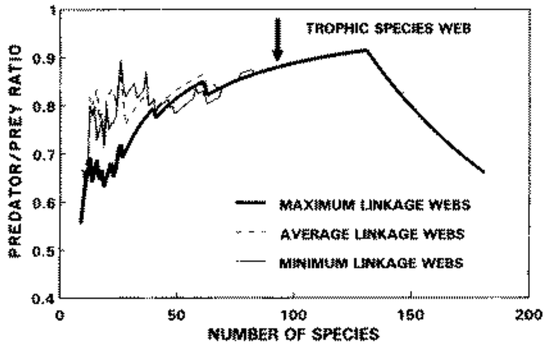

FIG. 9. Ratios of predators to prey in aggregated webs generated using the minimum-, average-, and maximum-linkage criteria. For comparison, the scale-invariant ratio of 1.13 predators to each prey in 62 community webs has been reported (Briand and Cohen 1984).

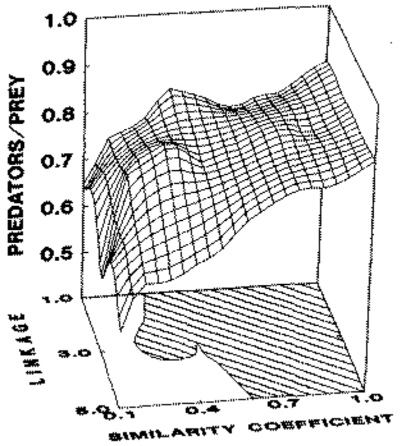

FIG. 10. Surface used for quantifying the robustness of the ratio of predators to prey. The surface describes the sensitivity of predators:prey to similarity coefficient and linkage criteria. The similarity coefficients correspond to the range of webs with 9 to 93 species. Only results from webs aggregated using the minimum (1), average (3), and maximum (5) linkage criteria (described in *Methods: Methods of assigning linkages*) are used to generate this surface. The hatched area below the contour surface indicates where directed connectance remains within 10% of its value in the trophic-species web (0.88); the hatched area covers 68% of the total possible area.

Fig. 11b describes the effects of aggregation on the proportions of intermediate-intermediate (I-I) links and basal-intermediate (B-I) links in aggregated webs generated using the minimum-, average-, and maximum-linkage criteria. With increased aggregation beyond the trophic species web, Fig. 11b shows a systematic decrease in the proportion of I-I links and a systematic increase in the proportion of B-I links. In the trophic-species web, 0.91 of the links are I-I links and 0.09 of the links are B-I links. The proporton of I-I links varies from 0.42 in highly aggregated minimum-linkage webs to 0.93 in webs with 130 species. The proportion of B-I links varies from 0.44 in minimum-linkage webs with ≈15 species to 0.07 in webs with 130 species. The higher proportions of B-I links can be seen in webs with <35 species. This range is also where the lowest proportions of I-I links are found. Highly aggregated minimum-linkage webs have the larger proportions of B-I links and smaller proportions of I-I links because taxa contained in several intermediate species in the average- and maximum-linkage webs have no prey in common. Therefore these species are considered basal species in the minimum-linkage webs. These high proportions of basal species and low proportions of intermediate species are artifacts of aggregation and linkage criteria.

DISCUSSION

Comparing webs

Variable aggregation and incompleteness of webs confound comparison of webs (May 1983*a*, Martinez 1988, Paine 1988, Lawton 1989). Perhaps the only generally employed standards that ease this problem are the community web (Cohen 1978) and trophic species definitions. The less rigorous standard, a *community food web,* simply includes all linkages among species that inhabit the same community (May 1983*a*). The more rigorous and easily employed standard, trophic species, downplays the taxonomic detail of webs and focuses on functional aspects of webs by "lumping" all organisms in a web that share the same set of predators and prey (Briand and Cohen 1984). Most reported patterns are based on community webs containing only trophic species. Since all linkages and species in a community may never be reliably determined, we are limited to definitions of linkages and co-occurring species that are often unstated and that currently differ substantially between studies.

It will be a continuing challenge to standardize documentation of webs so that patterns can more reliably be attributed to the web rather than to idiosyncrasies of data collection (Paine 1988, Peters 1988). An objective of this study is to contribute to such standard-

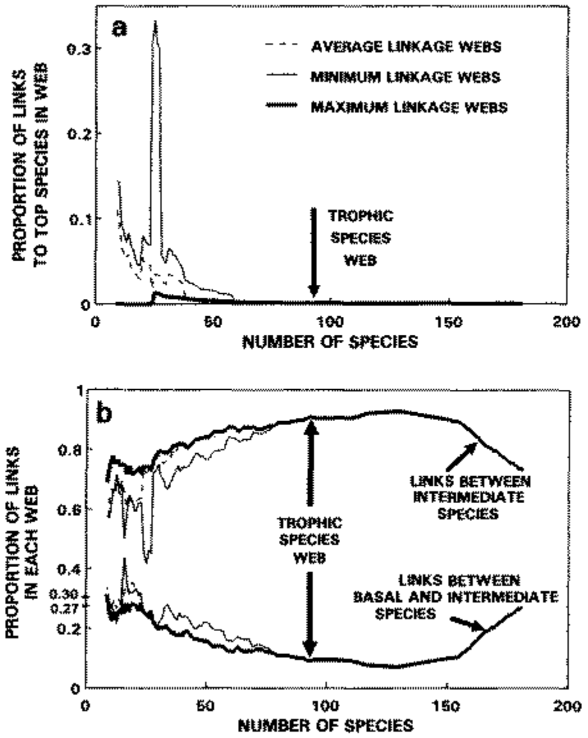

FIG. 11. Proportion of links to top species [basal–intermediate (B-I) links plus intermediate–top (I-T) links, a], and B-I and I-I links (b). The key in (a) also applies to (b). Only the most aggregated average- and maximum-linkage webs have significant proportions of links to top species. The trophic species web has 0.09 and 0.91 B-I and I-I links respectively. Previously reported scale-invariant proportions of 0.27 B-I links and 0.30 I-I links (Cohen and Briand 1984) are indicated on the *y* axis in (b) for comparison. The previously reported scale-invariant proportion of 0.43 links to top species (Cohen and Briand 1984) is off the *y* scale of part (a).

ization. While the web described here perfectly coincides with the definition of community webs (Cohen 1978), this web goes further by including all links among many co-occurring species from all trophic groups. Criteria for establishing links are explicitly defined and implemented during the original data documentation. I emphasize all trophic groups (producers, consumers, and decomposers) to address energy considerations of chain length and trophic status more reliably and to provide a touchstone for consistency in future food-web studies. Community food webs with relatively even emphasis on all trophic groups within an explicitly bounded ecosystem, and employing explicitly defined criteria for designating links, may be more precisely termed *ecosystem food webs.*

Since many difficult problems of community food-web data concern variability of definitions (Paine 1988, Lawton 1989), future use of ecosystem food webs may remedy several of these important problems. Communities are typically defined more arbitrarily than ecosystems. Whereas communities can include nearly any set of organisms as long as they occur within the same general area, ecosystems typically include a more trophically complete group of producers, consumers, and decomposers within an environment that is at least partially bounded, such as a lake, stream, forest, or grassland. In the same vein, ecosystem food webs constrain investigators to spatially and temporally bound the web, to attempt even resolution of all trophic groups within the bounds, and to include all trophic links among the organisms, including cannibalism and mutual predation (Polis 1991). These constraints decrease the dependence of food-web construction on the observer. Consequently, the increased consistency inherent in ecosystem web construction augments the abilities of other investigators to repeat and verifiably improve ecosystem food web construction compared to community food web construction. Additional food-web data from another ecosystem that follow this new definition are currently being assembled by the author.

In a strict sense, this study adds one very different web to the large and growing collection of community food webs (Briand and Cohen 1987, Sugihara et al. 1989). In another sense, this web may give us the most credible picture of a community food web that is currently available. The food web of Little Rock Lake is based on information provided by field ecologists for the purpose of describing the community food web of a whole ecosystem. Since these ecologists were thoroughly studying a particular field site, the number of species and linkages far surpasses those in other webs collected less directly from the literature (e.g., Briand and Cohen 1987, Sugihara et al. 1989). Most studies assume that the number of species in a web indicates the size of the community. This study examines the possibility that the number of species in a web indicates the level of resolution of the description of the web rather than community size.

Trophic aggregation reduces the resolution of Little Rock Lake's web to a level of resolution similar to that in previously described webs. Comparison of these similarly resolved webs addresses the degree to which previous webs may represent functionally aggregated versions of webs similar to this one, relatively complete, web from Little Rock Lake. One should not mistake the comparison in the present paper for a comparison of many webs with a large set of many other webs. The more valid description of this analysis is that many webs are being compared with many versions of one web. A question this analysis leaves outstanding is, "To what degree do previously described webs represent taxonomically aggregated versions or subsets of more complete webs?" Preliminary analyses of the Little Rock Lake web suggest that the effects of taxonomic aggregation are similar to the effects of functional aggregation, largely due to the frequent correspondence between taxonomic and functional designations (N. D. Martinez, *unpublished manuscript*).

Inspection of previous webs (Briand 1983*a*, Sugihara 1983) suggests that unevenly severe functional aggregation, taxonomic aggregation, and omission are responsible for the small numbers of species and links in previous webs. Uneven aggregation will continue to be a problem as long as ecologists understand the trophic habits and identities of large organisms better than those of small organisms. I address this problem by including detailed information about the trophic habits of many small organisms and by aggregating large and small organisms evenhandedly. This study only focuses on the effect of functional aggregation on food-web patterns and leaves the effects of observing spatial and temporal subsets of complete webs (e.g., pelagic web, benthic web, summer web, winter web, etc.) for other investigations (see Warren 1989 and Winemiller 1990).

The results of the cluster analysis show that half the taxa in Little Rock Lake have a trophic niche that is identical or very similar to that of at least one other taxon in Little Rock Lake. Since trophically equivalent basal taxa are aggregated first, followed by invertebrates, webs with 182 to 93 species are progressively more biased toward resolving organisms at the highest trophic levels. Pimm (1982; also see May 1983*a*, *b*, Paine 1988) suggests that food-web data are biased toward higher resolution of trophically higher organisms. Therefore the behavior of food-web patterns in webs starting with 182 species and ending with 93 trophic species may be loosely interpreted as the effect of progressively reducing trophic redundancy, so that the webs become progressively more skewed toward the bias suggested by Pimm (1982). During the first 53 aggregation steps until the 129-species web, aggregating trophically equivalent basal species de-emphasizes the many taxonomic distinctions between algal taxa. The next 36 aggregation steps before the 93-trophic-species web de-emphasizes many taxonomic distinctions between invertebrate taxa by aggregating trophically equivalent invertebrate taxa. The 182-taxa web and the 93-trophic-species web, respectively, contain about twice as many taxa and trophic species as the largest previously published webs. The largest previous community food webs contain 87 unlumped taxa (Sugihara et al. 1989) and 48 trophic species (Briand and Cohen 1987).

Connectedness

Among connectedness measures we find both very robust and very variable statistics. Directed, interactive, and upper connectance are relatively robust, while links per species and linkage complexity dramatically and systematically decrease with aggregation beyond the 93 trophic species web.

Within the relatively small variation of the connectance measures, linkage criteria contribute more to the variability than does web size (Fig. 2a and c). That is, the connectance of webs of similar size generated using different linkage criteria varies more than the connectance of webs generated using one linkage criterion with different sizes. This dominance suggests that differences in linkage criteria confound the comparison of connectance between different webs more than does the degree of aggregation.

Connectance

Directed connectance is the most robust connectedness statistic to changes in resolution. Upper and interactive connectance are the next most robust. All three forms of connectance are much more robust in maximally connected webs than in minimally connected webs. The robustness of connectance suggests that distinctions made among webs based on connectance are more likely to reflect true differences in web structure (Briand 1983*a*, 1985) than distinctions based on connectivity or chain length measures. This suggestion is stronger if authors of food-web data generally link aggregates even if few members of one aggregate are linked to few members of the other aggregate (i.e., if authors tend to employ criteria similar to the maximum-linkage criterion). An important caveat is that in small, very highly aggregated webs with <25 species, connectance is highly variable.

Directed connectance is more concretely tied to raw food-web data than is upper connectance. Upper connectance designates an upper bound on connectance by making the assumption that all predators that share prey interact competitively (Yodzis 1980). This questionable assumption is not made to calculate directed connectance. Directed connectance is also based on more ecologically significant information than is upper connectance or interactive connectance. For example, it is ecologically important if one species of fish, which preys on the same zooplankton species as a second species of fish, also preys on that second fish species. Matrix elements used to calculate upper connectance make no distinction between whether the fishes feed on each other or share the same prey. Elements used to calculate interactive connectance make no distinction between which fish species feeds on which fish species—they just interact.

On the other hand, elements used to calculate directed connectance distinguish which fish species eats which fish species in the above example. Directed connectance would be higher if both fish species preyed on one another (mutual predation) than if only one fish preyed on the other. Neither upper nor interactive connectance is sensitive to such ecologically significant details. The robustness combined with the more ecologically significant nature of directed connectance suggests that directed connectance is the preferred connectedness statistic for comparing webs (Martinez, *in press*). If the robustness of directed connectance is upheld in future studies, the introduction of directed connectance may be one of the more significant contributions of this study. Even if the robustness is not upheld, food-web investigators may choose to employ directed connectance solely due to the quality of ecological information incorporated into this connectance measure.

Another point emphasizing the utility of directed connectance is the comparison of directed connectance among other webs (Fig. 2b). The average directed connectance of 113 trophic-species webs (Briand and Cohen 1987) and of 11 trophic-species webs of lakes (Briand 1985) is 0.127 ± 0.054 (mean ± 1 SD) and 0.120 ± 0.038, respectively. Both these averages are remarkably close to 0.120, the directed connectance in the Little Rock Lake trophic-species web. Averaging directed connectance among differently sized webs is valid if assumptions of hyperbolically decreasing connectance (Rejmánek and Starý 1979, Pimm 1980, Yodzis 1980) or other systematic trends in connectance with number of species in food webs are not made (Auerbach 1984, Martinez 1988, *in press*, Paine 1988, Winemiller 1989). These consistencies among webs suggest that food webs in general, and lake food webs in particular, possess very similar directed connectance.

Comparing connectance between webs has been avoided (Briand 1985) because of several studies indicating that connectance increases with decreasing web size (Rejmánek and Starý 1979, Pimm 1980, Yodzis 1980). But several authors have seriously questioned this assertion (Auerbach 1984, Martinez 1988, *in press*, Paine 1988, Winemiller 1989). The increase does not generally occur in Little Rock Lake webs without trophic redundancy. The increase does occur in Little Rock Lake's highly aggregated webs generated using minimum, average, and maximum linkage criteria (Figs. 2b and 3b). The decreasing connectance with increased web size may not be a "well established . . . empirical generalization" (Cohen and Newman 1988). Instead, my findings (Figs. 2b and 4a) suggest that the generalization is an artifact of severely aggregated data (Martinez 1988, *in press*, Paine 1988).

Briand (1983*a*) examined the relationship between upper connectance and species number for 40 webs with 5 to 45 species and found that 83% of the variance was explained by the regression (upper connectance = $2.20[\text{Species}]^{-0.65}$). A comparison of this regression line with the Little Rock Lake data (Fig. 2c) shows that while the regression is a poor fit, it closely matches maximum-linkage webs with 9 to 30 species. Thirty-three (83%) of Briand's 40 webs have 9 to 30 species. This suggests that Briand's regression may be limited to the range of web sizes on which the regression is based. It also raises the possibility that Briand's webs are a collection of maximum-linkage webs, and that Briand's regression is based on a possible tendency for the upper connectance of small, highly aggregated maximum-linkage webs to increase with aggregation (Fig. 2c).

Connectance may be forced to hyperbolically increase as small webs get smaller by the lower limit of connectance. This is because each species in a web with >1 species requires at least one link to be a member of the web. Therefore, the minimum number of links in a web is one less than the number of species (Martinez, *in press*). This minimum constrains directed connectance in webs with 8, 5, and 3 species to be at least 0.11, 0.16, and 0.22, respectively. It is clear from the average and standard deviations mentioned above that this constraint biases webs with few species toward high connectance. This bias may be achieved by either misrepresenting trophic specialists as generalists or by including only trophic generalists and leaving out specialists in small webs. This bias is partly responsible for not analyzing aggregated Little Rock Lake webs with <9 species. The other part of the reason is the large amount of violence done to the food web by aggregating taxa that share $<10\%$ of their predators and prey. In summary, I suggest that connectance in variably resolved large webs is a useful and robust food-web attribute. Yet, in webs with fewer than 10 or 20 species, connectance may be systematically overestimated and very sensitive to resolution.

Connectivity

Comparisons of connectivity among webs are consistent with the notion that Briand's (1985) lake webs and Briand and Cohen's (1987) 113 webs are highly aggregated versions of more elaborate webs similar to that of Little Rock Lake. The average linkage complexity of Briand's 12 lake webs (5.18, SD = 1.03) with an average of 16 trophic species is close to the linkage complexity of the 16-species maximum-linkage web of Little Rock Lake (4.33, Fig. 4b). The range of Briand's average linkage complexity plus and minus two standard deviations spans the linkage complexity of Little Rock Lake maximum-linkage webs with 11 to 38 species. This 11 to 38 species range practically includes the 9 to 22 (average 16) trophic-species range of the webs on which the average is based. It seems safe to assume that a more accurate portrait of webs in Briand's (1985) lakes includes substantially many more than 9 to 22 trophic species. The linkage complexity of the Little Rock Lake 93-trophic-species web (36.3) is >20 standard deviations from Briand's average. These discrepancies suggest linkage complexity is much higher than has previously been characterized by others, and that linkage complexity strongly depends on resolution of the food web. If these two suggestions are correct, linkage complexity is not as useful as directed connectance to distinguish the structure of a wide size range of webs.

After collecting and examining 62 webs with 3 to 33 trophic species, Cohen and Briand (1984) determined that the number of links is a constant proportion of the number of species, i.e., links per species = 1.86. This scale-invariant ratio, otherwise known as the "link-species scaling law" (Cohen and Newman 1985, 1988, Martinez 1988, *in press*), is independent of the number of species in the web. Briand and Cohen (1984) offer no statistical support for their law over constant connectance, but do offer an unconvincing visual inspection of regression lines. The law is also observed to do "no obvious violence to the data" (Briand and Cohen 1984). Cohen and Briand (1984) cite the link-species scaling law as support for Pimm's (1980) hypothesis that "each species in a community feeds on a number of species of prey that is independent of the total number of species in the community." The link-species scaling law is also a basic assumption in the cascade model, which predicts the quantity of different types of links in webs (Cohen and Newman 1985, Cohen et al. 1985).

Comparisons of links per species among Little Rock Lake webs and Cohen and Briand's (1987) 113 webs are consistent with the notion that the average number of links per species in highly resolved food webs is much higher than previously suggested. These comparisons are also consistent with the hypothesis that Briand and Cohen's webs are highly aggregated versions of more elaborate webs similar to that of Little Rock Lake (Fig. 4a). During aggregation, links per species decreases almost linearly from 11 as the number of non-redundant species decreases (Fig. 4a). The average ±1 SD) of each links-per-species ratio among Cohen and Briand's 113 webs (1.88 ± 0.72 links per species), with 3 to 48 trophic species plus and minus two standard deviations, coincides with the links per species of Little Rock Lake webs aggregated to between 9 and 42 species (Fig. 4a). It seems reasonable that food webs described with <20 species tend to have two links per species. In other words, each species tends to interact with an average of four other species in small webs. Yet, one might expect that when the highly aggregated species, such as fishes and zooplankton, in small webs are disaggregated, the number of predators and prey of each species would increase as seen in this study. An example of this effect of disaggregation is that yellow perch eat many species of zooplankton, which suggests many more links per species than does the observation that fish eat zooplankton. Other new and highly resolved food webs also suggest this effect of resolution on links per species (Hildrew et al. 1985, Warren 1989, Winemiller 1990; see Paine 1988). These new data and my results suggest that the scale-invariant, link-species scaling law of ≈2 links per species is an artifact of severely aggregated data (Martinez 1988, *in press*).

A recent study (Sugihara et al. 1989), which used food-web aggregation algorithms practically identical to those used here and developed earlier (Martinez 1988), concludes that links per species (*L/S*) or $S \cdot C$ calculated using C = directed connectance (K. Schoenly, *personal communication*, $S \cdot C = S \cdot (L/S^2) = L/S$), is insensitive to aggregation employing the maximum linkage criterion. Somewhat paradoxically, Sugihara et al. (1989) also point out that links per species decrease slightly with aggregation. This only slight sensitivity appears to be due to an incomplete analysis and less thorough aggregation than employed here (N. D. Martinez, *unpublished manuscript*). Most previous analyses (e.g., Cohen and Briand 1984, Briand and Cohen 1984, 1987) analyze trophic-species webs because such "lumping" or aggregation appears to ameliorate the distortion of food-web data due to uneven taxonomic expertise of the original investigator. Though they compared their results to trophic-species analyses, Sugihara et al. (1989) analyzed raw food webs. When trophic-species versions of their 60 webs are analyzed, the same trends observed in differently resolved Little Rock Lake webs were observed among their variably sized 60 webs (N. D. Martinez, *unpublished manuscript*).

Sugihara et al. (1989) examined the effects of resolution on food-web structure by aggregating 41 webs with >10 taxa, generating 41 sequences of maximum-linkage webs. It appears that about three quarters of the webs in these sequences were not aggregated beyond trophic species. As such, Sugihara et al. (1989) primarily examined the effects of eliminating trophic redundance in webs. As shown in Fig. 4a, eliminating trophic redundance may either increase or decrease the links per species of Little Rock Lake depending on whether the redundance of basal or intermediate species is being reduced. In contrast, aggregating beyond the trophic-species web consistently decreases the links per species of Little Rock Lake. This decrease is least dramatic in small maximum-linkage webs (Fig. 4a). This mild decrease is consistent with Sugihara et al.'s (1989) finding regarding the behavior of links per species in small webs. It should be noted that Sugihara et al. only reduced their webs to ½ their original size instead of $\frac{1}{20}$ as achieved here. I have found recently that reducing the resolution of trophic-species versions of Sugihara et al.'s webs by ½ leads to findings similar to those regarding Little Rock Lake. Indeed, these recent findings indicate that the effects of resolution on the food-web patterns described here are much more general than suggested by this analysis of one web. (N. D. Martinez, *unpublished manuscript*). These results clearly suggest that comparisons of connectivity among differently resolved webs are confounded by the severe scale-dependence of connectivity.

Chain length

Many authors (Elton 1927, Hutchinson 1959, Pimm and Lawton 1977, Pimm 1982) have asserted that the length of food chains is limited (Lawton 1989). Questions raised in the literature do not concern whether food chains are limited but why. Pimm (Pimm and Lawton 1977, Pimm 1982) champions the hypothesis that chains are limited to an average of 4 or 5 links because long chains are dynamically unstable. Yodzis (1981, 1984) has advocated the hypothesis that the thermodynamics of trophic energy exchange limits chain length. Briand and Cohen (1987) claim that the dimension of the web's environment is correlated with chain length. In their words, "environments that are three dimensional or solid . . . such as a forest canopy or the water column of the open ocean, have distinctly longer food chains than environments that are two dimensional or flat, such as a grassland or lake bottom." My findings suggest that these claims are premature. Using definitions comparable to those in other studies, the Little Rock Lake trophic-species web has much longer chain lengths (Fig. 6a and c) than previously characterized (Pimm 1982, Briand and Cohen 1987). Trends in my data suggest that chain lengths would increase further with increased resolution of the food web.

A serious problem with the assertion of much longer chain length is the difficulty of consistently defining chain length. The conventional algorithm analyzes the length of all possible chains to top species (Cohen 1978). Application of that definition to the Little Rock Lake webs leads to the trivial result that maximal and mean chain lengths of most, if not all, Little Rock Lake webs are 1 link. This is because the bivalve at trophic level 2 is the only formal top species in most Little Rock Lake webs.

To more rigorously support the assertion of unconventionally long chain lengths, I compared the first average chain length algorithm employed here with Cohen's (1978) mean chain length. This comparison was performed by calculating the chain lengths of 60 webs employing both Cohen's algorithm and my first algorithm, which excludes loop-forming species. The 60 webs are those assembled by Schoenly et al. (1991) and also analyzed by Sugihara et al. (1989). Both unlumped and trophic-species versions of these 60 webs yield similar results. Fig. 12 shows that in all 60 webs, my chain length algorithm calculates equal or shorter lengths than Cohen's. This conservative nature of my algorithm shows that my assertion of long chain lengths is not an artifact of differing chain length algorithms.

Another comparison between Little Rock Lake and previous webs can be made among conventionally defined maximal chain lengths of Briand and Cohen's (1987) 113 webs and maximal chain lengths of Little Rock Lake webs, calculated including chains through loop-forming species (Fig. 6a). Briand and Cohen's algorithm includes *all* possible chains without excluding loop-forming species. While such chains in the Little Rock Lake webs are not restricted to end at top species, the maximal chain lengths of Briand and Cohen's webs should not be longer if chains to intermediate species were also considered. The maximum lengths of chains calculated including loop-forming species in Little Rock Lake far exceed those observed in previous webs and those predicted by the cascade model (Newman and Cohen 1986).

Loop-forming species are generally absent from the Briand and Cohen (1987) data (Cohen et al. 1986), but loop-forming species are prevalent in the Little Rock Lake webs and in other more directly constructed webs (Hildrew et al. 1985, Sprules and Bowerman 1988, Warren 1989, Polis 1991). This discrepancy prompted the qualification that the cascade model, which is based on the Briand and Cohen (1987) data, is relevant only to the loop-free portion of webs (Cohen 1990). My chain length algorithm excluding loop-forming species represents an attempt to delineate a comparable loop-free structure in the Little Rock Lake web.

Excluding loop-forming species biases my results toward shorter chains (Fig. 6b). Still, the average chain length (excluding loop-forming species) of the Little Rock Lake 93-trophic-species web (7 links) is >4.5 standard deviations higher than the average (±1 SD) chain length of Briand and Cohen's (1987) 113 trophic-species webs of 2.9 ± 0.9 links). In contrast, Little Rock Lake webs with 9 to 50 species have average chain lengths (excluding loop-forming species) within 2 SDS of Briand and Cohen's (1987) average chain length. These and other discrepancies discussed here demonstrate that the prohibition of loops and the constraint of two links per species prescribed by the cascade model causes this model to inaccurately describe the patterns in Little Rock Lake.

The more profound suggestion of these analyses is that resolution of data, rather than ecological factors, limits the length of binary food chains. Other studies have also found longer chain lengths in relatively highly resolved and more directly documented webs (Hildrew et al. 1985, Sprules and Bowerman 1988, Warren 1989, Polis, *in press*). The general trend of increasing chain length with increasing web size or resolution may be obscured in the Briand and Cohen (1987) data by the variability introduced by different authors invoking different linkage criteria and uneven aggregation.

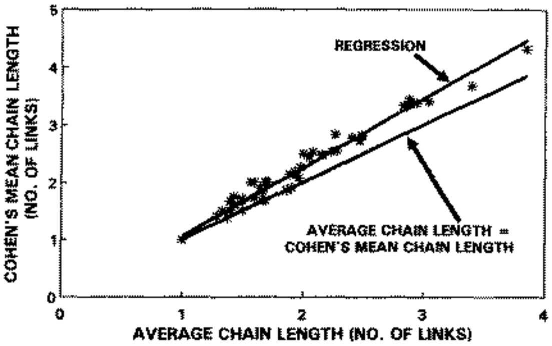

FIG. 12. Comparison of an average chain length algorithm employed in this study with Cohen's (1978) mean chain length. The points (*) represent the results from analyzing trophic species versions of 60 previously published webs (Sugihara et al. 1989, Schoenly et al. 1991). Identical analysis of the original unlumped versions of the 60 webs leads to similar results. When both algorithms generate the same result, the point falls on the lower line. This figure shows that the average chain-length algorithm that excludes loop-forming species (see description in *Methods: Chain calculations*) calculates shorter or equal chain lengths than Cohen's algorithm. The regression demonstrates that, in general, Cohen's mean chain length (Y) increases as a function of my average chain length (X) according to the equation $Y = 1.20X - 0.15$ ($\text{SE}_{slope} = 0.02$, $R^2 = 0.98$).

This critique addresses Briand and Cohen's (1987) assertion that the dimension of the environment affects chain length by suggesting that uneven resolution biases their findings. Three-dimensional environments (e.g., forest canopy, open ocean) afford ecologists more opportunities to make distinctions among species and their feeding habits than do two-dimensional environments (e.g., grasslands, lake bottoms). This allows people to resolve three-dimensional environments more highly and evenly because three-dimensional environments are those that people may observe from the inside. In two-dimensional environments, investigators are forced to observe from the outside. This means that differences between chain lengths in two- and three-dimensional environments may be due primarily to the differences in perspective inherent in observing such environments.

Previous studies (Martinez 1988, Sugihara et al. 1989) found that chain lengths are robust to aggregation of trophically redundant species. Sugihara et al. (1989) also concluded that chain lengths are robust to aggregation beyond trophic-species webs. This latter conclusion appears to be an artifact of incomplete analyses (see links per species discussion above). Had they aggregated their data more consistently, the systematic resolution-related trends shown in Fig. 6 would have been observed (N. D. Martinez, *unpublished manuscript*).

Average chain lengths in the Little Rock Lake webs are much less than those suggested by Newman and Cohen's (1986) rule that these lengths are roughly equal to twice the links per species ratio in a web. This bias exists at least partially because average chain length is calculated here as the average length of the chains to all the consumers in the web (Fig. 12). Other studies (Cohen et al. 1986, Briand and Cohen 1987, Sugihara et al. 1989) calculate average chain length to be the average length of chains to only top species. This convention inadequately addresses the Little Rock Lake web because none of the web's trophically highest organisms are top species. In the future, investigators may prefer to avoid statistics based on top species because it is questionable whether any species in a reasonably complete food web is free of predators (Winemiller 1990, Polis 1991).

Trophic levels

A corollary of the conventional assertions that food-chain lengths are limited is that organisms are roughly limited to trophic levels below 4 or 5 (Pimm 1982). This limit also exists in Little Rock Lake webs with 9 to 37 species (Fig. 7a). This range, 9 to 37 species, is similar to the size range of webs in which the limits were observed. Organisms in larger Little Rock Lake webs are not limited to trophic levels below 6. When loop-forming species are excluded from food chains, organisms at trophic level 9 are observed in Little Rock Lake's trophic-species web. Within a minimum-linkage web with 57 species, organisms at trophic level 12 are observed when loop-forming species are included in food chains. The trends in Fig. 7 suggest that organisms at higher trophic levels would be observed in more highly resolved webs.

These findings demonstrate greater potential for biomagnification of toxic chemicals into organisms at upper trophic levels than is currently appreciated. It might be possible that once quantities of energy associated with links are better known, we may find only trivial amounts of energy passing through the longer chains. Such a finding would invalidate the assumption used here and elsewhere (e.g., Pimm 1982) that chain lengths calculated using binary information indicate the absolute trophic level of a species. Still, since large fishes, leeches, and highly predaceous invertebrates are at the highest trophic levels of the Little Rock Lake webs, binary chain-length measures may accurately indicate the relative trophic level of a species.

Little Rock Lake webs with 9 to 137 species consistently contain the largest proportion of species in trophic level 2 (Fig. 7a and b). The large number of algae in the list of taxa suggests that trophic level 1 contains the most biological species (Appendix I). This discrepancy may be partly due to the fact that distinctions between trophically defined species above trophic level 1 are made considering both predators and prey. This situation allows more distinctions to be made between trophically defined species above trophic level 1 because trophic level 1 species are distinguished based only on their predators. Many species may be inaccurately assigned to trophic level 2 because many of these species consume fine organic matter, a severely aggregated taxon *assumed* to be at trophic level 1. This taxon is actually a rich community containing several trophic levels (Strayer 1985, 1986, Margulis 1986). Therefore, the relative abundance of species at trophic level 2 compared to those at higher levels may be an artifact of incomplete data and uneven resolution. Yet the robustness of this relative abundance to resolution suggests that this pattern may withstand the test of more highly resolved data.

Topologically described food-web attributes of chain length and trophic level are susceptible to changes in resolution. This susceptibility is to be expected given the definitions used for these investigations (e.g., binary link designations, quantities associated with links are ignored). It appears that observed chain lengths and trophic levels would increase beyond those presented here once the extent of food-web data expands (O'Neill et al. 1986) to include and evenly resolve all co-occurring organisms. Such an expansion would include, for example, microbes and killer whales in the same ecosystem web. To observe ecologically fixed constraints associated with chain lengths and trophic levels it may be necessary to incorporate energy flow measures (Finn 1980, Baird and Ulanowicz 1989) instead of relying on the topology of binary webs.

Proportions of links and species

The proportions of intermediate and bottom species and links among them are some of the most robust statistics examined. The robustness and trends of these proportions of species are similar to those reported by Sugihara et al. (1989). In contrast, proportions of top species and links to top species, which vary from their trophic species values by factors of 20 and 3000 (Figs. 8a and 11a), respectively, are among the least robust in highly aggregated webs. The values and systematic trends of these statistics in Little Rock Lake call into question previous generalizations of the proportions (Briand and Cohen 1984, Cohen and Briand 1984). Many extreme proportions and their widest variability are seen in webs with <35 species. These extreme values and their variability are also closest to those previously reported (Figs. 8 and 11) based on webs with <35 species (Briand and Cohen 1984, Cohen and Briand 1984, Briand 1985, Cohen and Newman 1985, Cohen et al. 1985). This suggests that generalizations of these proportions based on webs with <35 species are inaccurate and cannot withstand the test of better data.

The difference between the proportions reported here and elsewhere (Briand and Cohen 1984, Cohen and Briand 1984, Briand 1985, Cohen and Newman 1985, Cohen et al. 1985, Sugihara et al. 1989) is primarily due to much higher proportions of top species in the less directly collected data. It is unlikely that many, if any, species have no predator (Polis 1991). Certainly, almost all species have predators within the same community if parasitism and juvenile stages are considered

(Winemiller 1990). This analysis of a more directly collected ecosystem food web suggests that significant proportions of top species and links to top species are artifacts (see Warren 1989, Winemiller 1990). Since the proportions of 86% intermediate species (I) and 91% I-I links in the Little Rock Lake trophic-species web are relatively robust, these proportions may be much closer to the true proportions in ecosystem food webs than are previous estimates. Of course, this raises the problem of the different definitions of community food webs and ecosystem food webs. Future use of the ecosystem food web definition may resolve this problem by emphasizing complete and evenly resolved data.

The Little Rock Lake predator-to-prey ratio of 0.9 in the trophic-species web appears to be the most robust statistic examined. This robustness supports the reported scale-invariance of predators:prey (Cohen 1978, Briand and Cohen 1984, Jeffries and Lawton 1985, Cohen and Newman 1985, Sugihara et al. 1989). But these analyses have found average ratios >1 and few webs with ratios <1 (Briand and Cohen 1984, Sugihara et al. 1989). Predators:prey (mean = 2.31) among Schoenly et al.'s (1991, Sugihara et al. 1989) 60 webs appears to be roughly twice as high as among 113 other webs (mean = 1.13, Cohen and Newman 1986). This discrepancy is significantly reduced by aggregating the 60 webs into trophic-species webs. This aggregation reduces the mean (±1 SD) ratio among the 60 webs to 1.31 ± 0.32 (N. D. Martinez, *unpublished manuscript*). Briand and Cohen (1984) state that such aggregation "removes possible differences in the propensity to split (trophic species), among observers and trophic levels" and "tightens the relation between numbers of predators and prey." The above effect of aggregation on the 60 webs supports these statements. Briand and Cohen (1984) also assert that their analyses support "Pimm's (1982) suggestion that ecologists have exercised greater taxonomic refinement at high trophic levels than at low." The effects of resolution on predators:prey and value of predators:prey in Little Rock Lake appear to support all these quotes. Yet, due to their being few or no top species in highly resolved webs, predators:prey >1 appears unable to withstand the test of better data.

A predator-to-prey ratio >1 is the only conventional pattern not generated by reducing the resolution of the Little Rock Lake web. This result, Pimm's above suggestion, and omission of predation on "top" species (Polis 1991), suggest that previous webs are more fundamentally distorted than just by low resolution. Predator:prey ratios >1 indicate that there are more top species than basal species in most food webs. Even if top species occasionally exist, such a balance seems unlikely in evenly resolved ecosystem webs given significant proportions of basal species (Fig. 8b).

CONCLUSION

We may never know all the species and feeding relations in a given natural ecosystem. Most food-web data contain a small number of often highly aggregated species. To investigate the role of these problems in articulating food-web regularities, I have documented a large, relatively complete web and investigated the web's sensitivity to resolution in terms of quantitative food-web patterns. Patterns that remain consistent over different degrees of resolution are more likely to be attributes of a system than artifacts of limited observation of that system (Allen et al. 1984). Consistent attributes, observable in all ecosystems, may point to rules governing ecosystem structure (Cohen 1989). Therefore a thorough analysis of the sensitivity of quantitative food-web patterns to resolution is necessary to check the claim that observed patterns represent ecosystem regularities or, even stronger, "laws." Results of this sensitivity analysis are summarized qualitatively in Table 2.

The trophic species web of Little Rock Lake is certainly not of the most trophically complex ecosystem. Yet it differs from previously described food webs by having more trophically different species, higher linkage complexity, more links per species, longer food chains, more loops, species at higher trophic levels, and higher proportions of intermediate species and links between them. The directed connectance of Little Rock Lake, however, is similar to that of previously described webs. It remains to be seen whether other highly resolved ecosystem food webs follow this pattern of differences and similarities. Though this is an open question, problems with previous data (Martinez 1988, Paine 1988, Lawton 1989) and my understanding of ecosystems persuade me that future patterns will generally follow the example set by Little Rock Lake (see Warren 1989, Polis 1991).

If food webs have species at unconventionally higher trophic levels, as suggested here, there may be much greater potential for biomagnification than current characterizations of community food webs suggest. Relatively low proportions of top and bottom species and links to top and bottom species in Little Rock Lake and possibly other communities are made more believable by the combination of the robustness and absolute values of these proportions in Little Rock Lake, similar observations in other directly documented webs (Warren 1989, Polis 1991), and the possible dependence of the top-species phenomenon on incomplete data (Polis 1991). Since links per species decrease with resolution, and since the link-species scaling law (Briand and Cohen 1984, Cohen and Newman 1985, 1988) fails to predict anywhere near the 1037 links in the Little Rock Lake trophic-species web (only 173 links are predicted by the law), the law may be an artifact of explaining the structure of poorly resolved webs with unevenly aggregated groups of organisms (Martinez, *in press*). Likewise, decreasing connectance with increasing species (Rejmánek and Starý 1979, Pimm 1980, Yodzis 1980) to the point of constant links per species also may be an artifact. Still, distinctions between types of webs based on connectance or closely related sta-

[redacted]

Table 2. Summary of sensitivity of food-web statistics. Entries under the "Sensitivity to aggregation" heading that are designated as "High" refer to large and clear systematic changes that occur with aggregation, "Medium" refers to substantial sensitivity, and "Low" corresponds to a statistic that is relatively robust (i.e., relative to the other statistics) to aggregation. Entries under the two right-hand columns refer to the statistic's sensitivity relative to the statistic's sensitivity to aggregation. "High" means that the sensitivity of the statistic to the column heading is greater than the statistic's sensitivity to aggregation; "Medium" means that the sensitivity to the column heading is generally of the same magnitude as the statistic's sensitivity to aggregation; "Low" means the opposite of High.

	Statistic	Sensitivity to aggregation	Sensitivity to linkage criteria	Sensitivity to inclusion of loop-forming species
Connectance statistics	Interactive connectance	Medium	High	Not applicable
	Upper connectance	Medium	High	Not applicable
	Directed connectance	Low	Medium	Not applicable
Connectivity statistics	*L/S* (Links per Species)	High	Low	Not applicable
	SC (Linkage complexity)	High	Low	Not applicable
Chain length statistics	Average chain length	Medium	Low	Medium
	Maximum chain length	High	Medium	Medium
	Unimodal chain distribution	High	Not applied	Low
	Distribution among trophic levels	High	Not applied	Medium
Proportions of species	Top species	High	High	Not applicable
	Intermediate species	Low	Medium	Not applicable
	Basal species	High	Medium	Not applicable
	Predators/Prey	Low	Medium	Not applicable
Proportions of links	To Top species	High	High	Not applicable
	Intermediate–Intermediate links	Low	High	Not applicable
	Intermediate–Basal links	Medium	Medium	Not applicable

tistics (Briand 1983*a*, *b*, 1985) may withstand further scrutiny since connectance is relatively robust to variable resolution.

Connectedness, chain length statistics, trophic-level statistics, and several proportions of links and species of aggregated Little Rock Lake webs closely match the averages reported for similarly sized webs. This correspondence suggests the intriguing possibility that previously reported food webs are severely aggregated versions of more elaborate webs very similar to the trophic-species web of Little Rock Lake. The role of resolution in generating this consistency points toward less conventional explanations of the patterns. Previously articulated regularities, such as scale-invariant connectivity and short chain lengths, seem to be artifacts of low-resolution data, while observed values for connectance, especially directed connectance, may be important, robust attributes of food webs. Due to the unique qualities of directed connectance, comparability among webs, inclusion of more trophic information (direction of links, cannibalism, mutual predation), and robustness to changes in aggregation and linkage criteria, comparisons of directed connectance among webs may be more useful than is currently appreciated.

There are several other possible causes of the resemblance of our similarly sized webs. One possibility is that the resemblance is just a chance event stemming from using only one relatively complete web for comparison with relatively incomplete webs. We need other high-resolution ecosystem food webs to check this possibility. Another possibility is that, generally, webs are so similar that their resemblances are visible even in poorly resolved and unevenly aggregated data. This visibility could occur if the other webs are aggregated in a manner similar to the methods presented here (i.e., functionally) or if subsets of webs have quite similar structure to aggregated webs. I plan to examine this latter possibility in subsets of Little Rock Lake webs. This study leaves open the possibility that the structure of food webs is much less variable than previously reported, and the apparent variability results from different investigators employing different levels of resolution and different linkage criteria. An important check of my results is to compare results using null models (Cohen 1978). However, the development of null models is a difficult endeavor beyond the scope of this project.

Including more trophically redundant species affects quantitative food-web patterns in quite different ways than does adding trophically distinct species. Generally, food-web structure described in terms of connectivity, chain lengths, and distributions of species among trophic levels does not change as much when changing the number of trophically redundant species as it does when changing an equal number of trophically distinct species.

This is the first food-web study to use data originally collected to describe the complete, detailed food web of a large, whole, natural ecosystem. It is also the first to systematically examine the effects of resolution on food-web structure (Martinez 1988). As the first, it suggests different interpretations of previously articulated regularities in quantitative food-web patterns. I hope these results inspire food-web researchers to construct ecosystem food webs from the most knowledgeable site-specific sources as is possible rather than from one or a few published reports. We have recently developed our abilities to thoroughly and consistently describe the whole structure of particular ecosystems (Callahan 1984, Strayer et al. 1986). Now let us put these abilities to work.

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APPENDIX I

Taxa and taxonomic groups in the Little Rock Lake, Wisconsin, food web, with each taxon's identification number.

1, 3, 5, 7: Young of year fishes

1 Yellow perch (*Perca flavescens*)
3 Largemouth bass (*Micropterus salmoides*)
5 Rock bass (*Ambloplites rupestris*)
7 Black crappie (*Pomoxis nigromaculatus*)

11 Fish eggs

2, 4, 6, 8: Adult fishes

2 Yellow perch (*Perca flavescens*)
4 Largemouth bass (*Micropterus salmoides*)
6 Rock bass (*Ambloplites rupestris*)
8 Black crappie (*Pomoxis nigromaculatus*)

9, 10: Minnows

9 Mudminnow (*Umbra*)
10 Shiner (*Notemigonus crysoleucus*)

12–16: Pelagic copepods

12 *Diaptomus minutus*
13 *Diacyclops thomasi*
14 *Mesocyclops edax*
15 *Tropocyclops prasinus*
16 *Epischura lacustris*

17–24: Pelagic cladocera

17 *Bosmina longirostris*
18 *Eubosmina*
19 *Daphnia galeata mendotae*
20 *Daphnia parvula*
21 *Diaphanosoma birgei*
22 *Holopedium gibberum*
23 *Leptodora kindtii*
24 *Polyphemus pediculus*

25–38: Pelagic rotifers

25 *Conochilus unicornis*
26 *Conochiloides*
27 *Kellicottia longispina*
28 *Kellicottia bostoniensis*
29 *Keratella cochlearis*
30 *Keratella taurocephala*
31 *Keratella crassa*
32 *Keratella hiemalis*
33 *Polyarthra remata*
34 *Polyarthra vulgaris*
35 *Trichocerca cylindrica*
36 *Asplanchna*
37 *Gastropus*
38 *Synchaeta*

39–41: Juvenile pelagic zooplankton

39 Nauplii
40 Calanoid copepodids
41 Cyclopoid copepodids

42–53: Benthic cladocera

42 *Alona affinis*
43 *Alona quadrangularis*
44 *Alona rustica*
45 *Alona intermedia*
46 *Alonella excisa*
47 *Disparalona acutirostris*
48 *Chydorus* sp1
49 *Chydorus* sp2
50 *Acantholeberis curvirostris*
51 *Ophryoxus gracilis*
52 *Scapholeberis kingi*
53 *Sida crystallina*

54–59: Benthic copepods

54 *Macrocyclops albidus*
55 *Eucyclops serrulatus*
56 *Acanthocyclops*
57 *Microcyclops rubellus*
58 Harpacticoid copepods
59 Harpacticoid copepodids

60: Hemiptera *Gerris*

61, 76: Coleoptera

61 *Hydroporus*
76 *Gyrinus*

62–63: Ephemeroptera

62 *Leptophlebia*
63 *Caenis*

64–70: Trichoptera

64 *Oecetis*
65 *Mystacides*
66 *Limnephilus*
67 *Agrypnia*
68 *Banksiola*
69 *Molanna*
70 *Polycentropus*

71–74: Odonata

71 *Anisoptera epitheca*
72 *Libellula*
73 *Sympetrum*
74 *Enallagma*

75 Neuroptera *Climacia*

77 Hemiptera Veliidae

78 Hemiptera Notonectids

79 Magaloptera *Sialis*

80 Lepidoptera *Pyralidae eoparagyractis*

81–111: Diptera

81 *Bezzia*
82 *Sphaeromais*
83 *Chaoborus albatus*
84 *Chaoborus punctipennis*
85 *Albabesmyia*
86 *Clinotanypus*
87 *Djalmabatista*
88 *Guttipelopia*
89 *Larsia*
90 *Macropelopis*
91 *Procladius*
92 *Chaetocladius*
93 *Corynoneura*
94 *Cricotopus*
95 *Nanocladius*
96 *Micropsectra*
97 *Paratanytarsus*
98 *Tanytarsus*
99 *Chironomus*
100 *Cladopelma*
101 *Cryptochironomus*
102 *Endochironomus*

APPENDIX I. Continued.

103 *Glyptotendipes*
104 *Microtendipes*
105 *Parachironomus*
106 *Paratendipes*
107 *Polypedilum*
108 *Pseudochironomus*
109 *Stenochironomus*
110 *Stictochironomus*
111 *Xenochironomus*

112–114: Mollusca

112 Bivalvia
113 *Campeloma decisum*
114 *Sphaeriidae*

115 Annelida Oligochaete
116 Annelida Hirudinea
117 Turbellaria Tricladida
118 Amphipoda *Crangonyx gracilis*

119–121: Porifera

119 *Spongilla lacustris*
120 *Ephydatia muelleri*
121 *Corvomyenia everetti*

122 Arthropoda *Hydracarina*

123–147: Filamentous algae

123 *Bambusina*
124 *Batrachospermum*
125 *Binuclearia*
126 *Bulbochaete*
127 *Desmidium*
128 *Geminella*
129 *Groenbladia*
130 *Hapalosiphon*
131 *Hyalotheca*
132 *Lyngbya*
133 *Microchaete*
134 *Microcoleus*
135 *Mougeotia*
136 *Oedogonium*
137 *Oscillatoria*
138 *Phormidium*
139 *Plectonema*
140 *Radiofilum*
141 *Rhizoclonium*
142 *Schizothrix*
143 *Scytonema*
144 *Sphaerozosma*
145 *Spirogyra*
146 *Tribonema*
147 *Zygnema*

148–156: Cyanobacteria

148 *Chroococcus*
149 *Gloeothece*
150 *Merismopedia*
151 *Aphanocapsa*
152 *Gomphosphaeria*
153 *Coelosphaerium*
154 *Rhabdoderma*
155 *Aphanothece*
156 *Anabaena*

157–171: Green algae

157 *Arthrodesmus*
158 *Cosmarium*
159 *Crucigenia*
160 *Euastrum*
161 *Oöcystis*
162 *Pediastrum*
163 *Quadrigula*
164 *Schroederia*
165 *Spondylosium*
166 *Staurastrum*
167 *Tetraëdron*
168 *Ankistrodesmus*
169 *Xanthidium*
170 *Elaktothrix*
171 *Scenedesmus*

172–173: Euglenophyta

172 *Phacus*
173 *Trachelomonas*

174–175: Cryptophyta

174 *Chroomonas*
175 *Cryptomonas*

176–181: Chrysophyceae
176 *Asterionella*
177 *Dinobryon*
178 *Mallomonas*
179 *Synedra*
180 *Synura*
181 *Tabellaria*

182 Fine organic matter

APPENDIX II

LITTLE ROCK LAKE (WISCONSIN) ECOSYSTEM FOOD-WEB MATRIX

Each element of the matrix represents whether the predator identified by the vertical column number eats (1) or does not eat (0) the prey identified by the row number. All identification numbers refer to taxa in Appendix I. A computer-readable file is available from ECOWeB (Cohen 1989*b*).

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Prey
species no.                               Predator species number

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APPENDIX II. Continued.

Prey species no.	Predator species number
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