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Nonlinear scale dependence and spatiotemporal variability in planktonic food webs

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Zooplankton food webs of Lake Okeechobee, Florida, were analyzed in order to examine spatiotemporal variability and test for scale dependence of major food web properties. 46 webs were constructed from data collected during several years (1988–92) at six locations. For all these webs, the following food web properties were calculated: number of species, total links, links per species, connectance, percentage of top and intermediate species, and food chain length. We did not find any statistically significant spatiotemporal variation in these properties. Still, there were consistent differences seasonally (summer vs winter) and spatially (littoral vs pelagic habitats). There was also a very clear nonlinear scale dependence in most food web properties: links per species, food chain length, and proportions of top and intermediate species vs number of species. The scale dependence was strong for small webs, but became weaker for larger webs. The relatively simple food webs and consistently collected data used in our study provide some of the clearest and most statistically significant results to date. They help reconcile the debate about scale invariance vs dependence in major food web properties.

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Food webs have recently become a focus of attention for ecologists and limnologists (Lawton 1995a, Polis and Winemiller 1996). Studies have included experimental manipulations of predator-prey interactions (Carpenter et al. 1987, Power 1990), measurements of energy and materials flow (Pomeroy and Weibe 1988, Wylie and Currie 1991, Carpenter et al. 1992), and development of models of food web connectedness (Cohen and Newman 1985, Carney 1991, Martinez 1991, Havens 1992). In the study of connectedness webs, there have been several major controversies, including: (1) whether or not omnivory, defined as feeding on multiple trophic levels, is common in natural communities (Pimm 1982, Sprules and Bowerman 1988), (2) whether or not long food chains, with five or more trophic links, can exist in nature (Pimm 1982, Sprules and Bowerman 1988, Martinez 1991), and (3) whether or not natural food webs have "scale-dependent" properties – that is, whether food web structure, measured as the percent of species at different trophic positions, and complexity, measured as the number of trophic links per species, are related in a systematic manner with web size, measured as number of species (Cohen and Newman 1985, Sugihara et al. 1989, Martinez 1991, 1992, Havens 1992). It has been proposed that there is "scale invariance" in food web properties (Briand and Cohen 1984, Pimm et al. 1991). For example, proportions of basal (prey without prey), intermediate (prey with prey) and top (predators without predators) species do not vary with the number of species in a food web, and the number of links between species also does not vary (Briand and Cohen 1984,

Cohen and Briand 1984). The scale invariance or dependence of these food web properties has been tested and debated for both lake webs (Havens 1992, 1993, Martinez 1993, Deb 1995) and other types of webs (Pimm et al. 1991, Martinez 1994). A major problem has been the very high variance in the heterogeneous data used in these studies. This may obscure patterns that exist, so the issue remains unresolved. Thus, improved informaton and more critical tests are needed.

Another issue that is often not addressed, but may be of importance, is the use of "cumulative" data for constructing food webs. Nearly all studies, including multiple-habitat comparisons of simplistic webs (e.g., Briand 1983), and single-habitat analyses of complex webs (e.g., Martinez 1991) portray the community as a static assemblage of species and links with no consideration of spatial and temporal variability. Relatively few studies (Warren 1989, Schoenly and Cohen 1991, "Temporal and Spatial Scale" section in Polis and Winemiller 1996) have examined these kinds of variability.

For this study, zooplankton data have been collected uniformly during several years at many locations in a single large ecosystem, Lake Okeechobee. This provides a unique opportunity to analyze scale dependence and spatiotemporal variation. Consistently collected information on relatively small and simple plankton webs greatly reduces the heterogeneous data and resulting high variance of earlier studies. Like laboratory model systems (Lawton 1995b), such webs can provide powerful insights about patterns and dynamics of more complex and variable complete ecosystem food webs. We have found that the clear results with these webs help resolve some major questions about food web scale dependence vs invariance. We build on previous zooplankton food web studies (Sprules and Bowerman 1988, Havens 1991, Locke 1992). In this paper we present results of analyses of the Lake Okeechobee zooplankton food webs. The two major objectives are to (1) test for scale invariance vs dependence of major food web properties and (2) examine spatial and temporal variation in the structure of zooplankton webs of Lake Okeechobee.

Study site

Lake Okeechobee is a large (1730 km^2), shallow (mean depth less than 3 m) lake located in subtropical south–central Florida, USA. (Fig. 1). The lake is part of a vast interconnected aquatic ecosystem that includes the Kissimmee River, the Florida Everglades, and Florida Bay. The lake receives high inputs of nutrients from a predominantly agricultural watershed (Flaig and Havens 1995), experiences frequent algal blooms (Havens et al. 1996), and is classified as eutrophic (Stoermer et al. 1992). Due to the subtropical location, seasonal variations in water temperature are relatively small (from near 30°C in summer to near 15°C in winter), but seasonal changes in wind velocity, coupled with soft mud sediments, bring about a turbid winter season with low primary productivity, and a calm summer season with greater light availability and high primary productivity (Aldridge et al. 1995, Phlips et al. 1995). There also is considerable spatial heterogeneity. Approximately 25% of the lake's surface area is littoral marsh, and based on recent investigations, the pelagic zone is comprised of four distinct "ecological zones" (Phlips et al. 1993). The north pelagic region overlies mud sediments and has high nutrient levels (due to nearby tributary inputs) with relatively high algal biomass. In the larger central pelagic region, also overlying mud sediments and with high nutrient levels, algal biomass is lower because of the greater water column depth (4–5 m vs 2–3 m in the north). In the polymictic water column, phytoplankton are frequently transported below the aphotic depth of the central region. Along the periphery of the littoral zone, where the sediments are more consolidated sands, rocks, and peat, there is less sediment resuspension. A more favorable light climate favors phytoplankton growth, and nutrient limitation often occurs (Aldridge et al. 1995). A fourth transitional zone occurs between the littoral fringe and central mud zones of the lake.

In this lake, there have been extensive studies of most community components (Aumen and Wetzel 1995) and coarse-scale food webs have been constructed for both the pelagic and littoral regions (Havens et al. 1996). The plankton have been sampled at over 100 locations, from

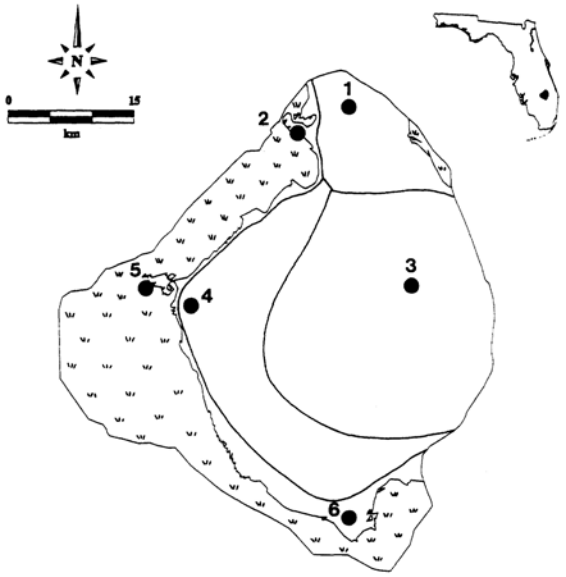

Fig. 1. Map of Lake Okeechobee, with sampling stations numbered. Stations 1, 3, 4, 5 and 6 each represent one of the five ecological zones delimited by the black lines, and station 2 borders two of these zones.

Table 1. Species in the Lake Okeechobee zooplankton food webs, with diet information.

Code	Species name	Type	Prey	Predators
1-DDOR	*Diaptomus dorsalis*	Copepod	3, 13–28	–
2-MEDA	*Mesocyclops edax*		3, 4, 6–28	–
3-NAUP	nauplii		28	1, 2, 4, 5
4-TPRA	*Tropocyclops prasinus*		3, 13–28	2, 5
5-AVER	*Acanthocyclops vernalis*		3, 4, 6–28	–
6-ETUB	*Eubosmina tubicen*	Cladoceran	28	2, 5
7-CRET	*Camptocercus rectirostris*		28	2, 5
8-CSPH	*Chydorus sphaericus*		28	2, 5
9-DAMB	*Daphnia ambigua*		28	2, 5
10-DBRA	*Diaphanosoma brachyurum*		28	2, 5
11-ALON	*Alona* sp.		28	2, 5
12-MROS	*Macrothrix rosea*		28	2, 5
13-AFIS	*Anuraeopsis fissa*	Rotifer	28	1, 2, 4, 5
14-ASCO	*Ascomorpha* sp.		28	1, 2, 4, 5
15-BHAV	*Brachionus havanaensis*		28	1, 2, 4, 5
16-BQUA	*Brachionus quadridentatis*		28	1, 2, 4, 5
17-CDOS	*Conochiloides dossuarius*		28	1, 2, 4, 5
18-EUCH	*Euchlanis* sp.		28	1, 2, 4, 5
19-FLON	*Filinia longiseta*		28	1, 2, 4, 5
20-KCOC	*Keratella cochlearis*		28	1, 2, 4, 5
21-KQUA	*Keratella quadrata*		28	1, 2, 4, 5
22-LECA	*Lecane* sp.		28	1, 2, 4, 5
23-PVUL	*Polyarthra vulgaris*		28	1, 2, 4, 5
24-SROS	*Scaridium rostrum*		28	1, 2, 4, 5
25-TLON	*Trichocerca longiseta*		28	1, 2, 4, 5
26-TMUL	*Trichocerca multicrinis*		28	1, 2, 4, 5
27-TRIC	*Tricocerca* sp.		28	1, 2, 4, 5
28-BASA	algae, bacteria, protozoa	Basal	–	1–27

1988 to 1992; approximately 20 sites were visited as frequently as once per month (Cichra et al. 1995, Crisman et al. 1995). In the present study, we considered zooplankton data from six of the most regularity visited locations (Fig. 1), which correspond to five ecologically distinct zones of the lake (Phlips et al. 1993).

Materials and methods

Details of field sampling and subsequent identification and enumeration are provided in Crisman et al. (1995). Briefly, the following procedures were used. At two- to three-week intervals, an integrated sampler, comprised of a 4-cm-diameter PVC pipe, was used to sample the entire water column at each site. Five such samples were collected during daylight hours, and the contents were collected on a 40-μm Nitex screen. The retained animals were preserved in 40% sucrose-formalin, and transported to the lab for enumeration and taxonomic identification at 100× magnification. All taxa were identified to the species level, and nauplii were considered separately from copepod adults and copepodids.

To make food web calculations, statistical analyses and comparisons more manageable, and for consistency between food webs, we chose to include only those species which contributed at least 5% of the total averaged densities for each location and time. This resulted in a total of 27 zooplankton species (Table 1). We then summed and averaged the field count data for each of six sites for two time periods during each year: winter (December to February) and summer (June to August). This produced a total of 46 food webs (Appendix 1).

All species occurring in these webs are listed with their prey and predators in Table 1. Feeding relations were determined with the best available information. The diets of *Diaptomus dorsalis*, *Mesocyclops edax*, *Eubosmina tubicen*, *Camptocercus rectirostris*, *Chydorus sphaericus*, *Daphnia ambigua*, *Diaphanosoma brachyurum*, and *Alona* sp. were determined from gut analyses and/or feeding experiments conducted at Lake Okeechobee. The diets of *Acanthocyclops vernalis*, cyclopoid nauplii, *Keratella cochlearis*, *Polyarthra vulgaris*, and *Trichocerca multicrinis* were determined from similar studies performed by K. Havens at other locales; and the diets of all other species were taken from published information (Stemberger 1979, Bogdan and Gilbert 1982, Sprules and Bowerman 1988, Adrian and Frost 1993).

Using the above information, we constructed pictorial food web models and binary predator-prey matrices (Cohen 1978) for each time and location. Fig. 2 shows the broad range of food webs constructed. The simplest web contained only 4 zooplankton species connected to a basal resource (Fig. 2A), while the most complex web had 14 zooplankton species and 44 links (Fig. 2C). The web which came closest to the average had 8 zooplankton species and 22 links (Fig. 2B). For consistency with earlier plankton studies we did not lump these species

into "trophic" species (groups of taxonomic species that have the same predators and prey). We feel that "trophic" species are too often poorly resolved aggregates of taxonomic species which do have different feeding relations. For consistency with other zooplankton and invertebrate web studies, other species feed on a single "basal" resource which is a complex mixture of algae, detritus and microheterotrophs. Also, we do not include larger swimming predators such as notonectids and fish.

After the food webs were constructed, the following food web properties were calculated: number of species (S), number of links (L), linkage density (L/S), connectance (C), number and percent of top predators, number and percent of intermediate species, modal food chain length, and average food chain length. Connectance (C) was calculated as in Briand (1983):

$$C = \frac{L}{S(S-1)}$$

where L is the number of links and S is the number of species in the system. Modal food chain length was calculated as in Cohen (1978). These properties are summarized in Table 2 for all webs.

Finally, we examined spatial and temporal variability in food web structure statistically. First, descriptive statistics of each food web property were calculated for the six locations and two time periods. These included means and several error estimates including variance, standard deviation and error, and 95% confidence limits. Then one-factor ANOVAs and multiple-comparison tests (Fisher PLSD, Scheffé F-test, Dunnett t) were used to test for significant differences between locations and seasons. The multiple-comparison tests were added to the ANOVAs because they provided more detailed pairwise comparisons for individual stations. Principal component analysis (PCA) was performed for multivariate comparisons of the stations according to the major food web properties.

Several properties (L, L/S, C, top and intermediate species, modal food chain length) were regressed against S to test for scale invariance vs dependence. Following Bersier and Sugihara (unpubl.) we analyzed a suite of competing models: linear, 2nd, 3rd and 4th order polynomial, power law ($Y = a \times S \wedge b$, with Y a property, and a and b fitted constants), exponential asymptotic ($Y = a + b \times \exp(-cS)$, with a, b and c fitted constants), and piecewise linear: ($Y = a_0 + b_0 \times S$

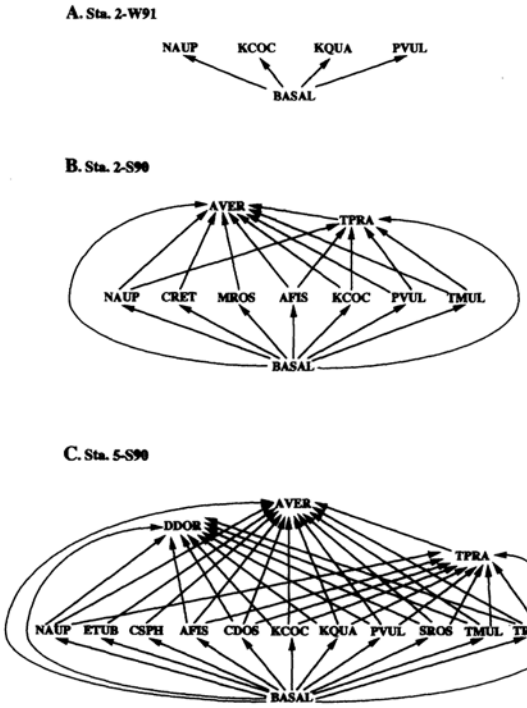

Fig. 2. Diagrams of three representative food webs: A. simplest, B. average, C. most complex. Full species names for the four-letter codes are provided in Table 1.

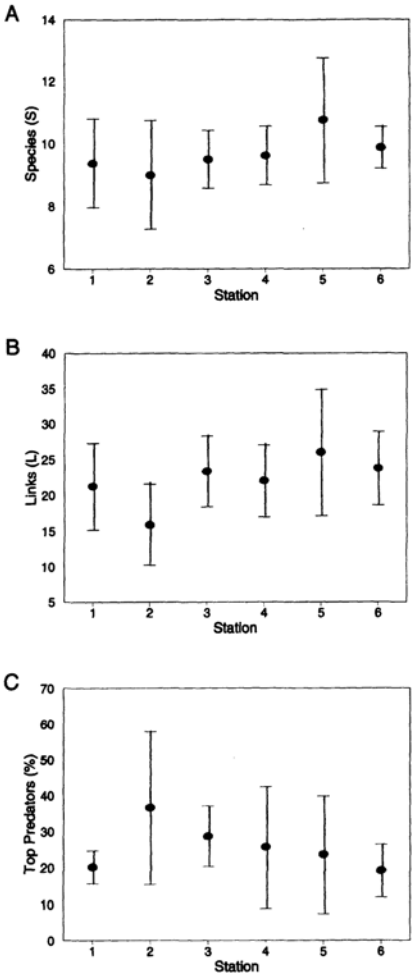

Fig. 3. Food web properties by station (±95% confidence limits): A. number of species per web, B. links, C. proportion of top predators.

[if $S \leqslant c$], $Y = a_1 + b_1 \times S$ [if $S > c$], with a_0, b_0, a_1, b_1, and c fitted constants). The suitability of a model was evaluated by inspecting its performance and the lack of systematic pattern in the residuals. To determine which model was the most appropriate given its number of parameters, we computed the Akaike Information Criterion [AIC] (Sakamoto et al. 1986). The model which minimized the AIC was considered to be the best one. A systematic error was evaluated in two ways, first by fitting polynomial regressions to the residuals to determine if higher order structure was present. Second, we evaluated the presence of heteroscedasticity by fitting a linear regression to the absolute values of the residuals (Zar 1984).

Results and discussion

Food web structure and spatiotemporal variation

Properties of the 46 Lake Okeechobee food webs are presented in Table 2. Average values for all webs are 9.7 species, 22 links, 2.2 links per species, and a connectance of 0.25. These results are in the range of previously published zooplankton food webs. In 53 Canadian lake zooplankton webs examined by Sprules and Bowerman (1988) there were 10.2 species per web and a mean links per species of 2.6. These somewhat higher average values were probably due to their inclusion of rarer taxa. By contrast, in 25 United States lakes analyzed by Havens (1991) there were averages of 5.4 zooplankton species per lake and 1.5 links per species. These lower values were clearly due to the acidification stress in many of the low pH lakes considered.

The major food web properties were generally similar for all sampling locations in Lake Okeechobee (Fig. 3). ANOVA and multiple pairwise comparisons did not detect any statistically significant differences between stations. Still, there were consistent differences between stations for most properties. For example, station 2 had the lowest average number of species and links, while

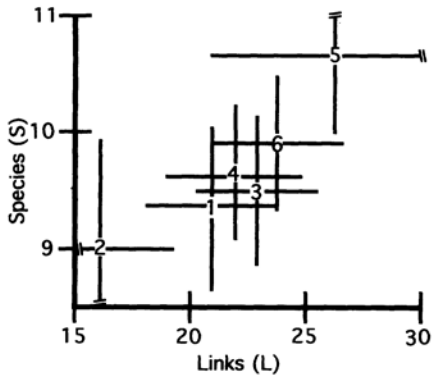

Fig. 4. Bivariate plot of number of species vs links per web (±S.E.) by station.

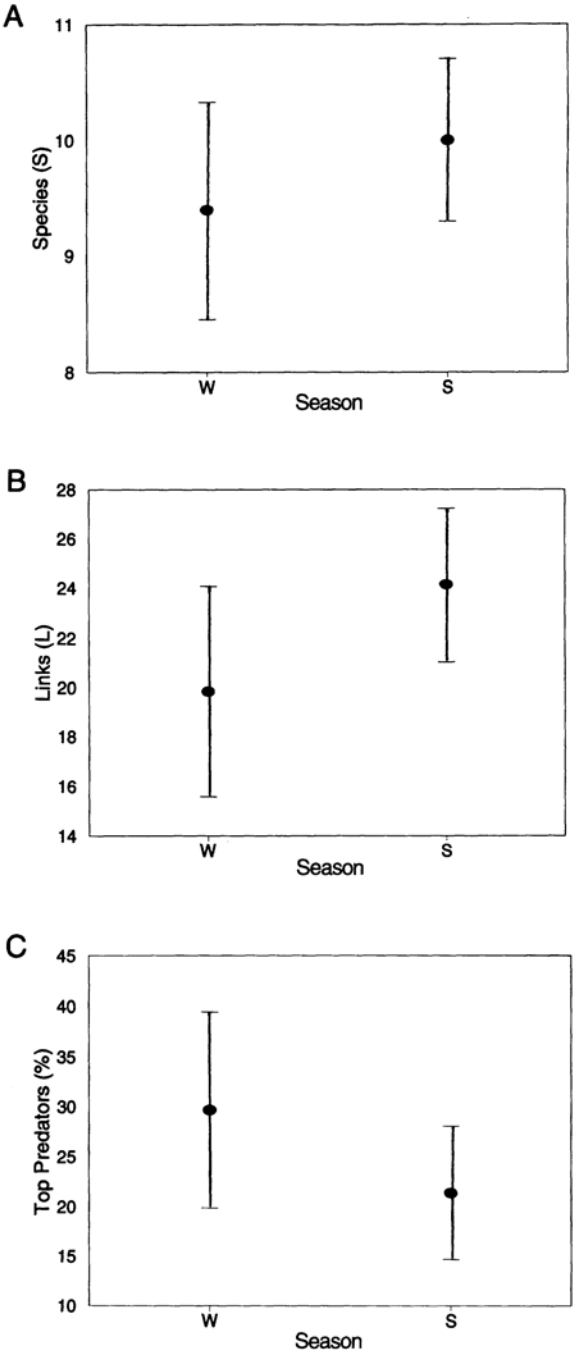

Fig. 5. Food web properties by season (±95% confidence limits): A. number of species per web, B. links, C. proportion of top predators. W = winter, and S = summer.

station 5 had the highest values of these properties. Corresponding with this, the proportion of top predators was highest in station 2. Principal component analysis (PCA) confirmed these patterns, but the major properties were highly correlated so the analysis did not distinguish the stations well. On the other hand, a bivariate plot of species vs links for the different loca-

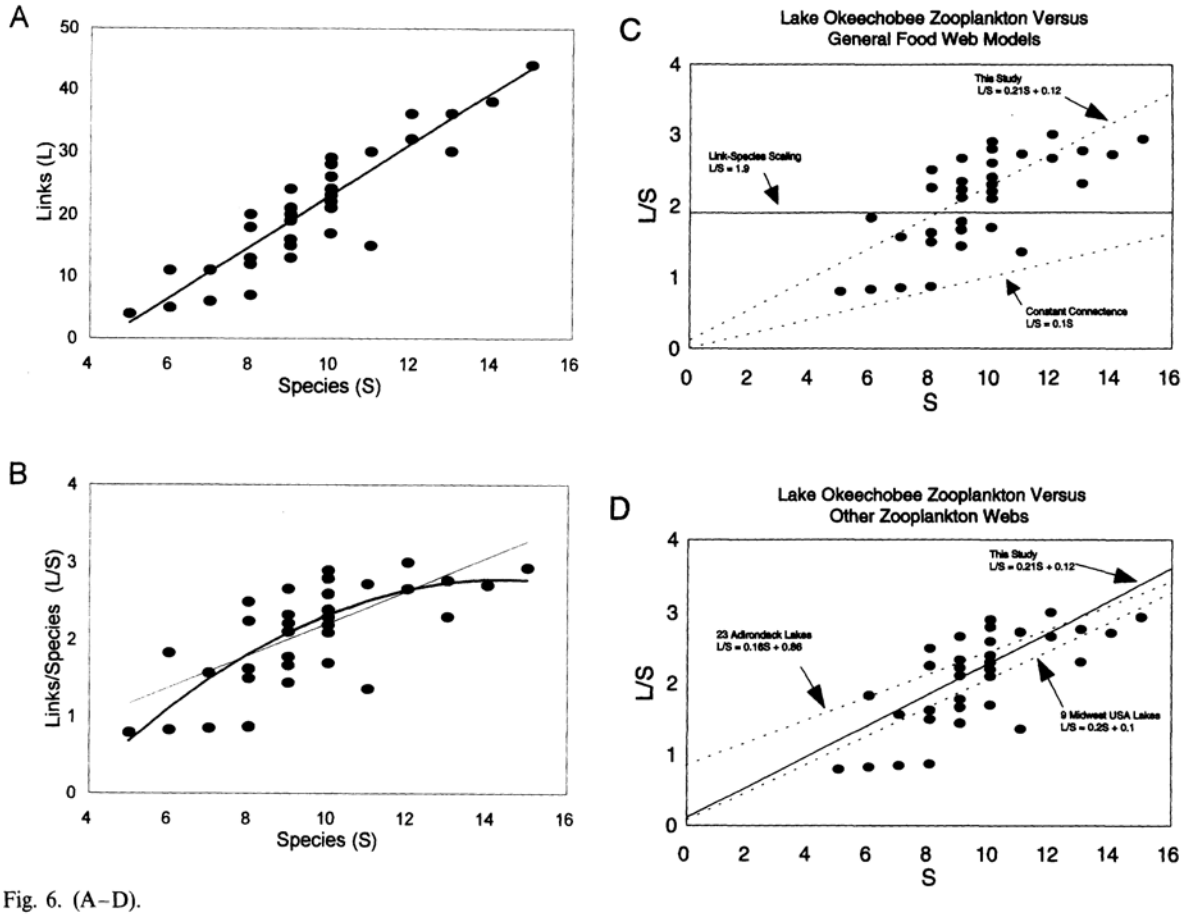

Fig. 6. (A–D).

tions (Fig. 4) clearly demonstrated the relative differences of stations 2 and 5.

Several explanations for these differences can be given. These two stations are closest to shore in the littoral region (Fig. 1). Station 2 is near the mouth of the Kissimmee River, the major inflow into Lake Okeechobee. Thus the station 2 food web may be simplified by the turbidity and other stresses in the river outflow. River effluent generally contains high levels of abiotic seston which negatively impacts crustacean herbivores (Kirk and Gilbert 1990). The waters of the Kissimmee can also have low oxygen concentrations (there have been fish kills due to anoxia) which could impact the zooplankton. At the other extreme, the more complex webs at station 5 may be due to the habitat heterogeneity and complex interactions which occur in nearshore areas in absence of tributary effects.

Seasonal differences are likewise not statistically significant according to ANOVA and multiple pairwise comparisons, but again there are consistent trends among properties (Fig. 5). Food webs are generally less complex, with fewer species and links, in the winter than in the summer. As in lakes of higher latitudes, this is probably due to the cooler temperatures, mixing and reduced biological activity during the winter. Lake Okeechobee clearly does not have the dramatic seasonal fluctuations which characterize lakes that freeze over during the winter. Still, these and other analyses (Crisman et al. 1995) indicate that it does have muted seasonality which can be found in many tropical and subtropical lakes (Richerson and Carney 1988).

In general, connectedness webs appear to have a limited ability to resolve spatial and temporal variation in community structure. This may be because they do not take into account species abundances. Preliminary results from cluster analyses which use relative species densities (Beaver and Havens unpubl.) indicate spatial variation more clearly. Web properties may still be easier to use when very substantial impacts such as pollution, species invasions or hurricanes dramatically alter food webs. For Lake Okeechobee, many kinds of spatiotemporal variation may be subtle because of the muted seasonality and the high mixing and turbulence in this large shallow system. Our analyses have of necessity been limited to relatively few times and locations. With larger data sets, analyses designed specifically to examine spatiotemporal variability (e.g. Legendre 1993) can be used to detect significant variation with more statistical rigor and power.

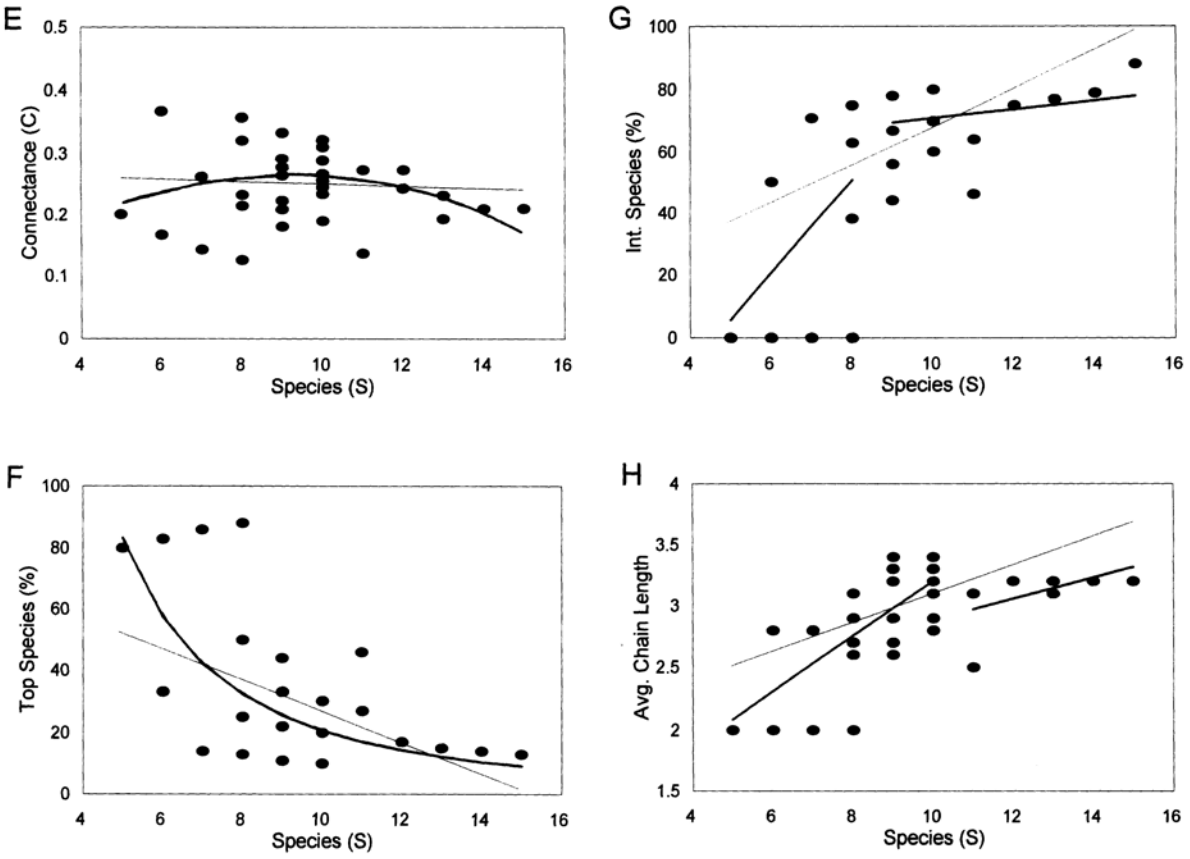

Fig. 6. Regressions of various food web properties vs number of species (S) per web: A. links (L), B. links per species (L/S), C. L/S in this study compared to link-species scaling law and constant connectance, D. L/S in this study compared to Adirondack and midwest lakes, E. connectance (C), F. percent of top species, G. percent of intermediate species, H. average food chain length. In B and E–H the regressions for the best models listed in Table 3 are shown (thick lines) and compared to simple linear models (thin lines).

Scale dependence in small plankton webs

One of the most striking features of the Lake Okeechobee webs is the high correlation of many food web properties with S and each other (Fig. 6). These clearly indicate a shift from scale dependence (Martinez 1993) at smaller web sizes to more scale invariance (Briand and Cohen 1984, Cohen and Briand 1984, Sugihara et al. 1989, Havens 1992) at larger web sizes. A simple linear regression of links (L) vs species (S) is highly significant ($p = 0.0001$, $R^2 = 0.82$, Fig. 6A). More complex nonlinear regressions also fit the data quite well. Since they were not substantial improvements, we present results of the simplest model here. This regression could be consistent with both scale dependence and invariance, so more critical tests are needed and provided below. The regression slope is 4.1 and webs range from 4 links at 5 species to 44 links at 15 species.

For the relationships of other major food web properties vs S, curvilinear and piecewise linear regressions are a decisive improvement over simple linear models (Table 3) when compared using AIC, R^2 and p values. This is because there is a clear and consistent shift from strong scale dependence in smaller webs to much more gradual trends in larger webs (Figs 6B–H). For example, for links per species (L/S) vs species (S), a second-order polynomial regression is the most appropriate model since it has the lowest AIC (59.7) (Table 3). L/S increases from 0.8 at 5 species to 3.0 at 12 species, so linkage density is clearly scale dependent. Four low-diversity webs contain only two major trophic levels (rotifers feeding on algae), so they average less than one link per species. They contribute greatly to the regression trend.

The overall relationship between L/S and S documented here is markedly different from that predicted by the link-species scaling "law" (Cohen and Newman 1985) (Fig. 6C). It comes closer to the prediction of the constant connectance hypothesis (Martinez 1992), but the slope is initially higher, and then declines dramatically. Also, the relationship is very similar to that observed among zooplankton webs of the Adirondack Mountains, NY (Havens 1991), and the mid-western USA (Havens unpubl.) (Fig. 6D). These

Table 2. Summary of major patterns for 46 Lake Okeechobee food webs. In the first column, "St" refers to station, which is followed by the station number. "W" and "S" refer to winter and summer, respectively, which are followed by the year.

Web	Species (S)	Links (L)	Links/sp. (L/S)	Connectance (C)	Top sp. (%)	Intermed. sp. (%)	Chain length (Av. FCL)
St1W88	14	38	2.71	0.21	14	79	3.2
St1W89	8	13	1.63	0.23	13	75	2.9
St1W90	7	11	1.57	0.26	14	71	2.8
St1W91	9	13	1.44	0.18	33	56	2.6
St2W88	10	17	1.7	0.19	10	80	2.9
St2W89	8	7	0.88	0.13	88	0	2.0
St2W90	6	11	1.83	0.37	33	50	2.8
St2W91	5	4	0.8	0.2	80	0	2.0
St3W89	11	30	2.73	0.27	27	64	3.1
St3W90	8	13	1.63	0.23	50	38	2.6
St3W91	10	24	2.4	0.27	20	70	3.1
St4W88	10	21	2.1	0.23	30	60	2.8
St4W89	12	32	2.67	0.24	17	75	3.2
St4W90	9	20	2.22	0.28	11	78	3.3
St4W91	10	26	2.6	0.29	20	70	3.2
St5W88	13	36	2.77	0.23	15	77	3.2
St5W89	8	12	1.5	0.21	25	63	2.7
St5W90	12	32	2.67	0.24	17	75	3.2
St5W91	6	5	0.83	0.17	83	0	2.0
St6W88	9	16	1.78	0.22	44	44	2.7
St6W89	12	36	3	0.27	17	75	3.2
St6W90	10	24	2.4	0.27	10	80	3.4
St6W91	9	15	1.67	0.21	11	78	2.9
St1S89	9	24	2.67	0.33	22	67	3.2
St1S90	8	20	2.5	0.36	25	63	3.1
St1S91	10	28	2.8	0.31	20	70	3.2
St1S92	10	23	2.3	0.26	20	70	2.9
St2S89	13	30	2.31	0.19	15	77	3.1
St2S90	10	22	2.2	0.24	10	80	3.3
St2S91	11	15	1.36	0.14	46	46	2.5
St2S92	9	21	2.33	0.29	11	78	3.4
St3S89	10	29	2.9	0.32	30	60	3.2
St3S90	10	26	2.6	0.29	20	70	3.2
St3S92	8	18	2.25	0.32	25	63	3.1
St4S89	10	26	2.6	0.29	20	70	3.2
St4S90	10	24	2.4	0.27	10	80	3.4
St4S91	9	21	2.33	0.29	11	78	3.4
St4S92	7	6	0.86	0.14	86	0	2.0
St5S89	9	19	2.11	0.26	11	78	3.2
St5S90	15	44	2.93	0.21	13	80	3.2
St5S91	13	36	2.77	0.23	15	77	3.2
St5S92	10	24	2.4	0.27	10	80	3.4
St6S89	10	28	2.8	0.31	20	70	3.2
St6S90	10	28	2.8	0.31	20	70	3.2
St6S91	10	28	2.8	0.31	20	70	3.2
St6S92	9	15	1.67	0.21	11	78	2.9
Average	9.70	21.98	2.18	0.25	26	64	3.0

results are consistent with hypotheses presented by Warren (1990) and Havens (1993) that food webs dominated by particle feeders display rapid increases of L/S with S, while other webs do not. In food webs with traditional predators, certain prey are captured and eaten one at a time, and the total number of prey species that a predator can exploit is limited by morphological constraints. As Pimm (1982) noted, "a tooth or beak designed for cracking or grinding seeds is not optimally suited for tearing flesh, or vice versa". In food webs dominated by particle-feeders, predation is size-based rather than species-based (Burns 1968, Geller and Muller 1981), and a very small or large number of prey species may fall into the particle size range that a predator can exploit. Consequently, the upper bound on the number of prey per predator is greatly enhanced, and the slope of L/S vs S can be very high, as observed herein. High L/S and connectance may also be due to the single basal resource category which includes many basal species. If we also lump the taxonomic zooplankton species into "trophic" species for the webs in Fig. 2, L/S decreases from 0.8–2.9 to 0.5–1.7.

For the Lake Okeechobee webs, connectance (C) is relatively constant in relation to number of species (adj. $R^2 < 0.001$, $p = 0.67$ for simple linear regression,

Table 3 and Fig. 6E). This is due to the high variance in connectance values (range 1.3–3.7) as well as to relative constancy. These data are qualitatively consistent with the constant connectance ($C = 0.1$) hypothesis (Martinez 1992) for webs of up to 93 trophic species, but our mean value of 0.25 is relatively high. If "trophic" species are used instead of taxonomic species, these values are even higher (for example, 0.3–0.5 for the webs in Fig. 2). This reflects a high number of links in relation to the number of species due to the reasons given above (see also Warren 1990, 1995). Martinez (1992) and Warren (1995) have also noted that smaller webs can have higher connectance. There is a very slight decrease in connectance with increasing S. A 2nd-order curvilinear relationship in which C declines gradually at higher S provides the best fit (adj. $R^2 = 0.040$, $p = 0.16$, AIC $= -317$) among the various models tested. This may have meaning for a broader range of food web sizes. For constant connectance, the total links in a web must be a constant proportion of the square of the total number of species, e.g. $L = 0.1S^2$. This requires an L/S of less than 1 for webs smaller than 10 species, and an L/S of greater than 10 for webs over 100 species. By comparison, our L/S values for small webs are all higher than the constant connectance prediction. And in much larger webs, a given species may have direct feeding links to a smaller proportion of all species in the web. This can lead to lower connectance when rare prey species are not included (H. Carney unpubl.). Thus the constant connectance model may provide the best fit to intermediate webs of 10–100 species.

For the proportions of top and intermediate species (Figs 6F and 6G) there are very clear, significant ($p < 0.001$) and interrelated patterns in relation to species number. A power law model best describes the relationship between the proportion of top species and S, while a piecewise linear model is the most appropriate for the proportion of intermediate species (Table 3). Top species decline from at least 80% in smaller webs to below 20% in the largest ones. Correspondingly, intermediate species increase from 0% in some smaller webs to over 70% in the most diverse webs. There are no intermediate species when only rotifers feed on algae in the smaller webs, but when these species are in turn fed upon in larger webs, there are few top species as in the cumulative web. While some of these explanations may be considered specific to plankton, the patterns may be quite general. They have been detected, albeit with much higher variance and lower R^2, in data sets which include both terrestrial and aquatic webs (Martinez 1994, Bersier and Sugihara unpubl.). Finally, and logically consistent with the above, there is a clear and significant increase in average food chain length from 2 in smaller webs to above 3 in the most diverse (Fig. 6H). This is due to the addition of intermediate species in the more speciose webs, so the curve is like the one in Fig. 6G for those species.

There is already additional evidence that these shifts in scale dependence occur in other kinds of food webs. Bersier and Sugihara (unpubl.) have analyzed the invertebrate food webs of Sugihara et al. (1989) and found a reduction in scale dependence at about 12 species. For

Table 3. Comparisons of simple linear vs several more complex regression models for some major food web properties. Abbreviations: adj. R^2 – adjusted R^2, AIC – Akaike Information Criterion, p (Het.) – p value for heteroscedasticity, p (H.O.S.) – p value for higher order structure. **Bold** numbering indicates the model which is most appropriate for each property according to AIC.

Property	L/S	C	$\%T$	$\%I$	Av.FCL
1) Linear					
adj. R^2	0.478	<0.001	0.260	0.337	0.308
AIC	68.09	−312.68	−100.60	−96.82	6.95
p	<0.001	0.674	<0.001	<0.001	<0.001
p (Het.)	0.239	0.004	<0.001	<0.001	0.033
p (H.O.S)	0.068	0.172	0.012	0.004	0.004
2) 2nd order polynomial					
adj. R^2	**0.529**	**0.040**	0.384	0.474	0.454
AIC	**59.69**	**−317.10**	−116.46	−117.03	−13.92
p	**<0.001**	**0.158**	<0.001	<0.001	<0.001
p (Het.)	**0.080**	**0.004**	<0.001	<0.001	0.009
p (H.O.S)	**0.830**	**0.934**	0.769	0.742	0.970
3) Power law					
adj. R^2	0.482	0	**0.397**	0.341	0.355
AIC	67.34	−312.33	**−119.44**	−97.41	0.498
p (Het.)	0.135	0.011	**<0.001**	<0.001	0.026
p (H.O.S)	0.081	0.158	**0.770**	0.005	0.016
4) Piecewise linear					
adj. R^2	0.542	0.056	0.405	**0.493**	**0.478**
AIC	79.34	−53.54	−58.70	**−122.87**	**−20.43**
p (Het. s.w.)	0.285	0.015	0.724	**0.728**	**0.015**
p (Het. l.w.)	0.028	0.022	0.048	**0.037**	**0.084**
p (H.O.S)	0.866	0.957	0.963	**0.975**	**0.970**

more complete aquatic webs with more species (Havens 1992) the shift appears to occur at a higher number of about 30 species.

Conclusions

The food web properties we have examined for Lake Okeechobee do not indicate striking temporal and spatial variability in biological structure and interactions. Still, we do find some clear trends which are consistent with muted seasonality, and some differences between littoral and pelagic habitats can be made clearer with additional analyses. We also find a clear nonlinear scale dependence in food web properties for these planktonic webs. This is especially the case for links per species, food chain length, and proportions of top and intermediate species vs number of species. These results thus help reconcile previous studies which supported either scale dependence or scale invariance in food web properties. The simpler and more consistent Lake Okeechobee data contribute to our clearer and statistically stronger results. What these results indicate most clearly is that there is a shift from strong scale dependence in smaller webs to much more gradual scale dependence or scale invariance in larger webs. What is less clear is how gradual scale dependence is in larger webs, whether there may be scale invariance for certain intervals, and how these relationships vary for different properties. Thus, additional testing is needed with improved information from other aquatic and terrestrial ecosystems.

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Appendix 1. Species composition of the 46 Lake Okeechobee food webs included in this study. Numerical codes of the species are listed. Names of the species are provided in Table 1.

Web	Species
St1W88	1, 3–6, 8, 10, 13, 15, 20, 22, 23, 26, 28
St1W89	3, 5, 17, 18, 20, 23, 26, 28
St1W90	1, 3, 18, 20, 23, 26, 28
St1W91	1, 3, 6, 8, 20, 21, 23, 26, 28
St2W88	3, 5 6, 10, 13, 15, 20, 23, 26, 28
St2W89	3, 6, 13, 17, 20, 23, 26, 28
St2W90	1, 5, 20, 21, 23, 28
St2W91	3, 20, 21, 23, 28
St3W89	1–6, 9, 10, 20, 23, 28
St3W90	1, 3, 4, 6, 9, 20, 23, 28
St3W91	1, 3–6, 9, 13, 20, 23, 28
St4W88	1, 3, 4, 6, 13, 15, 20, 23, 26, 28
St4W89	1, 3–6, 9, 17, 20, 21, 23, 26, 28
St4W90	3–6, 20, 21, 23, 26, 28
St4W91	1, 3–6, 20, 21, 23, 26, 28
St5W88	1, 3–6, 10, 13, 14, 20, 23, 25, 26, 28
St5W89	1, 9, 17, 18, 20, 21, 26, 28
St5W90	1, 4–6, 11, 13, 17, 20, 21, 23, 26, 28
St5W91	13, 20, 21, 23, 26, 28
St6W88	1, 3, 4, 8, 10, 20, 23, 26, 28
St6W89	1, 3, 4, 5, 15, 17, 18, 20, 21, 23, 26, 28
St6W90	3, 4, 5, 15, 18, 20, 21, 23, 26, 28
St6W91	1, 3, 15, 18, 20, 21, 23, 26, 28
St1S89	1, 3, 4, 5, 15, 20, 23, 26, 28
St1S90	1, 3, 4, 5, 15, 20, 23, 28
St1S91	1, 3, 4, 5, 15, 20, 21, 23, 26, 28
St1S92	1, 3, 5, 13, 17, 19, 20, 23, 26, 28
St2S89	1, 3–8, 10, 11, 20, 23, 26, 28
St2S90	3, 4, 5, 7, 12, 13, 20, 23, 26, 28
St2S91	1, 3, 6, 7, 11–13, 20, 23, 26, 28
St2S92	3, 4, 5, 13, 15, 20, 23, 26, 28
St3S89	1–5, 10, 20, 23, 26, 28
St3S90	1, 3, 4, 5, 10, 15, 20, 23, 26, 28
St3S92	1, 3, 4, 5, 10, 20, 23, 28
St4S89	1, 4, 5, 10, 13, 19, 20, 23, 26, 28
St4S90	3, 4, 5, 13, 15, 19, 20, 23, 26, 28
St4S91	3, 4, 5, 13, 15, 20, 23, 26, 28
St4S92	3, 13, 15, 20, 23, 26, 28
St5S89	4, 5, 6, 10, 13, 20, 23, 26, 28
St5S90	1, 3–6, 8, 13, 17, 20, 21, 23, 24, 26, 27, 28
St5S91	1, 3–6, 8, 13, 17, 20, 21, 23, 26, 28
St5S92	3, 4, 5, 13, 15, 17, 20, 21, 26, 28
St6S89	1, 3, 4, 5, 15, 19, 20, 23, 26, 28
St6S90	1, 3, 4, 5, 13, 15, 20, 23, 26, 28
St6S91	1, 3, 4, 5, 13, 15, 20, 23, 26, 28
St6S92	1, 3, 13, 15, 20, 21, 23, 26, 28