

the common conclusion that the tektite ejection process selectively samples only the top ~100 m of target material and, therefore, a thin veneer of carbonate over siliceous materials may be sufficient to produce the observed trends of chemical variation between the glasses. Proposed impact sites at both Manson, Iowa, and Chicxulub, Mexico, are in geologic terranes where appropriate mixtures of carbonate and silicate target materials are present (1–4).

REFERENCES AND NOTES

1. H. Sigurdsson *et al.*, *Nature* **353**, 839 (1991).
2. G. A. Izett, *J. Geophys. Res.* **96**, 20879 (1991).
3. A. R. Hildebrand *et al.*, *Geology* **19**, 867 (1991).
4. H. Sigurdsson, S. D'Hondt, S. Carey, *Earth Planet. Sci. Lett.* **109**, 543 (1992).
5. Samples were disaggregated by dissolving the carbonate matrix in dilute HCl. Spherules and fragments of unaltered black and yellow glass were hand-picked under a microscope.
6. A. R. Hildebrand and W. V. Boynton, *Science* **248**, 843 (1990).
7. H. Sigurdsson *et al.*, *Nature* **349**, 482 (1991).
8. F. J.-M. R. Maurrasse and G. Sen, *Science* **252**, 1690 (1991).
9. J. B. Lyons and C. B. Officer, *Earth Planet. Sci. Lett.* **109**, 205 (1992).
10. C. Jéhanno *et al.*, *ibid.*, p. 229.
11. C. B. Officer *et al.*, *GSA Today* **2**, 69 (1992).
12. Z. D. Sharp, *Geochim. Cosmochim. Acta* **54**, 1353 (1990).
13. C. P. Chamberlain and M. E. Conrad, *Science* **254**, 403 (1991).
14. Major element analyses were performed on 52 samples using a Cameca MBX electron microprobe. Analytical totals ranged from 94 to 98% (largely due to a poor polish necessitated by recovery of the samples) and were normalized to 100%.
15. J. Smit *et al.*, *Geology* **20**, 99 (1992).
16. Twenty-eight samples were recovered by dissolving away the acetone-soluble mounting medium and analyzed for oxygen isotopic composition. The apparatus is similar to that of Sharp (12), but differs in its laser beam delivery system. A 10-W continuous CO₂ laser beam was allowed to melt each sample in a BrF₅ atmosphere. After freezing the sample on a liquid nitrogen trap, the oxygen was passed through a mercury transfer pump to remove fluorine gas. The oxygen was then converted to CO₂ on a hot carbon rod. Samples ranged from 8.9 to 96.6 μmol of CO₂ and were analyzed for oxygen isotopic composition on a Finnigan Delta E mass spectrometer and are reported relative to standard mean ocean water (SMOW).
17. The uncertainty associated with the reported $\delta^{18}\text{O}$ values is estimated to be ± 0.2 per mil based on three independent experiments: (i) a rather large (10 mg) K-T glass spherule (sample A4a) was broken into three pieces and each was analyzed separately (Table 1); (ii) pairs of analyses made on two Australasian Muong Nong-type tektites (samples 8301 and 8319) agreed within 0.1 per mil (Table 1); and (iii) 30 replicate laser analyses of a quartz standard (38) with a conventional $\delta^{18}\text{O}$ = 11.7 per mil, yielded $\delta^{18}\text{O}$ = 11.7 ± 0.16 per mil (1σ).
18. H. P. Taylor and S. M. F. Sheppard, *Rev. Mineral.* **16**, 227 (Mineralogical Society of America, Washington, DC, 1986).
19. L. S. Walter and R. N. Clayton, *Science* **156**, 1357 (1967).
20. H. P. Taylor and S. Epstein, *J. Geophys. Res.* **74**, 6834 (1969).
21. N. Oskarsson *et al.*, *Lunar. Planet. Sci.* **XXII**, 1009 (1991).
22. W. R. Premo and G. A. Izett, *Meteoritics*, in press.
23. We use the term carbonate to represent a rock composed mainly of the mineral calcite (CaCO₃) but which also contains common impurities including dolomite and silicates.
24. We use the term sulfate-rich evaporite to represent a rock containing gypsum (CaSO₄·2H₂O) or anhydrite (CaSO₄).
25. T. Sharma and R. N. Clayton, *Geochim. Cosmochim. Acta* **29**, 1347 (1965).
26. M. B. Boslough *et al.*, *Earth Planet. Sci. Lett.* **61**, 166 (1982).
27. K. H. Wedepohl, in *Handbook of Geochemistry*, K. H. Wedepohl, Ed. (Springer-Verlag, Berlin, 1969), vol. 1, pp. 250–269.
28. J. R. O'Neil and R. N. Clayton, in *Isotopic and Cosmic Chemistry*, H. Craig, S. Miller, G. J. Wasserburg, Eds. (North-Holland, Amsterdam, 1964), pp. 157–168.
29. F. H. Stewart, *U.S. Geol. Surv. Prof. Pap.* **440-YY1** (1963).
30. G. E. Claypool *et al.*, *Chem. Geol.* **28**, 199 (1980).
31. A. P. Vinogradov and A. B. Ronov, *Geochemistry (U.S.S.R.) (Engl. Transl.)* **6**, 533 (1956).
32. L. S. Walter and M. K. Carren, *Geochim. Cosmochim. Acta* **28**, 937 (1964).
33. C. Koeberl and H. Sigurdsson, *ibid.* **56**, 2113 (1992).
34. J. D. O'Keefe and T. J. Ahrens, *Nature* **338**, 247 (1989).
35. W. von Engelhardt *et al.*, *Geochim. Cosmochim. Acta* **51**, 1425 (1987).
36. J. D. Blum *et al.*, *ibid.* **56**, 483 (1992).
37. L. W. Alvarez *et al.*, *Science* **208**, 1095 (1980).
38. M. E. Conrad and C. P. Chamberlain, *Geology*, in press.
39. B. P. Glass and C. Koeberl, *Meteoritics* **24**, 143 (1989).
40. We thank J. B. Lyons and C. B. Officer for providing the bulk Haitian sample, and C. Koeberl for providing the Muong Nong samples. This work was supported by grants from the National Science Foundation and a Burke Research Initiation Award from Dartmouth College.

3 April 1992; accepted 15 July 1992

Scale and Structure in Natural Food Webs

Karl Havens

The degree to which widely accepted generalizations about food web structure apply to natural communities was determined through examination of 50 pelagic webs sampled consistently with even taxonomic resolution of all trophic levels. The fraction of species in various trophic categories showed no significant overall trends as the number of species varied from 10 to 74. In contrast, the number of links per species increased fourfold over the range of species number, suggesting that the link-species scaling law, defined on the basis of aggregated webs, does not reflect a real ecological trend.

For over two decades, ecologists have tried to establish generalizations about the structure of natural food webs. From trends in published webs, three scaling laws (1–3) have been proposed. The first, the species scaling law, proposes that the basal (autotrophs and detritus), intermediate (preying on others and themselves preyed upon), and top (having no predators) fractions of species do not vary with the total number of species (S) in the web. The second, the link scaling law, proposes that the fractions of top-intermediate, top-basal, intermediate-intermediate, and intermediate-basal links do not vary with S . The third, the link-species scaling law, proposes that the total number of links (L) is proportional to S and that linkage density ($d = L/S$) does not vary with S .

These laws have been supported by studies, each including up to 113 webs (1–5). They have also been criticized for lack of uniformity in data collection, linkage criteria, and species aggregation in the food webs used to develop and test the laws (6, 7). For example, some webs present “whales” as several distinct trophic groups, whereas others make whales a single group that feeds on plankton, macroinvertebrates, and seals. Ag-

gregation tends to be uneven across trophic levels; basal species are often lumped into categories such as “plankton” while top species are aggregated only slightly or not at all (8). To address this problem, Briand and Cohen developed scaling laws for webs where biological taxa were first aggregated into “trophic species,” those having identical predators and prey (1). Others have argued that this aggregation disguises trophically important interactions (6, 9), and it remains uncertain whether the scaling laws reflect trends in natural nonaggregated webs. Recently Martinez (10) suggested that they do not, and Briand, Cohen, and others have proposed that link-species scaling in particular might be scale-dependent (2, 4, 11, 12). However, investigations have used either descriptions of webs from various sources that differ in sampling methods and completeness (13, 14) or a single, highly resolved web successively aggregated by computer algorithms (10).

I have analyzed the scaling laws using a large group of nonaggregated natural webs sampled consistently and constructed from identical linkage criteria (15, 16). The 50 webs represent the pelagic communities of small lakes and ponds in New York State sampled as part of the Adirondack Biota Project (17). Taxa at all trophic levels (fish, invertebrate predators, zooplankton, and phytoplankton) are resolved to genus

Department of Biological Sciences and Water Resources Research Institute, Kent State University, Kent, OH 44242.

or species and further resolved into life history stages where ontogenic changes in diet occur (for example, cyclopoid nauplii and larval fish). A total of 220 taxa are represented. The webs range in size from 10 to 74 species (Table 1), approximately the same range of S covered by the nonaggregated webs of Sugihara *et al.* (13) and a much greater range than covered by the original Briand (18) webs.

The data from the 50 natural webs (Fig. 1) support the species scaling law (1–3). The fractions of top (TF), intermediate (IF), and basal (BF) species are scale invariant, with means of 0.06, 0.44, and 0.50, respectively. Cohen and Briand (2) reported scale-invariant fractions with means of 0.19, 0.53, and 0.29. Martinez (10) reported means of 0.01, 0.86, and 0.13 and suggested that the greater

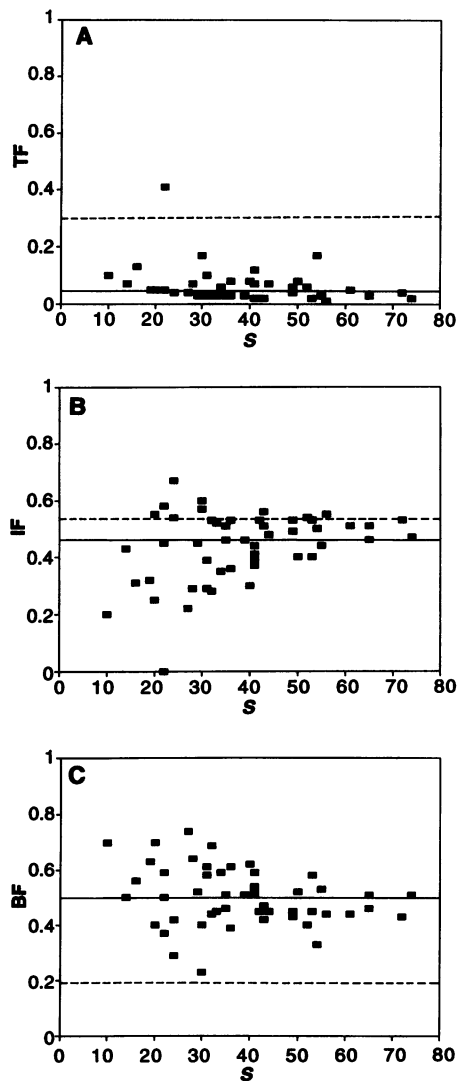


Fig. 1. Fraction of species in (A) top (TF), (B) intermediate (IF), and (C) basal (BF) trophic categories as a function of S . The solid lines represent the fraction means; the dashed lines indicate the fraction means predicted by the species scaling law.

fraction of top species given by Cohen and Briand was an artifact of aggregation. The present results indicate that for pelagic webs that view is correct; only a small fraction of species are top predators. Indeed, it is questionable whether any natural food webs contain top species as defined by Cohen and Briand (1, 2), which lack all predators includ-

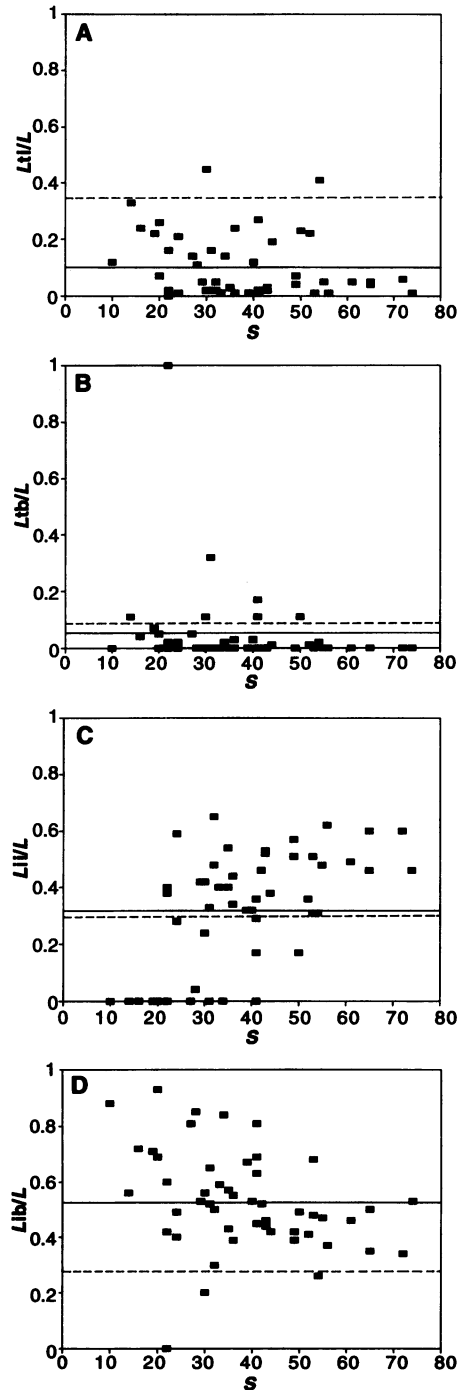


Fig. 2. Fraction of (A) top-intermediate (L_{ti}/L), (B) top-basal (L_{tb}/L), (C) intermediate-intermediate (L_{ii}/L), and (D) intermediate-basal (L_{ib}/L) links as a function of S . The solid lines represent the fraction means; the dashed lines indicate the fraction means predicted by the link scaling law.

ing cannibals (10). By convention (1–5), cannibalistic interactions were not considered when assigning species to the three trophic categories. Had they been included, none of the webs would have contained top species. In the smallest webs ($S < 20$) there is evidence of a reduced fraction of intermediate species and an increased fraction of basal species. These trends are not statistically significant but have been reported previously (1, 2, 10). The trends coincide with a reduction in the number of intermediate trophic levels from two to one.

The results in Fig. 2 support the link scaling law (1–3). The fractions of top-intermediate (L_{ti}/L), top-basal (L_{tb}/L), intermediate-intermediate (L_{ii}/L), and intermediate-basal (L_{ib}/L) links are scale invariant, with means of 0.10, 0.05, 0.32, and 0.53, respectively. Cohen and Briand (2) reported scale-invariant fractions with means of 0.35, 0.08, 0.30, and 0.27. More links to top species and fewer intermediate-basal links reflect inflated values for the fraction of top species in their webs (10). In the smallest webs herein, the fraction of top-basal links is increased while the fraction of intermediate-intermediate links is reduced to zero. The trends are not statistically significant but have been previously observed (1, 2, 10). In this case, they reflect the loss of intermediate-intermediate links in webs where the number of trophic levels is less than four.

Overall, the results support Briand and

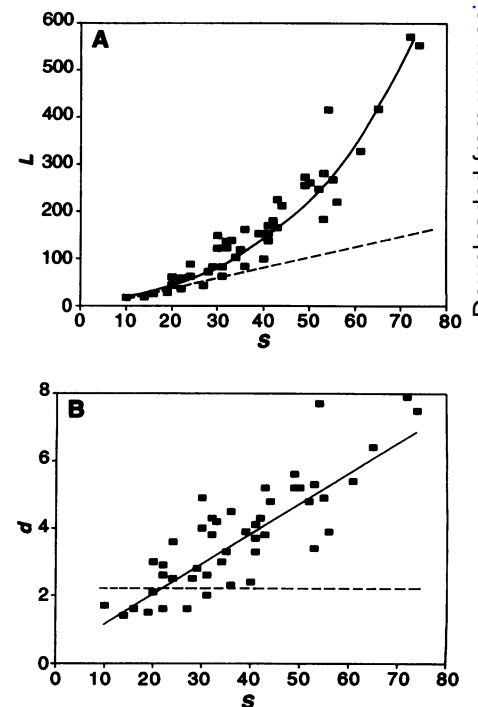


Fig. 3. (A) Links (L) and (B) linkage density (d) as a function of S . The solid lines are fitted to the data points; the dashed lines indicate the relations predicted by the link-species scaling law.

Table 1. Properties of the 50 food webs (22).

Lake name	S	L	d	TF	IF	BF	Lti/L	Ltb/L	Lii/L	Lib/L
Alford	56	220	3.9	0.01	0.55	0.44	0.01	0	0.62	0.37
Balsom	50	261	5.2	0.08	0.4	0.52	0.23	0.11	0.17	0.49
Beaver	55	267	4.9	0.03	0.44	0.53	0.05	0	0.48	0.47
Big Hope	61	328	5.4	0.05	0.51	0.44	0.05	0	0.49	0.46
Bridge Brook	74	553	7.5	0.02	0.47	0.51	0.01	0	0.46	0.53
Brandy	30	121	4	0.17	0.6	0.23	0.45	0.11	0.24	0.2
Brook Trout	14	19	1.4	0.07	0.43	0.5	0.33	0.11	0	0.56
Buck	41	153	3.7	0.07	0.41	0.52	0.02	0.17	0	0.81
Burntbridge	53	183	3.4	0.02	0.4	0.58	0.01	0	0.31	0.68
Cascade	35	118	3.3	0.03	0.46	0.51	0.03	0	0.4	0.57
Chub	36	83	2.3	0.03	0.36	0.61	0.01	0	0.44	0.55
Chub Pond	54	416	7.7	0.17	0.5	0.33	0.41	0.02	0.31	0.26
Connery	65	418	6.4	0.03	0.46	0.51	0.04	0	0.46	0.5
Constable	31	61	2	0.1	0.29	0.61	0.16	0.32	0	0.52
Deep	19	28	1.5	0.05	0.32	0.63	0.22	0.07	0	0.71
Emerald	22	58	2.9	0.05	0.45	0.5	0.16	0.02	0.4	0.42
Falls	39	152	3.9	0.03	0.46	0.51	0.01	0	0.32	0.67
Fawn	32	122	3.8	0.03	0.53	0.44	0.02	0	0.48	0.5
Federation	22	57	2.6	0.05	0.58	0.37	0.02	0	0.38	0.6
Goose	40	98	2.4	0.08	0.3	0.62	0.12	0.03	0.32	0.53
Grass	43	165	3.8	0.02	0.51	0.47	0.02	0	0.52	0.46
Gull	44	212	4.8	0.07	0.48	0.45	0.19	0.01	0.38	0.42
Gull North	16	25	1.6	0.13	0.31	0.56	0.24	0.04	0	0.72
Helldiver	41	169	4.1	0.12	0.37	0.51	0.27	0.11	0.17	0.45
High	24	87	3.6	0.04	0.67	0.29	0.01	0	0.59	0.4
Hoel	72	571	7.9	0.04	0.53	0.43	0.06	0	0.6	0.34
Horseshoe	49	255	5.2	0.06	0.49	0.45	0.07	0	0.51	0.42
Indian	34	102	3	0.06	0.35	0.59	0.14	0.02	0	0.84
L Rainbow	52	247	4.8	0.06	0.54	0.4	0.22	0.01	0.36	0.41
Long	65	417	6.4	0.03	0.51	0.46	0.05	0	0.6	0.35
Loon	35	118	3.3	0.03	0.51	0.46	0.03	0	0.54	0.43
Lost	30	148	4.9	0.03	0.57	0.4	0.02	0	0.42	0.56
Lost East	41	137	3.3	0.02	0.44	0.54	0.01	0	0.36	0.63
Lower Sister	36	161	4.5	0.08	0.53	0.39	0.24	0.03	0.34	0.39
Oswego	33	138	4.2	0.03	0.52	0.45	0.01	0	0.4	0.59
Owl	28	71	2.5	0.07	0.29	0.64	0.11	0	0.04	0.85
Rat	49	273	5.6	0.04	0.53	0.43	0.04	0	0.57	0.39
Razorback	42	179	4.3	0.02	0.53	0.45	0.02	0	0.46	0.52
Rock	20	43	2.1	0.05	0.55	0.4	0.26	0.05	0	0.69
Russian	24	61	2.5	0.04	0.54	0.42	0.21	0.02	0.28	0.49
Safford	43	225	5.2	0.02	0.56	0.42	0.03	0	0.53	0.44
Sand	29	82	2.8	0.03	0.45	0.52	0.05	0	0.42	0.53
South	22	36	1.6	0.41	0	0.59	0	1	0	0
Squaw	41	169	4.1	0.02	0.39	0.59	0.02	0	0.29	0.69
Stink	53	281	5.3	0.02	0.53	0.45	0.01	0	0.51	0.48
Twelfth Tee	31	82	2.6	0.03	0.39	0.58	0.02	0	0.33	0.65
Twin East	10	17	1.7	0.1	0.2	0.7	0.12	0	0	0.88
Twin West	20	60	3	0.05	0.25	0.7	0.07	0	0	0.93
Whipple	32	136	4.3	0.03	0.28	0.69	0.05	0	0.65	0.3
Wolf	27	42	1.6	0.04	0.22	0.74	0.14	0.05	0	0.81

Cohen's view (1–5) that the "shape" of food webs as described by both the species and link fractions is a scale-invariant property. The results also demonstrate the validity of community assembly models, which have predicted similar scale-invariant patterns (19, 20).

The results do not support the link-species scaling law. In these natural nonaggregated pelagic webs, linkage density is not scale invariant (Fig. 3). The relation between L and S can instead be approximated by a power function ($L = S^{1.4}$), as proposed by Pimm, Lawton, and Cohen (12) and recently demonstrated by Martinez (14) for a set of 175 aggregated food webs taken from previous findings. Such a scale-variant

relation is likely to exist in all food webs having indiscriminant herbivores. Particle feeders including many planktivorous fish and zooplankton consume a potentially limitless number of prey species because linkage is not so much a species-dependent phenomenon as it is a size-dependent one.

Powerful patterns in community structure do exist in nature, albeit some are independent of scale and others are not. Ecologists must now turn to the more interesting question of what causes those patterns.

REFERENCES AND NOTES

1. F. Briand and J. E. Cohen, *Nature* **307**, 264 (1984).
2. J. E. Cohen and F. Briand, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 4105 (1984).
3. J. E. Cohen and C. M. Newman, *Proc. R. Soc. London Ser. B* **224**, 421 (1985).
4. J. E. Cohen *et al.*, *ibid.* **228**, 317 (1986).
5. F. Briand and J. E. Cohen, *Science* **238**, 956 (1987).
6. R. T. Paine, *Ecology* **69**, 1648 (1988).
7. S. L. Pimm and R. L. Kitching, *ibid.*, p. 1669.
8. S. L. Pimm, *Food Webs* (Population and Community Biology Series, Chapman & Hall, London, 1982).
9. Even the nonaggregated webs such as those presented by F. Briand [*Ecology* **64**, 253 (1983)] contain severe lumping of species into categories such as "plankton," "herbs," "omnivores," "large carnivores," "other fish," and "mixed-food consumers."
10. N. Martinez, *Ecol. Monogr.* **61**, 367 (1991).
11. T. W. Schoener, *Ecology* **70**, 1559 (1989).
12. S. L. Pimm *et al.*, *Nature* **350**, 669 (1991).
13. G. Sugihara *et al.*, *Science* **245**, 48 (1989).
14. N. Martinez, *Am. Nat.* **139**, 1208 (1992).
15. The 50 lakes sampled were selected by a stratified random design (17) with samples taken once during the summer 1984. Phytoplankton samples were taken from mid-epilimnion; zooplankton were collected with vertical tows of a plankton net (76 μ m for rotifers and 158 μ m for crustaceans). Fish were sampled with overnight gill nets and minnow traps. The first step in constructing the food webs was to produce a cumulative list of species collected in the 50 lakes. Diet information was obtained from Martinez (10), Havens (21), W. B. Scott and E. J. Crossman [*Freshwater Fishes of Canada* (Fisheries Research Board of Canada, Ottawa, 1973)], K. Bogdan and J. J. Gilbert [*Proc. Natl. Acad. Sci. U.S.A.* **81**, 6427 (1984)], K. Havens and J. DeCosta [*J. Plankton Res.* **7**, 207 (1985)], and W. G. Sprules and J. E. Bowerman [*Ecology* **69**, 418 (1988)] and used to construct a cumulative matrix of predator-prey interactions among the 220 taxa. Individual matrices for the 50 lakes were derived from the rows and columns corresponding to the species present. In some cases the lake matrices were edited by removal of "dangling species" (17) that lacked trophic links to the web. The cumulative web approach was taken because direct measurements of feeding relations were not taken in the 50 lakes. To do so would have required gut content analyses of all predators and limited the study to a small number of lakes. Predator selectivity does not vary from lake to lake, according to the cumulative web approach. That is, if species A eats species B in one community, it eats B in all other communities where both are present, regardless of availability of alternate prey. This assumption may not be entirely valid. However, because the web models include only data on the existence (or lack thereof) of interactions and not information regarding interaction strength, the assumption is more robust.
16. The food webs used herein were not aggregated into trophic species because the objective was to determine whether the scaling laws accurately predict trends in the natural biological communities and not in their aggregates.
17. J. W. Sutherland, "Field surveys of the biota and selected water chemistry parameters in 50 Adirondack Mountain lakes" (New York State Department of Environmental Conservation, Albany, NY, 1989).
18. F. Briand, *Ecology* **64**, 258 (1983).
19. J. A. Drake, *J. Theor. Biol.* **147**, 213 (1990).
20. P. Yodanis, *ibid.* **92**, 103 (1981).
21. K. E. Havens, *Can. J. Fish. Aquat. Sci.* **48**, 1846 (1991).
22. Species lists are presented in (17) and the 50 food web matrices are contained in ECOWeb [J. E. Cohen, *Ecologists Co-operative Web Bank, Version 1.0* (Rockefeller University, New York, 1990)].
23. I thank R. Carlson, R. Heath, and S. Pimm for their comments on an earlier version of the manuscript.

8 May 1992; accepted 8 July 1992