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Predation and food web structure along a habitat duration gradient

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Abstract Food web statistics showed a complex relationship with measures of habitat variability in temporary ponds. Connectance was highest in short-duration, highly variable habitats, and lowest in habitats of intermediate duration and variability. The number of links and links/taxon increased with increasing duration. Much of the variation in the food web statistics could be explained by a strong linear relationship between number of taxa and number of links/taxon and a quadratic relationship of taxa number with the number of links. However, after accounting for this variation, there remained a relationship of duration with links and links/taxon. The relationship between the food web statistics and duration corresponded to experimental evaluations of predation in these habitats that showed an increasing importance of predation in long-duration habitats. The food web statistics, however, missed threshold effects in the relationship between predation and habitat duration. Differences in food web statistics before and after a regional drought could be explained by a decrease in taxa number after the drought. Connectance was the most robust statistic in relation to taxa number, but was also the least sensitive to changes in habitat characteristics.

Key words Food webs · Predation · Habitat variability · Temporary ponds · Connectance

Introduction

A number of researchers have tried to relate food web statistics to characteristics of the habitat, such as productivity (Jenkins et al. 1992), stress (Havens 1994; Locke and Sprules 1994), biogeography (Beaver 1985; Sprules and Bowerman 1988) and other factors (Bengston 1994). In particular, because the food web sta-

tistic of connectance is related to stability (May 1972), a number of authors have examined the response of food web statistics to habitat characteristics related to stability, like environmental variability (Briand 1983; Jenkins et al. 1992; Closs and Lake 1994).

Briand (1983) suggested that connectance, or the proportion of potential feeding links realized in a community, should be inversely related to environmental variability: more variable habitats have lower connectance. Other studies, however, have produced conflicting results. Locke and Sprules (1994) compared the food webs of unacidified lakes and lakes whose pH had declined and then recovered to predisturbance conditions and found no differences in food web statistics. Closs and Lake (1994) documented food webs in temporary streams subject to different frequencies of drying. They found no difference in connectance or other food web characteristics across the habitats, although they did find seasonal differences within habitats. Comparisons of food web statistics across habitats, such as that of Briand (1983), are also made difficult by the imprecise definition of habitat variability. Disturbance frequency, variation around the mean disturbance frequency, and the occurrence of unusually harsh conditions all contribute to variability in habitats and need to be considered in evaluating the effects of habitat variability on food web structure.

In addition, researchers have shown that regularities thought to occur in food webs may be artifacts of the manner in which the food webs were generated (Paine 1988; Sprules and Bowerman 1988; Martinez 1991; Polis 1991; Havens 1992; Warren 1994; Bengston 1994). Bengston (1994) identified web size as a characteristic of food webs that could confound analyses of web structure, because many of the characteristics of webs, such as connectance or linkage density, varied with web size. However, as communities change, one of the characteristics of key ecological interest is species number. It thus becomes difficult to ascertain what characteristics of a food web change with habitat characteristics independent of changes in species rich-

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ness. The important question is whether features of the habitat control food web structure directly, as suggested by Briand (1983), or whether food web structure simply covaries with the effect of habitat on species number. Only by partitioning out the independent relation of food web structure to habitat characteristics will we achieve a better understanding of the structure and function of communities through examination of the statistical properties of food web matrices.

In this paper I evaluate food web structure in temporary pond communities lying along a gradient of habitat duration. I compare food web statistics among habitats along a clearly defined gradient of duration and variability. All habitats were sampled by the same investigator and all food webs were characterized to the same level of taxonomic resolution. In addition, the importance of predation in structuring these communities was independently evaluated in a series of feeding experiments (Schneider and Frost 1996), allowing comparisons between food web statistics and other methods of evaluating trophic structure. I analyze several scales of variability in these habitats: mean habitat duration, variance in habitat duration, and periodic, large-scale disturbances.

Methods

I analyzed the food webs of seven temporary pond communities in Vilas County, northern Wisconsin, United States. These ponds are all within 0.5 km of each other, and are acidic, low conductivity habitats. Table 1 shows some of the physical and chemical characteristics of the pond on the day of maximum depth in 1985, which was not necessarily the same day for each pond. They lie along a gradient of mean habitat duration (disturbance frequency), ranging from 3 to 330 days per year (Table 1). Habitat duration was measured for 6 years, allowing characterization of variability in duration (Fig. 1). The coefficient of variation of duration for these seven ponds ranged from 16 to 140% (Table 1). The winter of 1987 and the summer of 1988 were particularly dry. During this regional drought, several ponds never formed, while perennial ponds dried. I sampled the communities in 1985, prior to the drought, and again in 1989, after the drought.

All ponds were sampled approximately weekly from melting in April to September, and bi-weekly from September to ice-on in November. Larger crustaceans, mollusks, insects and amphibians were sampled with a D-frame insect net. Sweeps were taken through the water column, aquatic vegetation and bottom of the ponds, for approximately 45 min at each pond. Zooplankton, mosquitoes and fairy shrimp (Anostraca) were sampled using a 3-l dip bucket. Usually eight 3-l subsamples were taken at various areas throughout the pond, filtered through a 53- μ m zooplankton

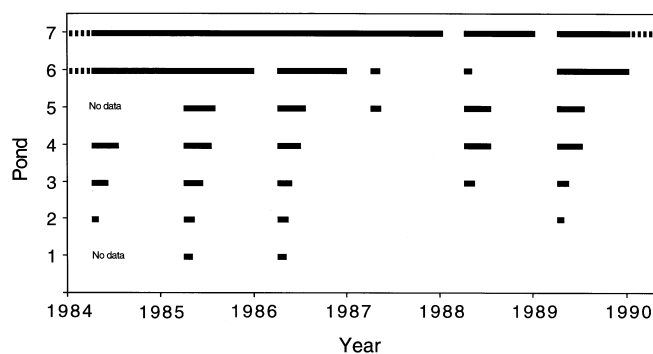


Fig. 1 Habitat variability gradient. Bars show wet periods of ponds from 1984 to 1990. Dotted lines indicate presumed wet periods. Ponds 1 and 5 were not examined in 1984

mesh and pooled. Clam shrimp (Conchostraca) were sampled using a funnel trap. All ponds were sampled with equal effort, and taxa identified to genus, with the exception of cyclopoid copepods, anurans, leeches and chironomids. Many of the taxa are detritivores. Because I did not characterize the detritus and seston, detritus in these webs is a single food group, and may encompass algae, protozoa, and bacteria as well. Ontogenetic stages with different feeding habitats were not separated.

The trophic relations among the temporary pond taxa were determined from experiments (Schneider and Frost 1996), from observations of feeding in the pond (D.W. Schneider, unpublished work), and from the literature on trophic interactions of zooplankton, benthic invertebrates, and amphibians. From these data, I constructed a table of feeding relations (Table 2). Of 956 total feeding links in the table, 109 were measured or inferred from experiments and observations in the temporary ponds and 592 were determined from literature studies conducted in similar habitats (temporary, semipermanent, or permanent ponds). The remainder were either from lakes, or the study habitat could not be determined, although most are likely to be from pond habitats as well, as many of the pond taxa are not found in habitats with fish. Webs for each pond were then constructed by drawing feeding relations from the table for all taxa present in a particular pond (Sprules and Bowerman 1988; Havens 1992).

The number of predation links (L) was calculated as the total number of non-zero entries in the food web matrix, and includes cannibalistic interactions as well as loops. Links/taxon was calculated as L/S and connectance as $L/(S^2)$ (termed "directed connectance," Martinez 1991), where L is the number of predation links in the food web and S is the number of taxa. Basal taxa feed only on detritus. Omnivores feed on more than one trophic level, and top predators are predators or omnivores with no predators.

I used analysis of variance and covariance to evaluate the changes in the food web structure-habitat duration relationship before and after the drought. To partition out the relative importance of taxa number in affecting food web structure, I used analysis of covariance. The number of taxa (S) entered the model as a covariate first, to remove the effect of S on the response of food web statistics to year and habitat duration. Duration or CV and

Table 1 Physical and chemical features of temporary ponds

Pond	Mean duration	CV of duration	Temperature ^a	Conductivity ^a	pH ^a	Dissolved oxygen ^a
1	3.4 days	140%	4.8°C	17 μ S · cm ⁻¹	5.2	3.2mg · l ⁻¹ ^b
2	8.0	99	4.0	19	5.1	4.1 ^b
3	29.1	64	12.5	28	5.4	5.1
4	67.0	50	12.5	37	5.6	3.6
5	75.0	42	12.1	28	5.8	6.2
6	190.2	77	12.0	29	5.9	4.1
7	330.2	16	16.5	29	6.1	6.9

^a Measured on day of maximum volume

^b Measured 5 days after maximum volume

Table 2 Feeding relationships of temporary pond taxa. Distribution of taxa in ponds across years indicated by number: 0 absent 1985 and 1989; 1 present 1985, absent 1989; 2 absent 1985, present 1989, 3 present 1985 and 1989. *Numbers* in prey column refer to taxa number in *Key* column. Feeding relation determined from experiments, observation and Arts et al. (1981), Baker and Clifford (1981), Balduf (1935), Brandl and Fernando (1978), Caldwell et al. (1980), Cloarec (1975), Cullen (1969), Davies et al. (1982), Dodson

and Dodson (1971), Ellis and Borden (1970), Giguere (1979), Helgen (1989), Hungerford (1917), James (1957, 1961, 1966), Leech and Chandler (1956), Li and Li (1979), Menke (1979), Merritt and Cummins (eds) (1984), Nummelin (1989), Parma (1971), Pritchard (1964), Raney and Lachner (1942), Rankin (1935), Sephton (1987), Sprules and Bowerman (1988), Vinyard and Menger (1980), Winterbourn (1971), Zalom and Grigarick (1980)

Key	Predator	Distribution in ponds 1,2,3,4,5,6,7	Prey
1	<i>Acilius</i>	0,1,1,3,3,3,3	2,3,8,11,13,20–23,27,29,31–33,39,40,44–47,55,57,58,62,63,65,71,73,75,77
2	<i>Aedes</i>	1,3,3,3,3,3,3	25
3	<i>Aeshna</i>	0,0,0,0,1,3	1,2,4,8,11,13,14,17,19,21–24,27,28,30–33,36–40,43–50,52,53,55,56,59–63,68,70,74,77
4	<i>Agabus</i>	0,0,3,3,3,3,3	2,5,14,16,21,23,26,33,63,71
5	<i>Alonella</i>	0,0,0,0,0,2,1	25
6	<i>Ambystoma</i>	0,0,0,1,3,3,3	5,12–14,16,23,26,27,39,41,62,63,65,68,71,72,74
7	<i>Anabolia</i>	0,0,0,0,1,1,1	25
8	<i>Anacaena</i>	0,0,0,3,3,3,0	5,14,16,23,25,26,71
9	<i>Anopheles</i>	0,0,0,0,0,1,0	25
10	<i>Banksiola</i>	0,0,0,0,0,0,1	14,26,27,31,55,59
11	<i>Belostoma</i>	0,0,0,0,0,0,3	1,2,4,6,7,10–12,14,17,19–21,29,30,31,36,39,41,44,45,47,50,52,53,55,57–59,62,68,70,72,73,75,77
12	<i>Callicorixa</i>	0,0,1,0,2,3,1	2,21,25
13	<i>Chaoborus</i>	0,0,1,1,3,3,3	2,13,18,21,23,26,27,34,42,51,54,67,71,76
14	<i>Chironomid</i>	0,0,3,3,3,3,3	25
15	<i>Chrysemis</i>	0,0,0,0,0,0,1	1,4,7,8,14,19,22,24,25,28,30,32,36–40,44–50,52,53,59,60–62,68,70,74,77
16	<i>Chydorus</i>	0,0,0,0,0,2,3	25
17	<i>Colymbetes</i>	0,0,0,0,0,1,0	2,5,16,21,23,71
18	<i>Conochilus</i>	0,2,1,0,0,3,3	25
19	<i>Coptotomus</i>	0,0,0,0,0,0,1	14,19,24,31,33,38,48,49,52,53,55,57,60,61,63,75
20	<i>Cordulia</i>	0,0,0,0,0,1,3	1,2,4,5,8,11,14,16,17,19,21–24,26–33,36–40,43–50,52,53,55,56,60–63,70,71,74,77
21	<i>Culex</i>	0,0,0,2,0,2,3	25
22	<i>Cymbiodyta</i>	0,0,0,0,1,1,3	5,8,14,16,23,25,26,32,40,46,71
23	<i>Daphnia</i>	0,0,1,3,3,3,3	25
24	<i>Desmopachria</i>	0,0,0,0,0,1,0	2,5,16,21,23,71
25	<i>Detritus</i>	3,3,3,3,3,3,3	
26	<i>Diacyclops/ Acanthocyclops</i>	1,3,3,3,3,3,3	18,25–27,34,42,51,54,67,76
27	<i>Diaptomus</i>	0,0,0,0,0,3,3	18,25–27,34,42,51,54,67,76
28	<i>Dineutus</i>	0,0,0,0,0,3,3	2,9,14,28,31,55
29	<i>Dorocordulia</i>	0,0,0,0,0,1,3	1,2,4,5,8,11,14,16,17,19,21–24,26–33,36–40,43–50,52,53,55,56,60–63,70,71,74,77
30	<i>Dytiscus</i>	0,0,1,3,3,3,3	1–4,6,7,10–12,17,19–21,24,29–31,33,35,36,38,39,41,48,49,50,52,53,55–63,65,68–70,72,73,75
31	<i>Enallagma</i>	0,0,0,0,0,1,1	5,13,14,16,23,26,27,31,33,34,42,51,54,55,67,71,76
32	<i>Enochrus</i>	0,0,0,1,0,1,3	5,14,16,23,25,26,71
33	<i>Eubbranchipus</i>	0,0,3,3,3,3,0	25
34	<i>Gastropus</i>	1,0,1,3,3,3,3	25
35	<i>Gerris</i>	0,1,3,3,3,3,3	9,14,35,39,62,65
36	<i>Graphoderus</i>	0,0,0,0,0,1,3	2,3,8,11,13,20–23,27–29,31–33,37,39,40,45–47,55–58,62,63,65,71,73,75,77
37	<i>Gyrinus</i>	0,0,1,1,3,3,3	2,9,14,21,25,31,37,55
38	<i>Haliplus</i>	0,0,0,3,1,1,3	25
39	<i>Helisoma</i>	0,0,0,0,0,0,1	25
40	<i>Helophorus</i>	0,0,1,1,0,0,0	5,14,16,23,25,26,71
41	<i>Hesperocorixa</i>	0,1,3,2,2,3,3	25
42	<i>Hexarthra</i>	0,0,0,0,3,0,0	25
43	<i>Hirudenea</i>	0,0,0,0,0,2,3	5,14,16,23,26,27,71
44	<i>Hydrobius</i>	0,0,0,3,2,3,3	5,8,14,16,22,23,25,26,31,32,40,44,46,55,71
45	<i>Hydrochara</i>	0,0,0,3,2,3,3	5,8,14,16,22,23,25,26,31,32,39,40,44–46,55,62,68,71,77
46	<i>Hydrochus</i>	0,0,0,0,0,1,3	5,14,16,23,25,26,71

Table 2 (continued)

Key	Predator	Distribution in ponds 1,2,3,4,5,6,7	Prey
47	<i>Hydrophilus</i>	0,0,0,0,1,0	1,3–5,7,8,10,11,14,16,17,19,20,22,23–26,28–32,36–40, 45–50,52,53,55–62,66,68,70,71,73,75,77
48	<i>Hydroporus</i>	1,3,3,3,3,3,3	2,5,14,16,21,23,26,27,33,71
49	<i>Hygrotus</i>	0,0,0,0,0,3,3	2,5,14,16,21,23,26,27,33,71
50	<i>Ilybius</i>	0,0,0,0,1,1,0	2,5,14,16,21,23,33,63,71
51	<i>Keratella</i>	0,0,1,3,3,3,3	25
52	<i>Laccophilus</i>	0,0,0,0,0,3,3	2,14,21,24,27,33,38,48,52,53,60,61,63
53	<i>Laccornis</i>	0,0,0,0,0,0,1	2,14,21,24,27,33,38,48,53,60,61,63
54	<i>Lepadella</i>	0,3,3,3,3,3,3	25
55	<i>Lestes</i>	0,0,0,0,0,1,3	5,13,14,16,18,23,26,27,31,33,34,42,51,54,55,67,71,76
56	<i>Lethocerus</i>	0,0,0,0,0,0,3	1,4,6,7,10–12,20,29–31,36,41,44,45,47,50,55,57–59,68,70, 72,73,75,77
57	<i>Leucorhinia</i>	0,0,0,0,0,1,3	1,2,4,5,14,16,17,19,21,23,24,26–28,30,31,33,36,37,38,39,43, 48–50,52,53,55,59–63,70,71,74
58	<i>Libellula</i>	0,0,0,0,0,1,3	1,2,4,5,8,11,14,16,17,19,21–24,26–28,30–33,36–40,43–50,52, 53,55,56,60–63,70,71,74,77
59	<i>Limnephilus</i>	0,0,0,3,1,1,1	2,21
60	<i>Liodessus</i>	0,0,1,1,2,3,3	2,5,16,21,23,26,27,33,71
61	<i>Lissonotus</i>	0,0,0,1,0,0,1	25
62	<i>Lymnaea</i>	0,0,0,0,0,1,0	25
63	<i>Lynceus</i>	0,0,0,3,3,3,3	25
64	<i>Mochlonyx</i>	0,2,1,3,3,1,1	2,18,21,23,26,27,34,42,51,54,64,67,71,76
65	<i>Notonecta</i>	0,0,0,0,0,1,3	2,9,12–14,21,23,26,28,33,41,63,65,71,72
66	<i>Oecetis</i>	0,0,0,0,0,1,0	2,14,21,25–27,33
67	<i>Polyarthra</i>	0,0,0,3,1,3,3	25
68	<i>Rana/Hyla</i>	0,0,1,3,3,3,3	25
69	<i>Ranatra</i>	0,0,0,2,0,1,3	2,9,14,21,23,26,27,33,39,62,63,71
70	<i>Rhantus</i>	0,0,1,0,0,3,2	2,4,5,14,16,21,23,33,50,63,71
71	<i>Scapholeberis</i>	0,1,1,0,3,3,3	25
72	<i>Sigara</i>	0,0,2,3,3,3,3	25
73	<i>Somatochlora</i>	0,0,0,0,0,1,3	1,2,4,5,8,14,16,17,19,21–24,26–28,30–33,36–40,43–50,52,53, 55,60–63,70,71,74,77
74	<i>Sphaeridae</i>	0,0,0,3,0,1,3	25
75	<i>Sympetrum</i>	0,0,0,0,0,0,1	1,2,4,5,14,16,17,19,21,23,24,26–28,30,31,33,36–39,43,48–50, 52,53,55,59–63,70,71,74
76	<i>Trichocerca</i>	0,0,1,0,2,3,3	25
77	<i>Tropisternus</i>	0,0,1,1,1,1,3	5,8,14,16,22,23,25,26,31,32,39,40,44,46,55,62,68,71,77

year entered the ANOVA model last, after the effect of taxa on food web structure was accounted for. Type I sums of squares are thus reported for S and type III sums of squares for the other variables. All analyses were performed using SAS, version 6.10 for Microsoft Windows (SAS Institute 1994).

Results

Measures of food web connectivity – links, links/taxon and connectance – all varied with measures of habitat variability (Fig. 2). The number of feeding links and the links/taxon both increased linearly with increasing habitat duration. Connectance, on the other hand, initially declined sharply with increasing duration, and then increased slowly with further increases in duration (Fig. 2).

The relation between duration and both links and links/taxon differed between the two years sampled (Table 3). Ponds had fewer links after the drought than before, and the rate at which links increased with duration was lower following the drought. The number of links/taxon was also lower following the drought. In

contrast, the relation between duration and connectance did not change between years.

Patterns in relation to the coefficient of variation of duration were more complex. Both the number of links and the links/taxon showed a general trend towards lower values at high variability, although one pond, pond 6, did not fit this general trend (Fig. 3). Connectance was at a minimum in ponds of moderate variability in duration, and was higher in ponds of both low and high variability. Patterns between years were not significantly different for any of the three food web statistics (Table 4).

All three food web statistics also varied considerably with the number of taxa in the web (Fig. 4). Links increased as the square of taxa number ($\text{links} = 0.163S^2$, $r^2 = 0.983$) while Links/taxon increased more linearly with increasing taxa ($L/S = 0.166S - 0.475$, $r^2 = 0.942$). Connectance showed a U-shaped relation to taxa richness, decreasing with increasing taxa number at lower values of taxa richness, and increasing at higher values.

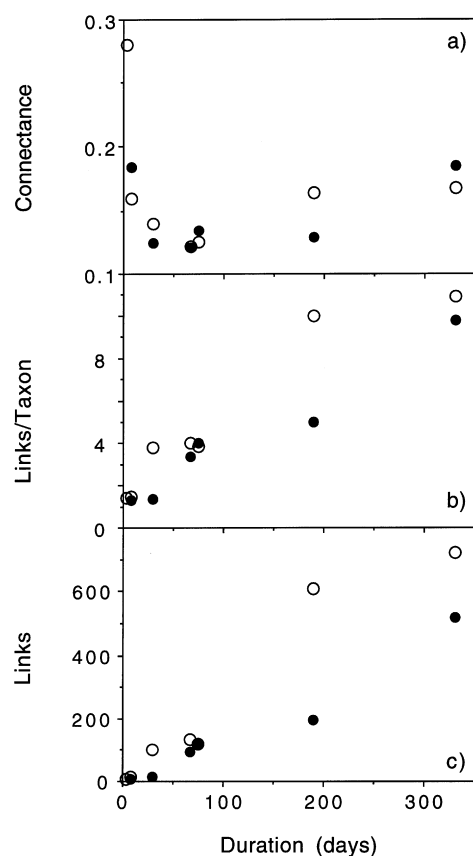


Fig. 2a–c Relation of food web statistics to mean habitat duration. *Open circles* are pre-drought, 1985 data and *closed circles* are post-drought, 1989 data. **a** Connectance **b** links/taxon, **c** Links. Symbols: ○ pre-drought; ● post-drought

Table 3 Analysis of variance (links) and covariance (links/taxon and connectance) of effect of year on food web statistics, using duration as a covariate

Source	<i>df</i>	Sum of squares	<i>F</i> -ratio	<i>P</i>
Links^a				
Year	1	825.399	0.17814	0.000
Duration	1	605171	130.61	0.6829
Year × Duration	1	29599.5	6.3883	0.0324
Error	9	41700.6		
Links/taxon				
Year	1	6.0314	5.0364	0.0487
Duration	1	126.46	105.59	0.0000
Error	10	11.976		
Connectance				
Year	1	0.0072	0.43307	0.5253
Duration	1	0.00362	0.21785	0.6507
Error	10	0.16625		

^a The year × duration interaction was significant for links, so analysis of covariance could not be done. For links/taxon and connectance, the interaction term was not significant

As pond duration increased, taxa richness also increased in both years (Fig. 5a). But when the relationship between taxa number and links, and links/taxon was taken into account, there was still a significant effect

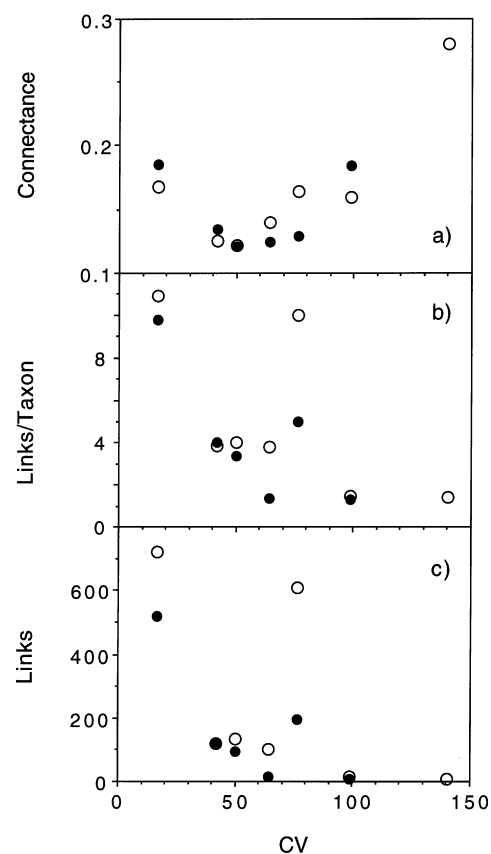


Fig. 3a–c Relation of food web statistics to the coefficient of variation of habitat duration. *Open circles* are pre-drought, 1985 data and *closed circles* are post-drought, 1989 data. **a** Connectance **b** links/taxon, **c** links. Symbols: ○ pre-drought; ● post-drought

Table 4 Analysis of covariance of effect of year on food web statistics, using coefficient of variation of duration as a covariate

Source	<i>df</i>	Sum of squares	<i>F</i> -ratio	<i>P</i>
Links				
Year	1	57016.2	1.2998	0.2808
CV	1	259245	5.9102	0.0354
Error	10	438643		
Links/taxon				
Year	1	8.99389	1.17061	0.3047
CV	1	61.60514	8.01830	0.0178
Error	10	78.83063		
Connectance				
Year	1	0.00161	0.16873	0.6899
CV	1	0.07450	7.81141	0.0190
Error	10	0.09537		

of duration (Table 5). Both the number of links and links/taxon increased with increasing duration, independent of taxa number. The difference in the number of links before and after the drought, however, can be explained by the change in the number of taxa in these two years, and not by any effect of drought (year effect) directly on food web structure (Table 5).

The distribution of trophic categories in the food webs changed with duration (Fig. 5b–d). Top predators

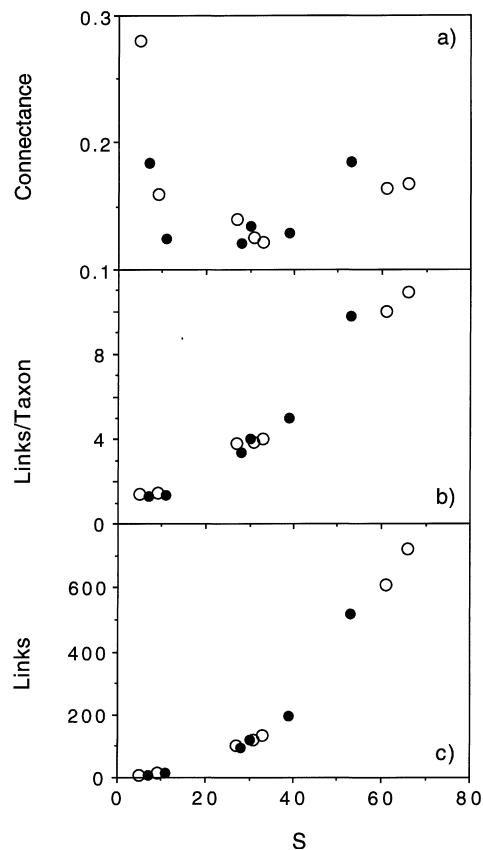


Fig. 4a–c Relation of food web statistics to taxa number. *Open circles* are pre-drought, 1985 data and *closed circles* are post-drought, 1989 data **a** Connectance **b** links/taxon **c** links *Symbols*: ○ pre-drought; ● post-drought

were rare in all but the shortest duration ponds. Top predators in the short-duration ponds were *Hydroporus*, *Acilius*, and *Agabus*, all dytiscid beetles. While these taxa were all present in the long-duration ponds, they had numerous predators in those systems. In the long-duration ponds, the top predators were leeches and painted turtles. The proportion of basal taxa increased initially with increasing duration, and then declined in the longest-duration ponds. The proportion of omnivores initially increased with increasing duration, and levelled off in long-duration ponds.

Discussion

These food webs were determined primarily from literature data for the feeding relationships of pond taxa, as well as from measured feeding links in the temporary ponds. Hall and Raffaelli (in press) term such webs “imaginable” as opposed to “likely” or “empirical” and suggest that feeding links realized by a set of taxa in a habitat are often fewer than those possible or documented from the region. The effect of this overestimation, however, is difficult to predict. Hall and Raffaelli found a significant impact on L/S and food chain length,

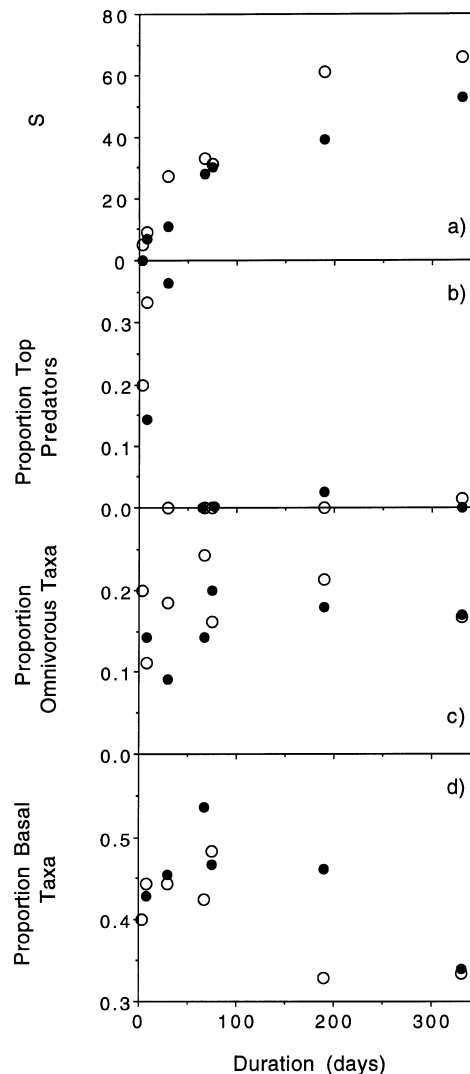


Fig. 5a–d Relation of food web characteristics to habitat duration. *Open circles* are pre-drought, 1985 data and *closed circles* are post-drought, 1989 data **a** Taxa number **b** proportion of taxa that have no predators **c** proportion of taxa that are omnivores **d** proportion of taxa that feed only on algae and detritus. *Symbols*: ○ pre-drought; ● post-drought

but calculations of connectance made from their data show the impact on this parameter was less pronounced. In contrast, Warren (1995) suggests that for aquatic habitats, absolute values of food web statistics calculated from the potential feeding interactions of a regional taxa pool may still be valid. He documented the pair-wise trophic interactions of a set of species that could potentially interact but did not necessarily co-occur. Using this regional food web to assemble local food webs of arbitrarily selected taxa he found little difference with statistics of “real” food webs. These studies suggest using potential interactions to construct food webs may yield meaningful results, although they need to be interpreted with caution. In addition, increasing taxa number might spuriously affect characteristics of food webs in which actual feeding relationships have not been

Table 5 Analysis of covariance of the effect of year and duration on food web statistics, using S (number of taxa) and duration as covariates

Source	<i>df</i>	Sum of squares ^a	<i>F</i> -ratio	<i>P</i>
Links				
S	1	636792.86	159.29	0.0001
Year	1	279.41	0.07	0.7982
Duration	1	45148.65	11.29	0.0099
Year \times Duration	1	16421.50	4.11	0.0772
Error	8	31981.91		
Total	12	720905.08		
Links/taxon				
S	1	133.53	284.81	0.0001
Year	1	0.392	0.84	0.3869
Duration	1	3.705	7.90	0.0228
Year \times Duration	1	0.036	0.08	0.7887
Error	8	3.751		
Total	12	141.145		
Connectance				
S	1	0.0222	1.84	0.2121
Year	1	0.0222	1.84	0.2118
Duration	1	0.0438	3.63	0.0932
Year \times Duration	1	0.0000307	0.00	0.961
Error	8	0.0965		
Total	12	0.1779		

^a Type I SS are reported for S , and type III SS for other variables. As a result, sums of squares will not equal the total SS

evaluated. I account for this possibility by explicitly factoring out the effects of taxa number in the analyses of covariance.

The structure of the food webs of these temporary ponds contradicts many of the generalizations drawn from the analyses of published food webs. Patterns from early published webs are coming under increasing criticism as ecologists analyze an increasing variety and number of food webs using consistent methodologies (Polis 1991). Connectance did not decline with increasing taxa number, contradicting the so-called link-scaling law, in which $L \times S$ is presumed to be a constant (Cohen 1989). Rather, connectance declined initially with increasing taxa number, but then increased again. Wine-miller (1989) examining tropical fish assemblages found either constant or increasing connectance with increasing taxa number. The slope of the relation between the number of links and taxa in the temporary ponds was not constant. Instead, the number of links increased with the square of the number of taxa. A similar pattern was found by both Warren (1990) and Martinez (1992). Because cannibalism and loops were relatively common features of these food webs there were very few top predators (Fig. 5). Omnivory was also common (Fig. 5). These characteristics appear to be common in aquatic ecosystems (Sprules and Bowerman 1988) as well as in habitats such as deserts (Polis 1991) and probably in other webs if high-resolution data are obtained. By ignoring cannibalistic links and loops, many published food webs are likely to be highly incomplete. Martinez (1991) cautioned against drawing generalizations from such webs.

Contrary to the predictions of Briand (1983), connectance in temporary pond food webs showed a complex relation to habitat variability and depended on the measures of both connectivity and variability used. There were no strong relationships between any measure of connectivity and the coefficient of variation of duration, a measure of how variable habitat duration was among years. In contrast, connectivity was related to variability when measured as the mean habitat duration, a measure of the time available for establishment of biotic interactions (Schneider and Frost 1996). Short-duration, highly variable ponds had the most highly connected habitats in this study and connectance initially decreased with increasing duration, or decreasing variability. Only after this initial decrease did connectance then increase with decreasing variability as suggested by Briand (1983).

When measured as the number of links or links/taxon, however, connectivity within food webs did increase with decreasing variability. The number of links and the links/taxon both increased with increasing habitat duration and decreasing variability. This was true even when the relation between links and taxa number was taken into account. Another measure of variability, the occurrence of periodic, large-scale disturbances, like drought, also produced changes in food web structure. Links and links/taxon were both lower in the ponds following the drought. However this effect could be attributed to the relationship between these variables and taxa richness, and the changes in taxa number following the drought.

Havens (1994) similarly found a decline in links/taxon in planktonic food webs stressed with copper. Locke and Sprules (1994) found a complex relation between connectance and a pH stress gradient. At low pH, stressed lakes had highly variable values of connectance, while connectance remained relatively stable at higher pH. They attributed much of the difference in food web structure of acidified lakes to the effects of lake chemistry on taxa number, rather than some direct effect of acidification on feeding relationships. As species dropped out of acidified lakes, links and links/species declined correspondingly. Similarly, Jenkins et al. (1992) showed that drought caused a reduction in the number of predators found in experimental container habitats and a reduction in the number of links in the food web. Neither Havens (1994), Locke and Sprules (1994) nor Jenkins et al. (1992) quantitatively separated the effects of species number on food webs from other factors. When taxa number was taken into account in my temporary pond food webs, a significant effect of duration on food web structure remained.

Some of the patterns of food web structure across the habitat duration gradient corresponded to the experimental analysis of predation in these systems. Experiments evaluating community predation rate and predator preferences demonstrated that the importance of predation increased with increasing pond duration (Schneider and Frost 1996). Prey clearance rates by the

entire predator community increased with increasing duration. In addition, individual predator taxa had higher per-predator feeding rates on the same prey in longer duration ponds. In the food web analysis, the number of links and links/taxon increased with increasing duration, consistent with the experimental evaluation of the importance of predation in structuring these communities.

There was evidence of reduced predation rates in the ponds following the drought. These changes in the ponds were reflected in the changes in food web structure. Both the number of links and links/taxon were lower following the drought, although this effect could be attributed to the reduced number of taxa in the ponds (Fig. 5). The pond with the greatest change in taxa composition, pond 6, also showed the largest shift in food web structure. The extreme reduction in connectivity in pond 6 corresponds to a temporal refuge from predation for prey taxa like mosquitoes and fairy shrimp that was caused by the effect of drying on the predator community (Schneider and Frost 1996). Fairy shrimp and mosquitoes, which had been rare or absent in pond 6 prior to the drought, reached high abundances in 1989. These same prey were the preferred food for predators, such as odonates and *Notonecta*, that were common before the drought but absent after. In the food web analysis, this pond showed the greatest reduction in the number of links, links/taxon, and connectance following the drought.

Although the changes in food web statistics corresponded to the general trends revealed by the experiments (Schneider and Frost 1996), the food web statistics were insensitive to thresholds in the importance of predation across the habitat duration gradient. In the experimental study, predation rates increased monotonically with increasing duration, but only in long-duration ponds was predation intensity high enough to affect populations of planktonic prey (Schneider and Frost 1996). Predatory interactions were common in short duration ponds, but predator diversity and abundance were too low to affect prey populations. Links and links/taxon in the food webs also increased monotonically with increasing duration, paralleling the pattern of predation intensity with duration. The experimental results, however, suggested a threshold effect in the longest duration ponds. Evaluation of food web statistics alone would miss this qualitative shift in the importance of predation in regulating prey assemblages. Because food web connections in this analysis don't incorporate interaction strength, food web statistics appear to miss biologically important processes (Paine 1980, 1988, 1992).

Warren (1990, 1994, 1995) has suggested that morphological constraints on feeding can govern the statistical properties of food webs. In communities composed of generalist predators, there are few constraints on feeding relationships, and as species are added to the web, the number of species with which they can potentially interact will increase. In these webs, links will scale with the square of the number of species in the web. The

data from the temporary ponds support this suggestion. The taxa in the ponds are all generalized feeders, and the proportion of omnivorous taxa increased with increasing taxa number. As pond duration increased, taxa richness also increased because once a pond lasts long enough to support a particular taxon, that taxon tends to occur in all ponds of longer duration as well (Schneider and Frost 1996). This pattern of continuity in distribution may explain the proportionately greater number of predation links in long duration ponds. As new taxa are added, they add trophic links to the already existing web, as well as to each other. The number of predator taxa, their abundances, and the diversity of predator feeding types all increase with increasing duration (Schneider and Frost 1996). This increase results in overall increases in the intensity of predation in long-duration ponds. However, while food web statistics may reflect these quantitative changes in predation intensity, the statistics cannot illuminate shifts in the ecological importance of predation that were revealed in experimental studies.

Links and links/taxon were the statistics most sensitive to habitat variability in this study. However, they were also the most tightly correlated with taxa number, making the interpretation of the effects of habitat on food web structure difficult. Martinez (1991) concluded that directed connectance was the statistic most robust to arbitrary changes in the resolution of the food web. Similarly, in these ponds connectance was the measure least affected by the number of taxa in the webs. However, it was also the least sensitive to the changes in the community following drought, and patterns of connectance across the habitat duration gradient did not correlate with independent measures of the importance of predation in these habitats.

The effect of habitat variability on food web statistics also depended on the method of characterizing variability. Habitat variability was characterized by the mean habitat duration, the coefficient of variation around duration, and the occurrence of unusually dry weather. Only mean habitat duration affected food web statistics after the effect of taxa number was removed. The significant effect of duration on food web structure suggests that food webs may be affected by characteristics of the habitat independent of the effect on taxa richness. The effect of a temporal characteristic of the habitat, duration, on the food web statistics suggests that dynamic constraints may be important in structuring food webs.

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