



Nordic Society Oikos

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Source: *Oikos*, Vol. 55, No. 3 (Jul., 1989), pp. 299-311

Published by: [Blackwell Publishing](#) on behalf of [Nordic Society Oikos](#)

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Spatial and temporal variation in the structure of a freshwater food web

Philip H. Warren

Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. – *Oikos* 55: 299–311

Trophic interactions between benthic invertebrates in a large freshwater pond were established using analyses of gut contents, laboratory feeding trials and published information. The web was detritus based and contained 36 “species”. Spatial and temporal variation in food web structure was assessed by partitioning the overall food web into subwebs drawn up for two areas of the pond on each of five sampling dates over the course of a season. Substantial variation occurred between webs from the open water benthos and the pond margin areas, both within and between sampling dates. Webs became more complex (species rich) over the season and, within, the webs from each area, species composition and interactions varied due to body size and life history effects. In relation to published data the webs had high average connectance, high proportions of intermediate species (and links among intermediate species) and moderately high predator: prey ratios. Other food web statistics varied considerably, but most fell within the ranges of values from previous analyses. Omnivory was extensive and, due to size dependent predation, cannibalism and trophic loops occurred. The potential effects of spatial and temporal variation in the web on the dynamics of trophic interactions suggest that Cohen and Newman’s “cascade model”, which imposes simple, non-dynamic constraints on the distribution of trophic interactions, may be an appropriate explanation for web structure. However, simulated webs generated by the cascade model, using parameters derived from the webs in this study, indicated the model’s sensitivity to connectance, and suggested that, in its present form, the model adequately accounts for the proportions of basal, top and intermediate species, but may not be a sufficient explanation for observed food chain lengths.

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Introduction

Analyses of the structure of binary food webs (which show only the presence or absence of feeding links) are based on webs from many different sites, comprising diverse taxa and sampled or compiled on a variety of temporal and spatial scales. Despite the heterogeneous data, certain regularities are apparent in the structure of such webs (Cohen 1978, Pimm 1982, Briand and Cohen 1987, Lawton and Warren 1988, Lawton 1989). These include short food chains (Elton 1927, Pimm 1982); roughly constant proportions of top, intermediate and basal species (Briand and Cohen 1984) (or, similarly, a

constant ratio between the numbers of predator and prey species (Cohen 1978, Jeffries and Lawton 1985)); and roughly constant proportions of links between basal, intermediate and top species (Cohen and Briand 1984). A variety of explanations have been proposed for many of these features and for systematic differences between webs from different habitats (see reviews in Pimm 1982, Lawton 1989).

However food webs are not static entities and like most ecological systems may be studied on a number of spatial and temporal scales (Wiens et al. 1986, Giller and Gee 1987). Summary, or average, food webs may conceal substantial temporal and spatial variation in

Accepted 2 March 1989

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trophic structure (Kitching 1987). Definition of a food web usually reflects some obvious habitat boundary, for example a lake, but the spatial organisation within the lake, for example profundal, littoral and pelagic zones, may have important influences on the way species interact and result in functionally distinct food webs. Similarly webs may represent the community at one point in time or may be summed across longer periods. It is unclear how apparent patterns in the structure of published food webs are influenced by combining studies based on different spatial and temporal scales.

This paper presents an analysis of the structure of a freshwater invertebrate food web, studied over a period of one year, by partitioning the overall summary web into subwebs from spatially distinct habitats and different times through the season. The aims of the study were to contribute a new, detailed, web to the existing data on food web structure; to analyse the magnitude and effects of spatial and temporal variation in the web; and to consider the implications of the results for static and dynamic theories of web structure.

Methods

Site

The study site was an acidic (pH 4.0–4.5) permanent pond, 0.25 ha in area and up to 1 m deep, on Skipwith Common, North Yorkshire, England (53°40'N 0°59'W). Most of the pond margin was densely vegetated with stands of *Juncus effusus* L. A few sparse patches of *Juncus bulbosus* L. and aquatic moss (predominantly *Fontinalis* sp.) occurred in the open water areas. The moss cover was initially very sparse (March 1986) but spread extensively over the course of the study. The bottom of the pond was composed of sand and fine detritus. Around the margin of the pond the bases of *Juncus* clumps and substantial accumulation of *Juncus* litter created a structurally more complex environment.

Sampling

On the basis of preliminary sampling and observation the site was divided into two areas for sampling purposes, the structurally simple open water region, and the more complex pond margin. The open water area was sampled at randomly chosen points using a cylindrical metal corer (0.125 m² cross sectional area, 1 m height) which, when dropped vertically into the water, rapidly enclosed an area of the pond bottom and water column. The contents of the core (animals, vegetation and detritus) were then extracted using a 0.3 mm mesh pond net, until no further invertebrates were observed in four successive nets. Material was preserved in 4% formaldehyde solution.

Vegetation and accumulated litter made core sampling impractical for the margin of the pond which instead was sampled at randomly chosen points along the

bank by taking five net sweeps, in the same place, from the pond bottom about 0.25 m from the bank up through the litter and vegetation to the water surface.

Samples were taken from these two habitats on each of the following dates during 1986: 1) 12–13 March, 2) 22–23 May, 3) 7–8 June, 4) 21–23 August, 5) 3–4 October. Five to seven samples from each area were taken on each date (though for date 2 one sample could not be analysed because of poorly preserved material). On sample date 4 the open water region could be clearly divided into an area of extensive moss growth and a comparatively unvegetated region; these were sampled separately, resulting in two sets of open water samples for this date.

In the laboratory, sieving and subsequent hand sorting were used to extract all larger invertebrates. The very abundant and smallest species were then counted in single subsamples (3% of the whole) from each main sample. Abundances cannot be directly compared between open and margin samples, so the mean abundances of each taxon from each set of samples were converted to relative abundance classes to summarise the data. Body lengths of all individuals (or a subsample of the more abundant) were recorded to the nearest 0.25 mm. For each individual sample the geometric mean of the maximum and minimum size of each species, and the average of these means (across samples) was calculated.

In addition to the regular samples, extensive qualitative sampling was conducted throughout 1986 and 1987.

Analysis of trophic links

Feeding interactions in the community were determined by experimental feeding trials in the laboratory and by analysis of the gut contents of field collected animals. For species which fed by extracting the body fluids of their prey (Hemiptera, dytiscid larvae) gut contents analyses were not possible, but analyses of gut contents or faecal pellets could be carried out for the larvae of *Sialis lutaria* (L.) (Megaloptera), odonates, chironomids, trichopterans and for adult dytiscid beetles and copepods. Animals collected from the open water and margin areas, during June 1986 and June, July and August 1987, were placed immediately in separate vials of clean water and taken back to the laboratory. Odonates and some *Sialis* were kept in vials at 15°C for 48 h and any faecal pellets produced were collected. Other species were killed in 70% alcohol and their guts dissected out. Dissected faecal pellets and guts were slide mounted in polyvinyl lactophenol and examined for identifiable prey remains.

Feeding trials were carried out in 250 ml beakers, each containing water, a little sand and some 10 mm mesh nylon netting. For each experiment a number of potential prey (between 1 and 10 depending on species) were placed in replicate beakers and a single predator,

Tab. 1. Occurrence and relative abundances of species included in the food web at all sample dates in each habitat area. Relative abundance classes (proportions of total abundance) are: 1=0.00001–0.0001, 2=0.0001–0.001, 3=0.001–0.01, 4=0.01–0.1, 5=0.1–1.0 (Dashes indicate zero values). Sample date 4 had two sets of samples: 4a, open without moss; 4b, open with moss.
* – Oribatid mites were not counted but occurred regularly in samples.

Taxon	Sample										
	Open						Margin				
	1	2	3	4a	4b	5	1	2	3	4	5
Tricladida											
1. <i>Polycelis tenuis</i> (Ijima)	–	–	–	–	2	2	3	–	3	2	1
Oligochaeta											
2. Small oligochaetes (principally Enchytraeidae)	5	5	5	4	4	4	5	5	4	4	4
3. <i>Lumbriculus variegatus</i> (Muller)	–	–	–	–	–	2	2	–	–	–	1
Arachnida											
4. Oribatei sp.*	–	–	–	–	–	1	–	1	3	2	2
5. <i>Argyroneta aquatica</i> (Clerk)	–	–	–	–	–	1	–	1	3	2	2
Cladocera											
6. <i>Scaphaloberis mucronata</i> (Muller)	–	–	–	–	–	–	–	–	3	3	–
7. <i>Chydorus latus</i> Sars	4	4	4	–	5	5	5	5	5	5	4
Copepoda											
8. <i>Acanthocyclops vernalis</i> (Fischer)	5	5	4	4	4	4	5	5	5	4	4
Odonata											
9. <i>Enallagma cyathigerum</i> (Charpentier)	–	–	–	3	4	3	1	–	1	3	3
10. <i>Lestes sponsa</i> (Hansemann)	–	–	–	–	–	–	–	1	2	–	1
11. <i>Aeshna juncea</i> (L.)	–	–	–	–	–	–	1	1	1	–	2
12. <i>Sympetrum scoticum</i> (Donovan)	–	–	1	–	1	–	–	–	1	1	1
Hemiptera											
13. <i>Notonecta glauca</i> L.	–	–	–	–	–	–	1	–	–	2	2
14. <i>Callicorixa praeusta</i> (Fieber)	2	1	2	2	2	3	4	2	3	2	2
15. <i>Corixa dentipes</i> (Thomson)	–	–	–	–	–	–	1	1	–	1	1
16. <i>Corixa punctata</i> (Illinger)	–	–	–	2	2	2	2	1	1	2	2
17. <i>Hesperocorixa linnei</i> (Fieber)	–	–	1	–	–	–	1	–	1	–	2
18. <i>Hesperocorixa sahlbergi</i> (Fieber)	–	–	–	–	–	1	1	–	–	1	1
19. <i>Arctocorixa germari</i> (Fieber)	3	2	2	3	2	2	2	–	1	1	1
20. <i>Sigaria semistraiata</i> (Fieber)	–	–	–	–	2	–	3	1	–	–	1
21. Corixidae nymphs	–	2	3	3	4	2	–	4	4	4	3
Coleoptera											
22. <i>Hydroporus erythrocephalus</i> (L.)	–	–	–	–	1	–	–	–	–	1	–
23. <i>Agabus sturmi</i> (Gyllenhal)	–	–	–	–	–	–	–	–	–	3	2
24. <i>Agabus bipustulatus</i> (L.)	–	–	–	–	–	–	–	–	–	1	1
25. <i>Ilybius fuliginosus</i> (Fabricius)	–	–	–	–	–	–	–	–	–	1	1
26. <i>Agabus/Ilybius</i> larvae	2	2	4	–	2	3	3	3	3	3	3
27. <i>Dytiscus marginalis</i> L.	–	–	–	–	–	–	–	–	1	1	–
Megaloptera											
28. <i>Sialis lutaria</i> (L.)	1	–	3	3	3	3	2	–	–	2	3
Trichoptera											
29. <i>Holocentropus picicornis</i> (Stephens)	–	–	1	2	3	4	3	2	4	5	5
30. <i>Limnephilus marmoratus</i> Curtis	1	1	–	–	1	1	3	2	2	2	3
Diptera											
31. <i>Procladius sagittalis</i> (Kieffer)	1	–	4	–	2	4	4	2	4	4	4
32. <i>Corynoneura scutellata</i> Winnertz	1	–	–	3	4	4	2	–	3	4	4
33. <i>Chironomus dorsalis</i> Meigen	4	4	4	4	4	4	2	1	–	3	4
34. <i>Glyptotendipes pallens</i> (Meigen)	4	3	4	4	4	4	5	4	5	5	5
35. <i>Tanytarsus bruchonius</i> Reiss & Fittkau	5	5	5	5	5	5	5	5	4	5	5
36. Other Chironomidae	–	–	4	4	4	4	–	–	5	4	4

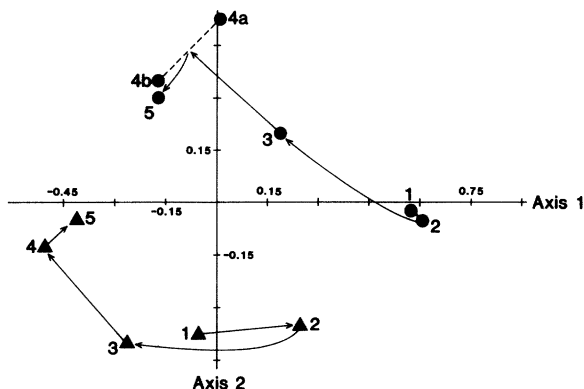


Fig. 1. Ordination based on principal coordinates analysis of samples based on the abundance classes given in Table 1. Samples are plotted on the first two axes derived from the analysis, which account for 46% of the variance. Arrows indicate the sequence of sample dates within each habitat. Circles = open water samples, Triangles = margin samples. The two open water samples from date 4 are represented separately (4a & 4b – see also Table 1), linked by a broken line.

starved for 36–48 h beforehand, was added to each. Further beakers, with prey but no predators, acted as controls. Experiments were left for 24 h under a 12:12 L:D cycle at 15°C and then prey mortality was compared between beakers with and without predators. Results from these experiments were usually unequivocal and predation was often observed directly. Tests giving uncertain results were repeated or allowed to run for longer periods. Not every size combination of predators and prey could be tested, so individuals used were chosen to cover a moderate range of sizes around the middle of the total size range for a species, except where the experiment explicitly set out to test for predation between extreme size combinations.

It was not possible to test every predator-prey combination so the likelihood of a few interactions had to be assessed using secondary information on the feeding ecology of similar species in the literature and inference from experiments done with other species in the web.

Compilation of the food webs

Food webs were drawn up based on the species found in each set of samples (open or margin) for each date together with information about potential feeding interactions. Nine species which occurred in the samples as isolated individuals on one or two occasions only, and which were not found regularly in the more extensive qualitative sampling, were excluded from the web.

Feeding links were included if the data suggested interactions between at least some size combinations of individuals present. Links were not included unless good evidence suggested they should occur. Use of a combination of feeding trials, gut contents analyses and other information to establish possible feeding links will tend to generate maximally connected webs.

The following conventions have been used in drawing the food webs. Species positions are constant between webs and species are identified by the template (Fig. 2 a). Links, unless otherwise indicated, are directed downwards from consumer to resource. The size of the circle representing each species denotes its mean body length. Boxes enclosing a group of species indicate that the adult and larval stages of those species occurred in the web, but that larval stages were not distinguished to species. The presence and size of such larvae is denoted by a circle attached to the box. Links which relate to the larval but not to the adult stage of a species (or vice versa) can therefore be distinguished. Circles which are attached to each other depict species whose trophic relations were considered to be the same and hence, for diagrammatic convenience, the links are represented only once for each group.

In calculations of the numbers of links, species and frequency distribution of food chain lengths all links to and from such species groups were counted for each of the species present. Where adults and larvae of potentially the same species were both present larvae were not treated as separate species; larval and adult feeding links were combined and assigned to each species as a whole. Where larvae (potentially of more than one species) were present in the absence of adults, they were treated as a single taxon, and their links counted only once.

Connectance (actual number of links as a proportion of the possible number of links) was calculated as $C = L / (S(S-1))$ (i.e. trophic connectance), where S is the number of species and L is the number of links. Predator-prey ratios were calculated using the same conventions as Jeffries and Lawton (1985). Species and linkage types followed the definitions of Cohen and Briand (1984) and Briand and Cohen (1984), i.e. top species feed on, but are not fed upon by, others in the web; intermediate species feed on, and are fed upon by others; and basal species are fed upon, but do not feed on any others in the web. Food chain lengths were calculated as the mode, mean and maximum of the frequency distribution of the lengths of all food chains in a web (Pimm 1982, Cohen et al. 1986). In the analyses of food chain lengths and numbers of links, intraspecific feeding has not been included, in keeping with other studies (e.g. Cohen and Newman 1985).

Results

Species occurrence and distribution

Sixty two invertebrate taxa were recorded from the pond over two seasons' sampling, but a substantial number of these, based on the criteria above, were not included in the analysis of the food web, reducing the food web for 1986 to 36 species (Tab. 1). No fish or

Tab. 2. Summary food web. Species are listed in their role as consumers along the top of the matrix and in their role as resources down the side. A non-zero element in the matrix indicates the consumer in that column feeds on the resource in that row. Species are designated by numbers as for Tab. 1, the trophic category "Detritus" is numbered 0. Adult and larval stages of a single species are not represented separately. 1=links based on direct experiment or gut contents analysis; 2=links based on good evidence from other studies and/or strong inference from similar species in this study. For species with adult and larval aquatic stages interactions are qualified by letters: a=consumer as larva; b=consumer as adult; c=resource as larva. No suffix=interactions common to both larva and adult.

		Consumer (species number)																																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	25	27	28	29	30	31	32	33	34	35	36	
Resource (species number)	0	.	1	1	2	.	2	1	2	2	2	2	2	2	2	2	1	.	1	1	1	1	2
	1	
	2	2	1	2	2	2	2	2	2	2	2	.	2	2	2	2	.	1	.	.	.
	3	2	.	.	.	2	.	.	.	1	1	1	2	2	1	2	2	2	2	.	2	.	.	.	1	.	.
	4	2	1	1	1	1	1b	2b	1b	2b	1	.	2	1
	5	2	2
	6	2	1	1	1	2	2	2	2	2	1	.	2	1	.	1	
	7	1	.	.	2	1	1	1	1	1a	2	1	1	.	1	
	8	2	.	.	2	1	1	1	1	2	2	2	2	2	.	1	1	.	1
	9	1	1	1	1	1	1	2	2	2
	10	2	1	1	2	2	1	2	2	2
	11	1	2a
	12	2a	2a
	13	2c	2c	2c	2c	2	2c	2c	2c	2c
	14	1	.	.	.	1c	1c	1c	1c	2c	1c	2c	1c	2c	1c	1c
	15	2c	.	.	.	1c	1c	1c	1c	2c	1c	1c	1c	2c	1c	1c
	16	2c	.	.	.	1c	1c	1c	1c	2c	1c	1c	1c	2c	1c	1c
	17	2c	.	.	.	1c	1c	1c	1c	2c	1c	2c	1c	2c	1c	1c
	18	2c	.	.	.	1c	1c	1c	1c	2c	1c	2c	1c	2c	1c	1c
	19	2c	.	.	.	1c	1c	1c	1c	2c	1c	2c	1c	2c	1c	1c
20	2c	.	.	.	1c	1c	1c	1	2c	1c	2c	1c	2c	1c	1c	
22	2c	2c	2	2	1c	2c	2c	2c	2c	2c	2c	
23	1c	1c	1c	1c	1c	2c	2c	2c	2c	2c	2c	
24	1c	1c	1c	1c	1c	2c	2c	2c	2c	2c	
25	1c	1c	1c	1c	1c	2c	2c	2c	2c	
27	2c
28	1	1	1	1	2	2a	1	2	2	2	1	
29	1	1	.	2	1	2	1	2	
30	1	1	.	2	1a	2a	2a	2a	
31	2	.	.	.	2	1	1	1	1	2	2b	2a	1	2	1	2	1	2	
32	2	.	.	.	2	.	.	2	1	2	1	1	2	2b	2a	2	2	1	2	2	2	2	2	2	.	.	.	
33	1	.	.	.	1	.	.	.	1	1	1	1	1	1b	2a	1	2	1	2	1	1	1	1	1	.	.	.	
34	1	.	.	.	1	.	.	.	1	1	1	1	1	2b	2a	1	2	1	2	1	1	1	1	1	.	.	.	
35	1	.	.	.	1	.	.	1	1	1	1	1	1	1b	2a	1	2	1	2	1	1	1	1	1	1	.	.	.
36	2	.	.	.	2	.	.	2	2	2	2	2	2	2b	2a	2	2	2	2	2	2	2	2	2

amphibia were found. Although different sampling methods were used for the marginal and open water areas, sampling effort curves flattened off markedly after about five samples in both areas, indicating that differences in species richness between the margin and open water areas (see Tab. 3) were not artefacts of the sampling methods.

Many species occurred regularly in the pond margin but were rarely, if ever, found in the open water; no species occurred only in the open water (Tab. 1). Thus the open water community was, in effect, a subset of that around the margin. Ordination of samples on the basis of the data in Tab. 1 shows consistent differences between open water and margin sites on all dates (Fig. 1). From Tab. 1 and Fig. 1 it can also be seen that, except for sample date 2, there was a broadly consistent seasonal trend in both areas towards more species rich webs.

Feeding relationships

Laboratory feeding trials and gut contents analysis of field collected animals produced consistent results. The combined information from both methods is included, without distinction, in the summary food web (Tab. 2). A selection of food webs based on this summary, compiled for each sample date/area combination is shown in Fig. 2.

Several predatory species were cannibalistic (Tab. 2), for example *Agabus sturmii*, *Sialis lutaria*, *Enallagma cyathigerum*, *Lestes sponsa* and *Aeshna juncea*. Feeding on conspecifics tended to be size dependent and was observed for some species in the field as well as in feeding trials. Size dependence is also important in interspecific predation. Many of the links (Tab. 2) occurred predominantly between certain size combinations of species. The results of some feeding trials could

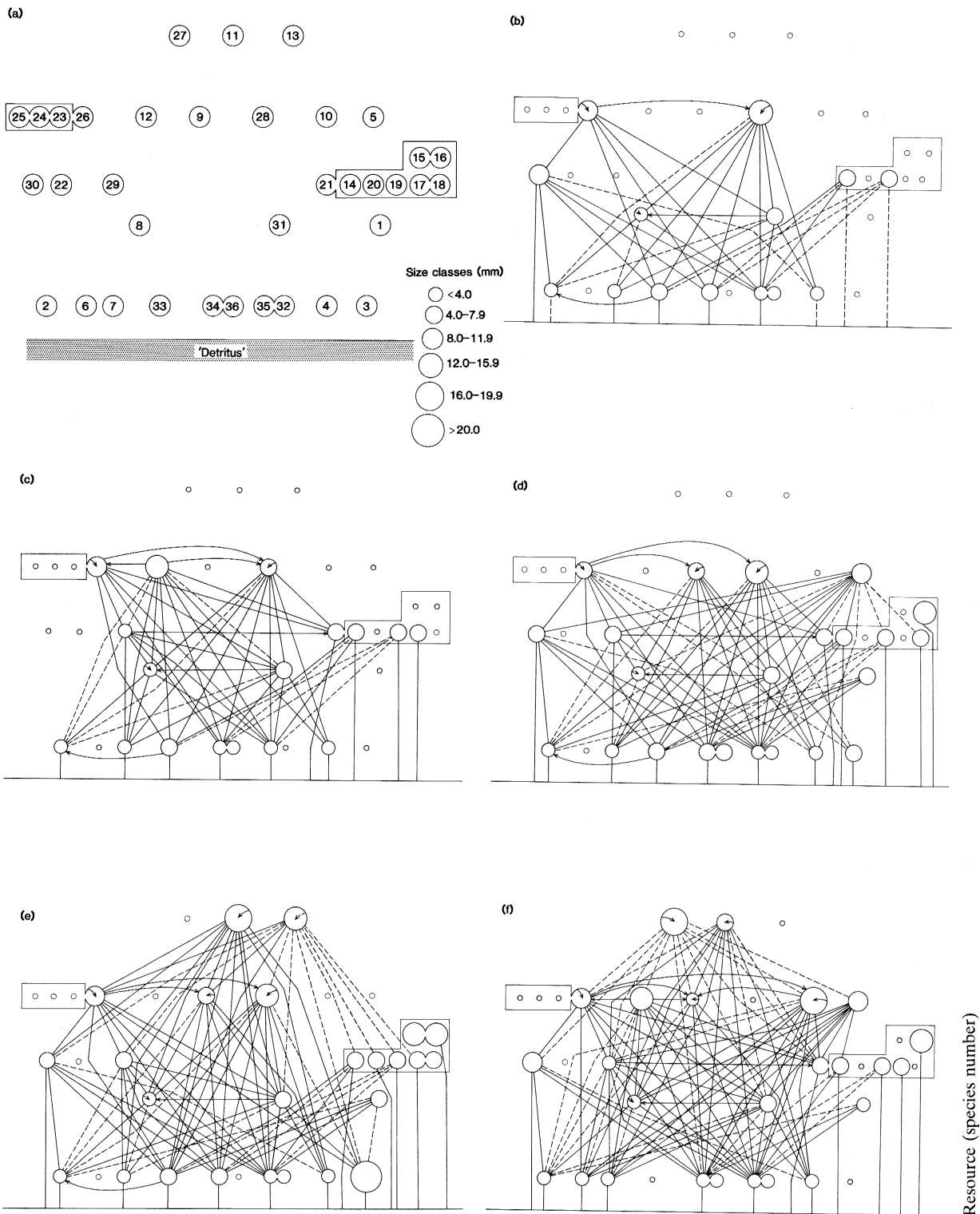


Fig. 2. Food web diagrams for selected date/habitat combinations. Species are represented by circles and links are directed downwards from consumer to resource unless otherwise indicated. Links within circles denote cannibalism. Very small circles (with no links) represent the positions (on the web template (a)) of species which were not found in that particular sample. The six sizes of larger circle indicate the mean size of species (see methods). The line at the base of the diagram represents a basal resource of detritus, fungi and microorganisms (see text). Broken lines show links derived from literature evidence or inference from other species in the web, solid lines links shown in feeding trials or by gut contents analysis. a) Web template. Species names are denoted by numbers corresponding to those in Table 1; b) Open water, March (date 1); c) Open water, June (date 3); d) (Open water, October (date 5); e) Margin, March (date 1); f) margin, June (date 3).

Resource (species number)

Tab. 3. Summary statistics for food webs from each sample and overall mean values. The significance of pairwise (t) tests of the differences between means of open water and margin samples for each characteristic are indicated by the conventional symbols – * = 0.05 > p > 0.01, ** = 0.01 > p > 0.001, *** = p < 0.001, NS = not significant. The values for the open water web at sample date 4 are the averages of the values for the open water (vegetated) areas.

Sample Date	Number of species	Connect- -ance	Pred./prey ratio	Food chain length:		
				Modal	Mean	Maximum
<i>Open</i>						
12–13 Mar	15	0.242	0.55	3	3.1	4
22–23 May	12	0.212	0.38	2	2.4	4
7– 8 Jun	17	0.279	0.6	4	4.0	6
21–23 Aug	19	0.268	0.58	3.5	3.3	5
3– 4 Oct	23	0.219	0.57	3	3.2	5
<i>Margin</i>						
12–13 Mar	26	0.167	0.6	4	4.1	6
22–23 May	19	0.248	0.7	4	3.9	7
7– 8 Jun	25	0.265	0.84	5	4.9	8
21–23 Aug	30	0.255	1.0	4	4.4	7
3– 4 Oct	32	0.252	0.82	4	4.4	7
<i>Mean (SE)</i>						
Open	17.2 (1.9)	0.244 (0.013)	0.53 (0.04)	3.1 (0.33)	3.22 (0.25)	4.8 (0.37)
Margin	26.4 (2.2)	0.237 (0.018)	0.79 (0.067)	4.2 (0.02)	4.32 (0.16)	7.0 (0.31)
Difference of means	***	NS	*	*	***	***
Overall	21.8 (2.1)	0.241 (0.01)	0.66 (0.057)	3.65 (0.26)	3.77 (0.23)	5.9 (0.43)

be reversed by altering the size combination of the two species involved. For example large individuals of *Lestes*, *Enallagma*, *Sialis* and dytiscid larvae would all feed on smaller individuals of each of the other species. Species which ingest only the body fluids of their prey (*Notonecta glauca* and larvae of *Agabus*, *Ilybius* and *Dytiscus*) could exploit prey of their own size or larger.

Further complications occur when larval and adult forms of one species have different trophic positions. Dytiscid beetle larvae (*Agabus*, *Ilybius*) can feed on some of the same prey as the adults and, while the latter are fed on by few, if any, predators, the larvae are prey to a number of other species, including Odonata and confamilial adults (Tab. 2, Fig. 2). Likewise relatively few species feed upon adult Corixidae (*Corixa*, *Hesperocorixa*, *Callicorixa*, *Arctocorixa*, *Sigaria*) but the larvae are consumed by a wide variety of predators (Tab. 2, Fig. 2).

Several of the species feeding predominantly on detritus were also found to be, to some extent, predatory. *Callicorixa praeusta* in feeding trials readily consumed Chironomidae, and other species in the genera *Callicorixa* and *Arctocorixa* have been recorded as predators (Southwood and Leston 1959, Reynolds 1975, Bakonyi 1978, Pajunen 1982). *Chironomus* larvae were observed to feed on small oligochaetes, and *Limnephilus*, partic-

ularly in later instars, attacked and consumed chironomid larvae (Tab. 2, Fig. 2).

The basal resource in the food web, referred to loosely as “detritus” is, in reality, a complex of living and dead organic material. Detritus feeders undoubtedly derive part of their nutrition from microorganisms ingested as part of the detrital material (Berrie 1976, Anderson and Cargill 1987), but it was beyond the scope of this study to tease out the trophic relationships at this level, which may be complex (Walker 1985). Similarly I have little information on the role of microinvertebrates as prey for the predators in the web. Nematoda, Protozoa (Ciliata) and Rotifera (mainly *Rotaria* sp.) were all found in detrital material and *Rotaria* sp. remains were found in gut contents of *Acanthocyclops vernalis*. Early instars of other predators (e.g. Odonata, Tanypodinae) almost certainly feed on microinvertebrates (e.g. Lawton 1970) but information was felt to be too fragmentary to include in the analyses.

Food web structure

As expected from Tab. 1 and Fig. 1, food webs classified by habitat and sample date show considerable variation in structure (Fig. 2). The margin area food webs appear

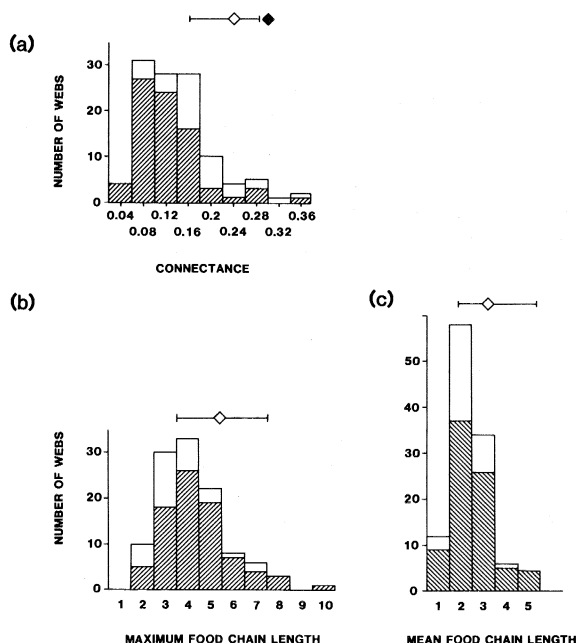


Fig. 3. Comparison of the average connectance and food chain lengths of webs from this study with those from the 113 published webs collected by Briand and Cohen (1987). The histograms show the distribution of connectance and chain lengths for all Briand and Cohen's webs and the hatched areas show the values for webs with species numbers in the same range as those in this study. In each case the open square and bars show the mean values and ranges for the webs from this study. a) Connectance (the solid square indicates the value for the summary web, Table 2). The values marked are the midpoints of each interval i.e. intervals are: $>0.02-0.06$, $>0.06-0.1$ etc. b) Maximum food chain length. c) Mean food chain length. Values marked are the midpoints of each interval.

consistently more complex than those from the open water due to their greater species richness; however the average connectance of webs from the two areas is almost identical (Tab. 3). Longer food chains occur in

the margin webs since the additional species found in the margin areas are predominantly large predators (Tab. 1); consequently the predator:prey species ratio is positively related to the number of species (Tab. 3).

Tab. 3 and Figs 3 and 4 show the summary descriptive statistics for the 10 food webs from the 1986 samples along with statistics documented from other food webs by Cohen and Briand (1984) and Briand and Cohen (1987). Food chain lengths, measured either as the maximum or mean length, fall within the range of values from the 113 webs studied by Briand and Cohen (1987) (Fig. 3 b,c), though with rather higher overall means. Connectance was generally higher, particularly in the summary web.

The webs in this study have a generally smaller proportion of basal and top species than webs from the literature (Figs 4a). The small proportion of basal species is almost certainly a product of classifying detritus as a single "trophic species" (sensu Briand and Cohen 1984). Recalculation of the proportions, assuming that detritus can be split into three, reasonably discrete, arbitrary basal resource categories (e.g. Hildrew et al. 1985, Kitching 1987), shifts the proportions closer to those found in other webs, but even in this case there are higher proportions of intermediate species and lower proportions of basal and top species than found by Briand and Cohen (1984).

The proportions of links in each of the categories basal-intermediate, intermediate-intermediate, intermediate-top and basal-top corresponded reasonably well with those from other webs (Fig. 4b). As expected from the species proportions (Fig. 4a) the average proportion of intermediate-intermediate links was comparatively high and the proportion of basal-top links was always low. Since the number of basal resources is constant, both species and linkage proportions are not independent of the number of species, so variation between

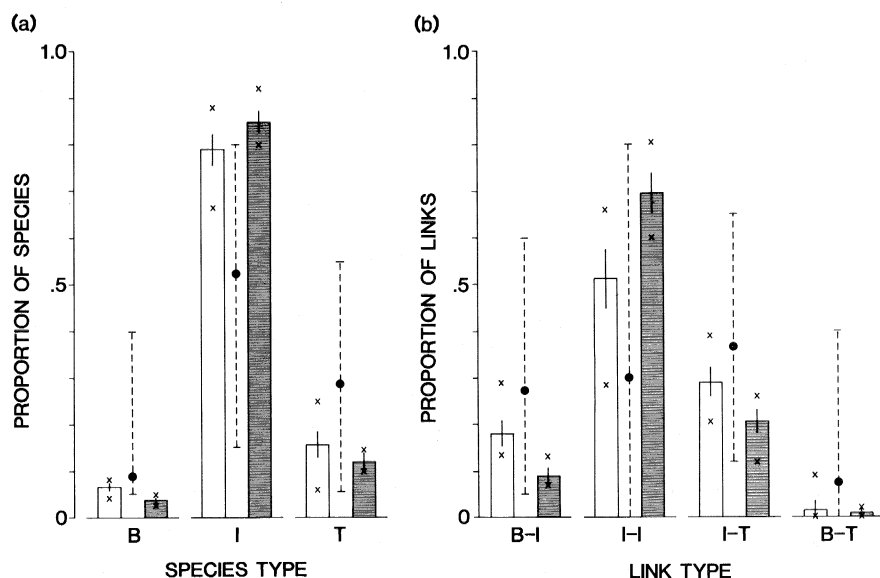


Fig. 4. Comparisons of species and linkage proportions. Histogram bars show the mean values (with SE) and range (crosses) of each statistic for the webs for this study. Unshaded bars indicate open water webs, shaded - margin webs. The solid circles and broken lines show the overall values and ranges for the 62 webs analysed by Cohen and Briand (1984). a) Proportions of basal (B), intermediate (I) and top (T) species. b) Proportions basal-intermediate (B-I), intermediate-intermediate (I-I), intermediate-top (I-T) and basal-top (B-T) links.

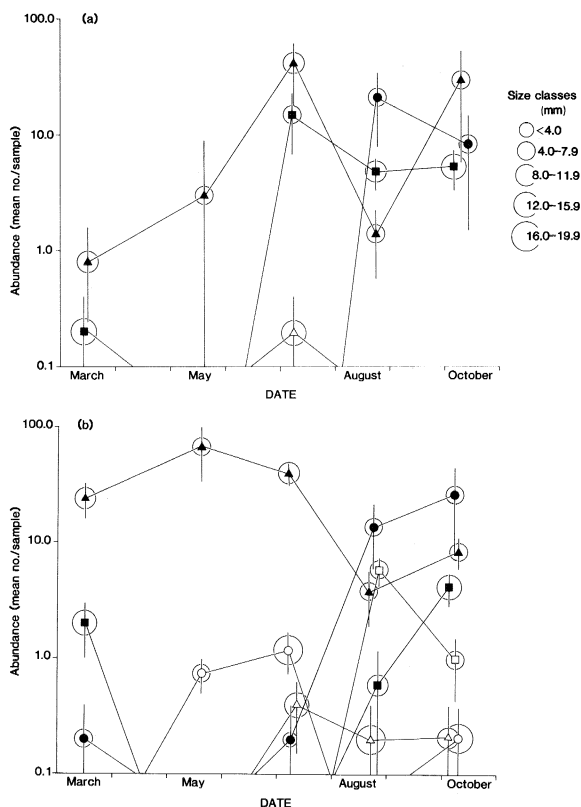


Fig. 5. The mean abundance and size of selected predators at each sampling date. Some points have been slightly displaced laterally for graphical clarity. The species are as follows: *Enallagma cyathigerum* (Odonata) (●); *Lestes sponsa* (Odonata) (○); *Sialis lutaria* (Megaloptera) (■); *Sympetrum scoticum* (Odonata) (△); *Agabus/Ilybius* larvae (Coleoptera) (▲); *Agabus sturmii* (Coleoptera) adults (□). Circles indicate body size as for Fig. 2. The bars are standard errors of abundance. a) Open water. b) Margin.

open water and margin webs is probably a consequence of differing species richness.

The difference between webs from the open and margin areas is maintained through the season, despite substantial variation in the presence and abundance of species at different sampling dates and a general trend towards increasing species richness at later dates (Tab. 1, Fig. 1). Much of the seasonal variation in species composition can be related to species life histories. Fig. 5 shows the sizes and abundances of several of the predator species from the margin and open water samples from March to October 1986. No species was consistently most abundant, even within one area of the pond, and some species appear to be absent on particular dates. Distinct effects of life cycle are most apparent for *Enallagma cyathigerum* (which emerges early and overwinters as a larva); *Lestes sponsa* (which has a short larval period, late summer emergence and overwinters in the egg stage) and *Sialis lutaria* (which pupates in the

spring); however, for *Sialis*, which generally has a two year life cycle (Elliott 1977), it is unclear why the previous year's larvae were not found in May samples. With the Dytiscidae, in which even congeners may have very different life cycles (Nilsson 1986), life history effects are harder to interpret.

Discussion

Food webs are not static entities. Even in the relatively simple community in this study substantial variation in trophic structure occurred within a single season and within what would typically be regarded as a single food web. The nature of the web and the variation within it lead to three considerations: the overall characteristics of the web in relation to theoretical predictions and other empirical studies; the nature of the variation; and the implications for theories concerning food web structure.

Characteristics of the web

The study web has, on average, high connectance and moderately long food chains. There is also considerable omnivory (i.e. species feeding at more than one trophic level (Pimm and Lawton 1978), many species feeding at more than one level in the web. Most models of food web dynamics predict that all three characteristics decrease the average stability or resilience of food webs and should therefore be rarely observed in natural systems and, when found, should be associated with stable environments (Pimm 1982). I have no formal measures of environmental variability for the study site, but observation over three years indicates that it was not subject to marked variations in water level, turbidity or temperature, though changes in the vegetation did occur over the study period (see Methods).

However, high values of connectance, omnivory and, perhaps to a lesser extent, food chain length and species proportions are all features sensitive to the thoroughness with which links are recorded. In this study the high values of omnivory and connectance were probably due to the use of both laboratory feeding studies and gut analyses along with consideration of the potential for interaction among different size combinations or developmental stages of species. Significantly, the mean of the connectance values for individual webs (Fig. 3a), although still high, is lower than that for the summary web in Tab. 2 (Fig. 3a). Given that observation of web linkage is very sensitive to the intensity of study, connectance, and hence omnivory and possibly maximum food chain length, seem likely to be underestimated, sometimes substantially so, in many published webs. However, even with more detailed data, the webs still fall roughly within the ranges of species and link propor-

tins noted as scale invariant by Cohen and Briand (1984).

Variation in the food web

Several interacting sources of variation are apparent from Tab. 1 and Figs 1 and 2: a marked difference between habitat areas, a general trend towards increasing complexity through the season and specific variation in the abundance or sizes of individual species. The two former sources of variation are primarily related to changes in the number of species although, due to changes in body sizes, links between particular species may also vary.

As species numbers increase (from open water to margin areas or through the season) predators and prey (*sensu* Jeffries and Lawton 1985) do not increase in equal proportions (Tab. 1). The additional species are principally predators. It can be seen from Fig. 2 that additional predator species do not feed only on species at higher trophic levels but take prey from all parts of the web. Food chain length however, still increases with number of species because links between top species and others at high levels in the web contribute many more chains to the final total than links between top species and those lower in the web.

It is not clear why the pond margin should consistently have more species than the open water areas. Increased invertebrate species richness in structurally more complex aquatic habitats has been associated with refuges from fish predation (Macan 1977, Crowder and Cooper 1982, Gilinsky 1984) though that cannot be the cause in this case since no fish or equivalent large predators were present. The occurrence of some species in more structurally complex habitats probably reflects modes of feeding or movement, for example net or web building (*Holocentropus* spp., *Argyroneta aquatica*) or perches for predators such as Odonata. The two areas seem unlikely to have marked differences in environmental predictability; however productivity may differ since the bulk of detritus entering the system is litter from fringing vegetation, and is therefore concentrated around the pond margin. This latter factor raises the intriguing possibility that, while food chains do not appear to be consistently longer in more productive environments (Pimm and Lawton 1977, Briand and Cohen 1987, Pimm and Kitching 1987 – though see also Yodzis 1984, Lawton 1989) at this fine scale, species number and (hence) food chain length may be related to energy input.

Increasing food web complexity (in both open water and margin areas) through the season seems to result from two factors. First (see Fig. 5), many species were either absent (as larvae) or nearing the end of their larval period (and hence at their least abundant) during late winter and early spring, generating webs with fewer species early in the season. Second, as already noted, there were structural changes in the open water habitat.

The initially sparse patches of submerged mosses spread markedly through the season and a number of species initially associated with the marginal vegetation (e.g. *Argyroneta aquatica*, *Polycelis tenuis*) were found later in the year in the open water samples. The difference between the webs from the vegetated and unvegetated open water areas (on sample date 4) indicate this effect (Fig. 1).

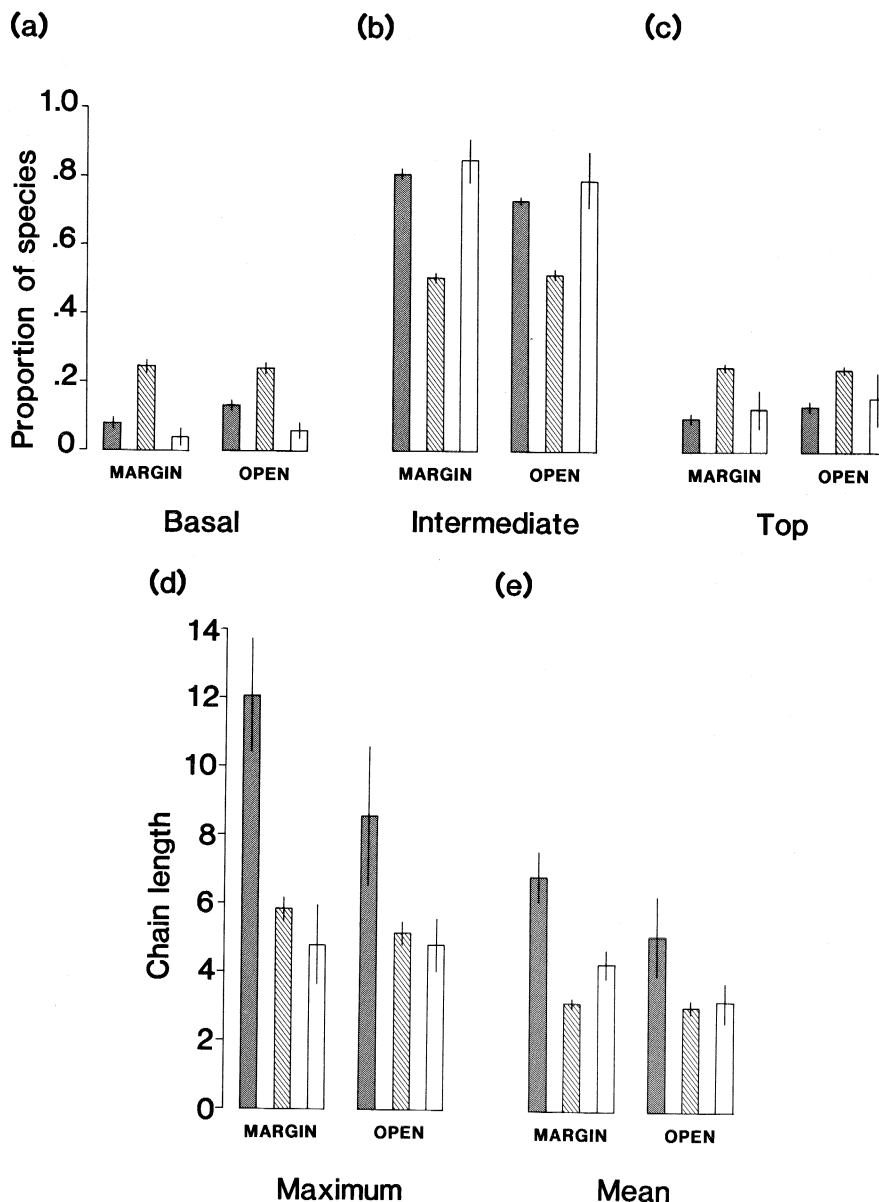
Nested within the overall trends in spatial and temporal variation are specific changes in trophic relationships between species. Size has major influences on trophic interactions in the community and the temporal variation in population size structure creates potential for varied, dynamic patterns of trophic structure (Cousins 1980, Werner and Gilliam 1984, Pimm and Rice 1987, Southwood 1987). Despite the complexity of Tab. 2, the range of potential interactions between different sizes of species in the web is probably still an underestimate; it is not difficult to envisage a number of further possible links, between extreme size combinations of species, which have not been included. Consideration of all life stages of a species also increases the estimate of omnivory in the web and makes trophic loops much more common. Trophic loops and “life-stage omnivory” (Pimm and Rice 1987) may arise at a particular point in time (if species co-occur at a sufficient range of sizes) or, more commonly, may occur when interactions are summed through time (for example in Tab. 2: *Lestes* – *Sialis* – dytiscid larvae – *Lestes* forms a trophic loop). Both features can lead to instability in food web models (Pimm 1982, Pimm and Rice 1987).

Constraints on food web organisation

A number of theoretical explanations have been proposed for observed patterns in the structure of food webs (Pimm 1982, Lawton 1989). One such body of theory is based on analyses of the local stability properties of particular multispecies population dynamics models (May 1973, Pimm 1982). How does variability in food web structure bear upon this theory?

One consequence of heterogeneity in the web is that many potential predator and prey populations will only partly overlap in space or time, resulting in seasonally ephemeral or spatially restricted interactions, with two possible consequences. First, some dynamically important links may be missed in short term studies. Second, and probably more significant, the nature and realised strength of the interactions between species may be substantially altered. Spatially or temporally restricted interactions, averaged over generation time, may have negligible consequences for the population dynamics of consumer and/or resource. For example a consumer feeding only in a limited area of the habitat, on prey occurring over a much wider area, is one situation likely to lead to “donor-controlled” interactions (Pimm 1982:96), in which consumers have little effect on the resource dynamics. Overall it is difficult to imagine that

Fig. 6. Comparison of observed and simulated webs. a) Proportions of basal species. b) Proportions of intermediate species. c) Proportions of top species. d) Maximum food chain length. e) Mean food chain length. Each bar shows the average of all observed webs (open bars), or the corresponding simulated webs (light and dark shaded bars), from each habitat area, across all sample dates. Simulations were carried out with observed values (dark shaded bars) and the literature derived values (light shaded bars) for the links: species ratio (see text). Error bars are 1 standard deviation.



individual seasonally and spatially defined webs (Fig. 2) include all dynamically important links. Equally, the summary web (Tab. 2) almost certainly contains a high proportion of links which are of little or no dynamic consequence.

The predictions of dynamic food web models depend substantially on assumptions made about the strength of species interactions, particularly with regard to "donor-control" (DeAngelis 1975, Pimm 1982, May 1979, Lawton 1989). Models of food webs which assume predominantly closely coupled, reciprocal, consumer-resource interactions ("Lotka-Volterra" models – Pimm 1982, Lawton 1989) will be poor predictors of web structure if most links are actually weak or donor-controlled.

Given this sensitivity in the models, and the potential effect of web heterogeneity in moderating the strength of interactions, it seems improbable that Lotka-Volterra models provide a sufficient explanation of food web structure in this system. By implication, the same problems must exist in many other webs.

A very different explanation for several of the patterns in published webs has been suggested by Cohen and Newman (1985) and Cohen et al. (1985). They proposed a non-dynamic model in which species can be arranged a priori into a hierarchy or "cascade" such that a species may feed upon any of those below it in the hierarchy and be fed on by any of those above (an idea also used as the basis for a null model of food webs

(Pimm 1980)). Within this constraint links are assigned independently, with fixed probability such that the density of links (i.e. links:species ratio) matches that observed in published webs. The model appears to make approximately correct predictions of the proportions of basal, intermediate and top species; of the proportions of links between each of these; and of the frequency distribution of food chain lengths, for most published webs. One possible mechanism leading to the type of hierarchy required by the model is an ordering of species based on size, with the restriction that species feed only on others smaller than themselves (Warren and Lawton 1987, Cohen and Newman 1988). The independence of this general mechanism from the species dynamics and the spatial and temporal scale on which a web is studied, suggests that despite heterogeneity in the data, webs should have broadly similar average structure and would thus appear to be a widely applicable explanation for patterns in food webs, though it does not exclude the possibility of other processes having a part in shaping food webs.

Interestingly, as is evident from a comparison of the summary web (Tab. 2) and the individual webs (Fig. 2), the assumptions of the cascade model may best be met in webs drawn at one point in time rather than for webs summarising links over longer periods. In a summary web, if species sizes change markedly over time and feeding interactions alter correspondingly, it may be impossible to meaningfully order species on the basis of size. To retain a size based trophic hierarchy in such webs, size classes of a species must be depicted separately (e.g. Hardy 1924).

Since, in compiling the Skipwith pond webs, it was sometimes necessary to make judgements about the likelihood of interactions between particular sizes of species, the distributions of links in the webs are not wholly independent of assumptions about size, and these webs cannot therefore be used to test the idea that body size generates the trophic hierarchy assumed by the cascade model. However, for subsets of data from this food web, for which links and body sizes can be derived independently, the assumption of a trophic hierarchy based on size is reasonable (Warren and Lawton 1987, Warren 1988). The relationship between the predictions of the cascade model and observed web structure can, however, be investigated by comparing webs from this system with model webs assembled under the assumption of a size-based trophic hierarchy. This was done using computer simulation.

Simulated webs were based on two parameters, the number of species and the links:species ratio. Species sizes were drawn independently from a uniform distribution and links, up to the density set by the links:species ratio, were assigned at random under the constraint that species feed only on others smaller than themselves. The model is closely equivalent to that analysed by Cohen et al. (1985). For each observed web a number of simulated webs (usually 50) were generated

and the average food chain lengths and proportions of basal, intermediate and top species were calculated. Proportions of links between basal, intermediate and top species were not analysed.

Simulations were carried out for each web in Tab. 3 using both the observed links:species ratio (i.e. a separate value for each web) and the constant 1.86, the average value from published webs, derived by Cohen and Briand (1984). Fig. 6 shows the average values of food chain length and species proportions for the observed webs from the open water and the margin, and the averages for the corresponding simulated webs.

It is evident from Fig. 6 that for webs with observed (high) links:species ratios the model predicts food chains that are too long (Fig. 6 d, e), but species proportions that are approximately correct (bearing in mind the arbitrary single basal "species") (Fig. 6 a, b, c). The reverse is true for simulations using the constant (and lower) links:species ratio derived from the published data. These predict food chain length more accurately, but species proportions rather badly.

Predictions of food chain length appear very sensitive to variation in the density of links in the food web, suggesting that the cascade model, in this form, may be a sufficient predictor of species proportions but not of food chain lengths. This may point to other factors acting to limit food chain length, for example energetic or dynamic considerations (Pimm 1982, Lawton 1989); it may also point to inadequacies in the model. In particular the simple uniform distributions of species sizes and the absence of prey-size selection by consumers are simplifications. Refining the model structure, for example by using more realistic species-size, and prey-size distributions, may help reconcile the disparate predictions in Fig. 6. However, initial analyses (Warren 1988) indicate that, while using more realistic species- and prey-size distributions can account for the higher proportions of top species over basal species observed in published data, the basic conclusions from the simulations described here still hold. The results also emphasise the need to test, independently of published food web data, hypotheses proposed to account for constraints on the links:species ratio (e.g. May 1973, 1986, Pimm 1982, Cohen and Newman 1988, Paine 1988).

It remains to be determined whether, in untangling the processes underlying patterns in web structure, any single factor explanation will prove sufficient (Lawton 1989). The detailed data on structure and connectance in food webs from the single system studied here indicates the importance of spatial and temporal scale in food web analyses, and the potential problems for interpreting patterns in web structure posed by combining studies on a variety of scales. Identification of the scale at which particular factors operate and of the independence, or interdependence of these factors may be necessary to develop an explanation sufficient to account for the composite patterns which determine the overall "shape" or structure of food webs.

Acknowledgements. – I would like to thank J. Lawton and R. Law for much helpful discussion and advice during the course of this study and for comments on the manuscript. Further useful comments and criticisms of the manuscript were provided by D. Reavey, K. Gaston, S. Hartley, S. Pimm and C. Otto; financial support was provided by an N.E.R.C. studentship and permission to work at Skipwith Common was kindly given by the Yorkshire Wildlife Trust. To all these people and organisations I am most grateful.

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