

Is resolution the solution? : the effect of taxonomic resolution on the calculated properties of three stream food webs.

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SUMMARY

1. The influence of level of taxonomic resolution on estimates of food-web properties was studied in three grassland streams in New Zealand. The food webs, each of which contained approximately 100 species of algae, macroinvertebrates and fish, were progressively aggregated into higher taxonomic groupings and the effect on food-web properties was assessed. Aggregation was also carried out differentially on particular taxonomic groups to mimic the usual approach to taxonomy in stream food-web studies.

2. Of the commonly used food-web properties mean chain length and linkage complexity varied little with the degree of taxonomic resolution. Estimates of connectance were markedly higher in coarsely resolved (family level) food webs, possibly as a result of a decrease in the number of web elements.

3. Connectance, linkage density, linkage complexity and prey:predator ratios, but not mean chain length, were strongly affected by inconsistency in the level of resolution used among different taxonomic groups within a food web.

4. In order to make meaningful comparisons among food webs a standardised approach to methodology, resolution and effort is needed.

Introduction

Connectivity food webs display the trophic interactions in a community. They have a long history (Elton, 1927) but the search for predictable patterns in food-web structure has been far from fruitful. In recent years, a series of damning reviews (e.g. Paine, 1988; Pimm and Kitching, 1988; Closs, 1991; Cohen, 1993a) have focused, in particular, on the considerable problems associated with the existing database of food webs. We agree with these concerns. However, the conclusion of Polis (1994) that ‘the connectivity approach is fatally and irrevocably flawed’ may be premature. Judgement should be reserved until a more standard approach to describing food webs provides a database that allows rigorous testing of hypotheses across communities (Townsend *et al.*, 1998).

Published food webs vary in the methodology used, the season of sampling, the criteria for defining a link and the level and standardisation of taxonomic resolution. Some of these factors have now been convincingly shown to affect estimates of food-web properties (Closs, 1991; Cohen *et al.*, 1993a; Tavares-Cromar & Williams, 1996). We focus on the complex issue of the influence of taxonomic resolution. Researchers have been criticised for a failure to resolve webs to the highest possible level of taxonomic resolution (Cohen *et al.*, 1993a) but increasing resolution involves a considerable increase in the effort required (e.g. Lancaster & Robertson, 1995). A related issue, which has rarely been discussed, is the standardisation of resolution in different groups within the same food web (e.g. algae, small and large invertebrates, fish). The construction of food webs that can

properly be compared requires understanding of the effects of low and/or variable taxonomic resolution.

In this study, the food webs of three New Zealand streams have been compiled with an emphasis on consistent methodology and a high level of taxonomic resolution. The purpose here is not to analyse these food webs exhaustively or comment on the patterns that they display as this has been done elsewhere (Jaarsma *et al.*, 1998; Townsend *et al.*, 1998). The existence of these three comparable food webs has allowed us to investigate rigorously the effects of variation in taxonomic resolution. Such an approach has been attempted before in Sugihara *et al.*'s (1989) review of invertebrate food webs and Martinez's (1991; 1992) work on lake communities. However, these reviews have included food webs gathered by many different researchers with high variation in the techniques used and effort expended. This study aims to determine what the effect on a selected group of food-web properties is of increasing taxonomic resolution 1) when it is increased across all taxonomic groups evenly and 2) when it is increased only for certain groups.

Like Sugihara *et al.* and Martinez we progressively aggregated our webs into coarser taxonomic groupings to determine how food-web properties are affected. However because we knew that the food webs varied only in taxonomic resolution, we were better able to investigate this effect. We also assessed the influence of differential aggregation of particular taxonomic groups (to mimic the traditional unevenness of taxonomic resolution in food-web studies). Most food-web papers have grouped certain taxonomic groups together based on their

biological characteristics. For instance it is not uncommon for algae to be grouped together into a single taxon, or for small invertebrates such as chironomids to be grouped together. Although our food webs group detritus into a single grouping, our ability to resolve the taxonomic identity of algae and most invertebrates places us in a unique position to investigate the consequences of increasing the evenness of taxonomic resolution across groups.

Methods

Study sites

The three study sites, Healy Creek (NZMS 260 : I41, 975015), an unnamed tributary of Three O’Clock Stream (described here as Dempsters Stream; NZMS 260 : I43, 052237) and Sutton Stream (NZMS 260 : H43, 467938), are second-order streams in the headwaters of the Taieri River in the South Island of New Zealand. They all have grassland catchments that are grazed by sheep and cattle and are broadly comparable in terms of water chemistry, physical characteristics (Table 1) and primary productivity (Townsend *et al.*, 1998). The area is characterised by a cool temperate climate with average rainfall of around 800mm.

Table 1 Summary of physico-chemical characteristics of the three sites.

	Healy Creek	Sutton Stream	Dempsters Creek
Altitude (m a.s.l)	660	520	300
Catchment area (km ²)	5.9	15.2	24.5
Average width (m)	3.03	2.40	3.72
Average depth (m)	0.16	0.12	0.14
NO ₃ +NO ₂ (µg/L ⁻¹)	7.3	1.5	21.2
Total N (µg/L ⁻¹)	75.4	219.1	219.1
DRP (µg/L ⁻¹)	4.6	13.0	13.0
Total P (µg/L ⁻¹)	9.1	16.2	38.9

Sampling and dietary analysis.

Sampling of each site was confined to a 30m reach. These reaches were chosen at random with the restriction that each site should contain at least one pool and one riffle. Algae and invertebrates at each site were sampled on 5 (Dempsters Stream), 12 (Sutton Stream) and 17 (Healy Creek) January 1995 (Austral summer).

Invertebrates were collected using 10 randomly located Surber samplers (0.06m², mesh size 250µm), sampling the top 5cm of substratum. On return to the laboratory these samples were used to construct food webs for each site. Samples were sorted without magnification excluding invertebrates less than 1.5mm in length, terrestrial invertebrates, partial invertebrates, pupae and empty insect cases. Meiofauna (invertebrates <1.5mm in length) were not included in this study as taxonomy on small

individuals is not sufficiently accurate for a study of this nature. The key of Winterbourn & Gregson (1989) was used for general invertebrate identification, with reference to specialist keys for hydraenid beetles (Ordish, 1984) and hydrobiosid caddis-flies (McFarlane, 1951). Identification was carried out to the highest level of resolution possible. In some cases, such as for chironomids and oligochaetes, keys to the New Zealand fauna are incomplete and the individuals were described according to morpho-species within major familial groupings. Subsequent microscopic taxonomy (by Dr Peter Cranston, CSIRO, Canberra) revealed that the chironomid morpho-species represented either a single species or a single genus. Using these methods, more than 90% of individuals were ascribed to either a species or morpho-species classification.

Invertebrate diets were analysed according to the methods of Jaarsma *et al.* (1998). Ten individuals of each species (or as many as were present if there were fewer than ten) were gutted by squeezing the gut contents on to permanent slides that were then inspected to identify the animal and plant contents. Individuals that had empty guts were ignored and another individual selected. Although the number of invertebrates gutted was considered a minimum, it was the largest number feasible for webs of this size. In each of the food webs around 40% of species did not achieve a gut sample size of ten (Dempsters Creek, 23 out of 55; Healy Creek 19 out of 48; Sutton Stream 14 out of 34), although three quarters of those still had more than five guts inspected.

Organic detritus was included as a single food item and was distinguished from non-organic material by the use of lignin pink as a stain. Taxonomy of algae in the guts was determined by Cathy Kilroy (National Institute for Water and Atmospheric Research, Christchurch, New Zealand) by reference to the texts of Bourelly (1981; 1985; 1988; 1990), Cassie (1989), Foged (1979), Krammer (1986), Patrick & Reimer (1966; 1975), Prescott (1973; 1981) and Whitford & Schumacher (1973). When the slide had been inspected, diatom species, invertebrate remains and organic detritus were attributed a score from 1 (rare) to 8 (abundant).

Fish were sampled by electro-fishing two to three days after the initial sampling visit. The study reaches were isolated with stop nets and three fishing runs were carried out. All the fish caught were identified in the field and a random sub-sample of 10 fish (or as many as possible if 10 were not caught) was chosen for gut analysis. These fish were killed and placed in formalin for return to the laboratory. The remaining fish were returned to the stream. In the laboratory the fish were dissected and the contents of the guts identified under 40x magnification.

Compilation of food webs.

Each food web was compiled in the form of a binary matrix. The presence of detritus, algal or invertebrate species in the gut of an animal species was recorded as a trophic link. Where a species occurred that was eaten but had not been found in field samples it was attributed the feeding links of the most closely taxonomically and trophically related species. This was necessary for a single species (from a total of 92) in Sutton Stream, for eight

species (of 107) in Dempsters Creek and for 10 species (of 96) in Healy Creek. Known suctorial feeders (Empididae and flatworms; never more than two species per food web) were omitted when gut analysis revealed no recognisable material in the gut contents.

Invertebrates were categorised into as predatory or non-predatory according to the score that they received for abundance of different food items in the gut. Any species that predominantly consumed invertebrates (invertebrate remains scoring greater than 4, organic detritus and algae scoring less than 4) was classified as a predator. Predatory taxa were precluded from linking with algal taxa to remove the chances of detecting false links due to prey within prey. Cannibalistic links were removed to simplify the computer analysis. Food-web properties were calculated using a simple Excel © macro that calculated the number of species (S), number of links (L), mean chain lengths (excluding loops) and the proportion of top, intermediate and basal species using recursive programming. These primary properties were used to calculate the linkage density (L/S), linkage complexity (SxC), trophic connectance (C) and prey:predator ratios (Cohen, 1977). Connectance was calculated by means of the formula in Jaarsma *et al.* (1998). This modifies the Warren's (1994) formula by calculating the number of possible links in the food web as the square of the total number of feeding taxa (ie non-basal taxa). This change was made to acknowledge the fact that an unusually high number of the taxa in our food webs are non-feeding (i.e. algae). We present results for five properties: connectance, linkage density, linkage complexity, mean chain length and prey:predator ratios.

Manipulation of taxonomic resolution.

The taxonomic resolution of the webs was manipulated by creating three levels of resolution. The first, termed ‘species’, was the initial web, in which more than 90% of individuals were resolved to species or morpho-species. The second and third levels, termed ‘genus’ and ‘family’, grouped species into these taxonomic divisions.

In a separate analysis, we used a further set of three protocols which resolved organisms from different taxonomic groups at different levels. In the ‘variable I’ protocol, fish and large macroinvertebrates were identified to species, small macroinvertebrates, namely chironomids and oligochaetes, were identified to family or class, and algal species were lumped as a single web element. This variable pattern of resolution was chosen to mimic the resolution used for previous stream food webs (Minshall, 1967; Hildrew *et al.*, 1985). To determine the effects of aggregating animals or algae alone, two intermediate variable protocols were created between the ‘species’ level and the ‘variable I’ level. In ‘variable II’ algae were grouped into a single category (as in ‘variable I’) but all macroinvertebrates and fish were identified to species. In ‘variable III’ invertebrates and fish were grouped as in ‘variable I’, while algae were identified to species level.

As we had no *a priori* reason for assuming that our properties were normally distributed, where possible distribution-free statistical techniques were used. The properties were analysed collectively using the program ‘Primer’ (Plymouth

Marine Laboratory, 1994). All the properties (normalised but not transformed) were used in a hierarchical agglomerative clustering technique (Clarke and Warwick, 1994) which was used to produce an ordination using non-metric multi-dimensional scaling (Kruskal and Wish, 1978). Simple non-parametric permutation tests (Clarke and Green, 1988) were then used to test for significance between different sites and treatments.

To test for differences in properties of food webs resolved to the species, genus and family level, a two factor ANOSIM without replication (ANOSIM2, Clarke and Warwick, 1994) was used, testing for differences between sites and level of taxonomic resolution nested within site. The same analysis was carried out to analyse for an effect of applying taxonomic resolution unevenly. However in this case an additional single factor analysis of similarities (ANOSIM, Clarke and Warwick, 1994) (testing for a significant difference between food webs which had had only algal species lumped together and all other webs) was also executed. Non-parametric two factor analysis of variance (Kruskal-Wallis test, Zar, 1984) was used to test for the effect of site and resolution on the individual food-web properties. These analyses were carried out testing for a stream effect, an effect of the 'species', 'genus' and 'family' taxonomic levels, and an interaction between these terms, on each property. A similar analysis was used to contrasted the 'species' level with the three 'variable' levels of resolution, by testing for an effect of site and of the different levels of resolution. An analysis of the interaction between these terms was not possible in this case due to insufficient degrees of freedom.

Results.

Effects of absolute level of taxonomic resolution.

When the effect of resolving the food webs to species, family or genus level was analysed, between-site variation alone was significant only for links per species, while taxonomic resolution alone did not significantly affect any property (Table 2, 3). More important in the present context, was the significant interaction for all properties between site and taxonomic resolution. All properties showed a significant effect of taxonomic resolution within each site. However the way in which variation in taxonomic resolution affected properties differed between sites. Sutton Stream, which was dominated by algal taxa, was little affected by reduction in resolution because most of the algal taxa were distantly related. Healy and Dempsters Streams however were strongly affected, as they had more invertebrate taxa, which tended to be more closely related taxonomically. In these sites reduction of resolution to family level resulted in an increase in connectance and prey:predator ratios and a decrease in the number of links per species. Linkage complexity and mean chain length were unaffected. When the properties are plotted together on an ordination (Fig 1) the site effect is apparent in the clustering of the three taxonomic levels from each site together, and distant from the other sites. However the wide spread of data within these clusters means that the site effect is not significant for this analysis (Global $\rho = 0.667$, $p=0.21$). It is readily apparent from the ordination that Sutton Stream is behaving

differently from the other two sites, which cluster together and show the same pattern of taxonomic resolution levels within the site clusters. The differences in the patterns between Healy and Dempsters Creeks as compared to Sutton Stream mean that no significant effect of taxonomic resolution is found (Global rho = -0.333, p=0.94).