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

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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

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