

## SPATIAL AND TEMPORAL VARIATION IN THE STRUCTURE OF AN INTERMITTENT-STREAM FOOD WEB<sup>1</sup>

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**Abstract.** Food webs from the Lerderderg River, an intermittent stream in Victoria, Australia, were compiled with the aim of examining changes in food web structure in a highly variable habitat. Emphasis was placed on a high degree of taxonomic precision. Spatial and temporal variation in the food webs was assessed by partitioning the study area into three sites, located  $\approx 1.5$  km apart along the river. Sites differed in overall stream width and the length of the low streamflow period during summer. Three separate webs for each site were compiled for four different times of the year.

Relatively little spatial variation in community structure was observed. In contrast, temporal variation was considerable, with species composition and the number of species in the community changing considerably over the year. The number of species increased dramatically as the period of constant streamflow lengthened. Detritivores dominated the community, both in terms of species and individual numbers. The proportion of predators in the community increased slightly by the end of the year, suggesting that recolonization of the community by predators lags behind that of detritivores. The increase in the number of predator species also resulted in an increase in the mean food chain length through the year.

Patterns observed in the food webs tended to fall within the range of values reported from several previous studies, suggesting that underlying constraints may structure certain aspects of food webs. However, the constancy of certain food web statistics was attributable either to methodological decisions made during compilation, or to an inherent property of the statistic itself. The potential sensitivity of several food web statistics to the methodology used to compile a food web render between-web comparisons difficult due to the confounding effects of methodology. This suggests that comparisons between food webs should be restricted to webs derived from similar habitats using a comparable methodology.

**Key words:** connectance; disturbance; food-chain length; food chains; food web patterns; food webs; food web theory; intermittent streams; predator–prey ratios; spatial and temporal variation; succession; trophic interactions.

### INTRODUCTION

Analyses of large collections of published food webs have suggested that food webs show consistent structural patterns (Cohen 1977, 1978, Pimm 1982, Briand and Cohen 1984, 1987, Cohen and Briand 1984, Briand 1985, Lawton and Warren 1988, Lawton 1989, Sugihara et al. 1989, Cohen et al. 1990, Pimm et al. 1991, Schoenly and Cohen 1991, Schoenly et al. 1991). These regular patterns include short food chains (Elton 1927, Pimm 1982); a constant number of links per species (Cohen and Briand 1984); an inverse relationship between web connectance and the number of species (May 1972, 1973, Rejmanek and Stary 1979, Pimm 1982); constant predator species to prey species ratios (Cohen 1977, 1978, Briand and Cohen 1984, Jeffries

and Lawton 1985, Lockwood et al. 1990, Warren and Gaston 1992); and constant proportions of top, intermediate, and basal species (Briand and Cohen 1984).

The observation of these patterns, and the possible reasons for their existence, have generated considerable debate. Views on the significance of different patterns have ranged from those who suggest that the patterns may be indicative of an underlying order in nature (e.g., Pimm et al. 1991) to those who view them as artifacts of food web compilation (e.g., Paine 1988) or mathematical artifacts (e.g., Closs et al. 1993). Several causative mechanisms for different patterns have been suggested, including the dynamics of predator–prey interactions (May 1972, 1973, Pimm 1982); inefficiencies in the transfer of energy between successive trophic levels (Elton 1927, Lindeman 1942, Yodzis 1981, 1984); biological size and design constraints (Elton 1927, Colinaux 1978, Pimm 1982, Warren and Lawton 1987); and topological or mathematical constraints (Auerbach 1984, Kenny and Loehle 1991, Closs et al. 1993).

Different aspects of these proposed mechanisms have been incorporated into theoretical food-web models,

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