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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 (Bengsston 1994). In particular, because the food web sta-

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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; Bengsston 1994). Bengsston (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-