## THE IMPORTANCE OF TEMPORAL RESOLUTION IN FOOD WEB ANALYSIS: EVIDENCE FROM A DETRITUS-BASED STREAM<sup>1</sup>

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Abstract. A series of time-specific food webs for the macroinvertebrate riffle community of Duffin Creek, Ontario was constructed using dietary information obtained from the analysis of gut contents. Trophic links were quantified using a dietary index of relative importance. Precision of the analysis was maintained at a high level by: (1) identifying dietary items as accurately as possible via direct gut analysis; (2) identifying web members to the species level, thus avoiding the taxonomic aggregation and lumping of size classes common in food web analyses; and (3) ensuring temporal resolution of the web by determining ontogenic variation in the diets of dominant members of the community.

The Duffin Creek webs are heavily detritus-based with a large proportion of top-to-basal, and intermediate-to-basal links. Top-to-basal links, proportions of top and intermediate species, and lower connectance (0.180–0.219) varied temporally. Trophic connectance ranged from 0.090 to 0.109, consistent with values expected for a web consisting largely of specialist feeders. Weak links made up the largest proportion of total links in the webs, whereas very strong links made up the smallest proportion. Omnivory was more common than indicated in other webs and can be attributed to ontogenic diet switching.

Comparison of the statistics for a summary web with those generated for the time-specific webs indicated that the total number of links per web, total number of species, number of top and intermediate species, and linkage density were much greater for the summary web. In view of these differences, the importance of temporal resolution when assessing food web structure and dynamics is emphasized. The possibility that some of the observed features in our web are common to other detritus-based webs is considered. Future studies of this calibre are justified.

Key words: aquatic macroinvertebrates; detritus-based; fresh water; life history omnivory; ontogenic diet switching; riffle community; temporal resolution; time-specific food webs.

## Introduction

This study of food web structure is considered to be important to the understanding of ecosystem function (Pimm 1982). In the last decade, food webs have been approached from a theoretical aspect, with emphasis on food web structure and the constituent patterns (Pimm and Rice 1987, Schoener 1989). Food web theory indicates that complex web interactions are not random, but highly patterned and limited by simple biological processes, namely dynamic and energetic constraints, and the structural design of animals (Pimm 1982, Yodzis 1989). Pimm (1982) has identified 12 patterns of food web design, some of which may be non-independent. Analyses of previously published webs have revealed common features, even among webs from different habitats with widely varying species numbers (Sugihara et al. 1989). However, limitations in the collection of data used for these analyses and results from recent analyses (Winemiller 1990, Martinez 1991, Polis 1991, Paine 1992) have cast doubt on these putative common food web features and their validity (Pimm et al. 1991, Polis 1991).

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Early food web studies often focused on a small subset of species from an entire community ("speciesspecific webs"; e.g., Hardy 1924, Paine 1966, Birkeland 1974, Hildrew et al. 1985). Although these studies provide important dietary information for specific members of an assemblage, they are of limited use in the assessment and/or development of food web theory at the community level. Since food webs are a community phenomenon, food web data sets should be community based. However, even community webs are plagued with inconsistencies, which include poor taxonomic resolution, inconsistent trophic accuracy (direct vs. implied trophic information), and poor quantification of links, all of which may bias the resulting food web statistics (Paine 1988, Lawton 1989, Sugihara et al. 1989, Hall and Rafaelli 1991, Martinez 1991, Pimm et al. 1991, Polis 1991). Recently, Cohen et al. (1993) proposed a list of recommendations to standardize food web analysis and make it more comparable with other studies. Their suggestions address many of the shortcomings of previous web studies and call for "more explicitness and more exhaustiveness."

Another important aspect of food web studies that has largely been ignored of late is temporal resolution. Perhaps the greatest impediment to understanding food