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Does food web theory work for marine ecosystems?

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ABSTRACT: More recent and extensive food web studies have questioned some of the prevailing paradigms of food web theory. Yet with few exceptions, most food webs and associated metrics are reported for freshwater or terrestrial systems. I analyzed the food web of the Northeast US Shelf ecosystem across a large spatial and temporal extent. This speciose food web exhibits a predator:prey ratio (0.95) and percentage of intermediate species (89%) similar to most other food webs. Other statistics, such as the percentage of omnivory (62%), percentage of cannibalistic species (31%), number of cycles (5%), and the total number of links (*L*; 1562) and species (*S*; 81) are similar to more recent and extensively studied food webs. Finally, this food web exhibits a linkage density (*L/S*; 19.3), connectivity (*C*; 48.2%), and Lyapunov stability proxy ($S \times C$; 39.1) that are an order of magnitude higher than other webs or are disproportionate to the number of species observed in this system. Although the exact *S* and *C* relationship is contentious, the connectivity of food webs with more than 40 species is approximately 10%, which is very different from the near 50% observed for this ecosystem. The openness of marine ecosystems, lack of specialists, long lifespans, and large size changes across the life histories of many marine species can collectively make marine food webs more highly connected than their terrestrial and freshwater counterparts, contrary to food web theory. Changes in connectivity also have ramifications for ecosystem functioning and Lyapunov stability. The high connectivity of this food web and the mathematical determinants for stability are consistent with the weak nature of species interactions that have been observed and that are required for system persistence. Yet the historically high exploitation rates of marine organisms obfuscate our understanding of marine food web stability. It is possible that marine food webs are inherently very different from their terrestrial or freshwater counterparts, implying the need for modified paradigms of food web theory.

KEY WORDS: Connectivity · Stability · Species interactions · Continental shelf · Predator · Prey · Food web dynamics

INTRODUCTION

Food webs are a useful framework to assess the magnitude and importance of trophic relationships in an ecosystem. Food webs have high heuristic value for ecological theory, and food web linkages ultimately determine the fate and flux of every population in an ecosystem, particularly upper trophic levels of fiscal importance (May 1973, Pimm 1982). Thus, in the past 2 decades food web synthesis has not only generated a host of theoretical debate that has been, mostly, fruitful and has directed a lot of empirical and experimental work, but has also often provided an interesting, if not useful, context for management applications (Crowder et al. 1996, Winemiller & Polis 1996). At the least, food web characterization is required as an initial step in understanding an ecosystem.

Several food web metrics can provide insight into the dynamics of biomass partitioning and production in an ecosystem (May 1973, Pimm 1982, Cohen et al. 1990). Central among these parameters are species richness (*S*) and the number of species interactions or links (*L*), with many other emergent properties and statistics

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