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The concept of trophic pyramids and energy flow in ecosystems has been of major interest to ecologists since the early 20th Century. Some recent papers documenting inverted trophic pyramids, whereby the majority of the biomass in the system is in the upper trophic levels, have renewed interest in these ideas, and generated considerable debate. Trebilco et al. review the history of trophic pyramids and size-based theory in ecology and highlight some of the differences that may be expected between terrestrial and aquatic ecosystems. A major breakthrough in the article is providing the first quantitative link between trophic pyramids and size spectra analysis, assessing the energetic principles of trophic transfer efficiency and predator-prey mass ratios that make different pyramid shapes possible. The authors argue that, in relatively intact systems, a trophic level biomass stack (whereby the biomass at different trophic levels is broadly equivalent) or column is much more likely than an inverted pyramid. They postulate that inverted pyramids may be described due to census biases or energy subsidies, whereby upper trophic level organisms are drawing energy from a wider prey base than the local area being surveyed. Finally, they provide a compelling case as to why size spectra should become a mainstream approach used in ecosystem ecology. This is an important review, which not only provides potential explanations to explain some recent results in the literature, but also offers a wide array of research avenues to better characterize trophic dynamics in ecosystems.

## Disclosures

Nick Graham has co-authored a paper with NK Dulvy in the last 4 years, but had no input to the current paper.

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## Abstract:

Biomass distribution and energy flow in ecosystems are traditionally described with trophic pyramids, and increasingly with size spectra, particularly in aquatic ecosystems. Here, we show that these methods are equivalent and interchangeable representations of the same information. Although pyramids are visually intuitive, explicitly linking them to size spectra connects pyramids to metabolic and size-based theory, and illuminates size-based constraints on pyramid shape. We show that bottom-heavy pyramids should predominate in the real world, whereas top-heavy pyramids indicate overestimation of predator abundance or energy subsidies. Making the link to ecological pyramids establishes size spectra as a central concept in ecosystem ecology, and provides a powerful framework both for understanding baseline expectations of community structure and for evaluating future scenarios under climate change and exploitation.

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