

## LETTER

# Mechanistic theory and modelling of complex food-web dynamics in Lake Constance

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## Abstract

Mechanistic understanding of consumer-resource dynamics is critical to predicting the effects of global change on ecosystem structure, function and services. Such understanding is severely limited by mechanistic models' inability to reproduce the dynamics of multiple populations interacting in the field. We surpass this limitation here by extending general consumer-resource network theory to the complex dynamics of a specific ecosystem comprised by the seasonal biomass and production patterns in a pelagic food web of a large, well-studied lake. We parameterised our allometric trophic network model of 24 guilds and 107 feeding relationships using the lake's food web structure, initial spring biomasses and body-masses. Adding activity respiration, the detrital loop, minimal abiotic forcing, prey resistance and several empirically observed rates substantially increased the model's fit to the observed seasonal dynamics and the size-abundance distribution. This process illuminates a promising approach towards improving food-web theory and dynamic models of specific habitats.

## Keywords

Allometric Trophic Network model, community ecology, food web, multi-trophic dynamics, seasonal plankton succession.

Ecology Letters (2012) 15: 594–602

## INTRODUCTION

Ecosystem functions and services critically depend on the dynamics of complex ecological communities. This dependence has long motivated a search for mechanistic explanations and predictions of community dynamics. However, the paucity of predictive community models suggests to many that such research on communities of interacting species has been largely misguided and scientifically unproductive (Lawton 1999; Ricklefs 2008). One exception to this criticism concerns food webs which represents a fruitful tradition of both empirical and theoretical network analysis (Lindeman 1942; MacArthur 1955; May 1973) and has led to ecological network theory that successfully predicts both general and specific system's structural properties (Williams & Martinez 2000, 2008; Dunne 2006; Allesina *et al.* 2008).

In contrast, progress predicting empirically observed population dynamics of many species feeding upon each other in the field has been more limited. Recent advances based on theoretical models such as the Allometric Trophic Network (ATN) model (Brose *et al.* 2006) integrate the above-mentioned structural theory with general metabolic consumer-resource theory of species' biomass gains from resource-based growth and loss to consumption and maintenance costs (Yodzis & Innes 1992) based on Rosenzweig-MacArthur models (Rosenzweig & MacArthur 1963). In addition to structural network parameters, this theory of dynamics requires species' body size and metabolic type as inputs. ATN models very generally model trophic interactions in a manner easily parameterised by allometric scaling rules which helps to develop basic theory of many dynamically interacting species. Other more applied models integrate locally focused hydrodynamic and

biogeochemical models with biological models for managing dynamics of specific ecosystems (Baretta *et al.* 1995; Mooij *et al.* 2010). However, the focus on locally relevant biogeochemical cycles impedes the generalisation of these models to other ecosystem types (Omlin *et al.* 2001; Mieleitner & Reichert 2006), and the difficulties in deriving functional group parameters from distinct (laboratory) experiments often require a decrease in trophic resolution to a few groups. Other related models of many interacting species designed for fisheries management (Pauly *et al.* 2000) are constrained by mass-balance and fixed diet proportions. These constraints greatly increase the need for many site-specific parameters, significantly limit model generality and would likely prevent the rapid changes of species' populations needed to reproduce seasonal plankton dynamics.

To bridge this gap between generality and specificity and better address ecological complexity, we developed ATN models of intermediate generality with high trophic resolution and minimal abiotic forcing to test whether and how easily the ATN approach can reproduce observed time series of multiple interacting species. While ATN models are increasingly used for developing ecological theory (Brose 2010), they have only been tested against a limited range of temporal patterns and dynamic processes in natural ecosystems (Koen-Alonso & Yodzis 2005; Otto *et al.* 2007; Berlow *et al.* 2009). Broadening this range could enable ATN models and associated theory to help explain and predict multi-species dynamics by refining and corroborating modelled mechanisms. Such advances could then be integrated with site-specific abiotic sub-models to more effectively inform management of specific ecosystems subjected to human exploitation and global change. This research strategy directly

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