



Using *Daphnia* physiology to drive food web dynamics: A theoretical revisit of Lotka–Volterra models



Gurbir Perhar, Noreen E. Kelly, Felicity J. Ni, Myrna J. Simpson, Andre J. Simpson, George B. Arhonditsis *

Department of Physical and Environmental Sciences, University of Toronto, 1265 Military Trail, Scarborough, Ontario M1C 1A4, Canada

ARTICLE INFO

Article history:

Received 3 February 2016

Received in revised form 7 July 2016

Accepted 8 July 2016

Available online 9 July 2016

Keywords:

Lotka–Volterra models

Daphnia ecophysiology

Food web dynamics

Metabolomics

Prey–predator interactions

ABSTRACT

The Lotka–Volterra model is the most commonly used framework to describe the dynamics of ecological systems in which two species interact, one as a predator and the other as prey. Theoretical ecologists have since built on variants of these equations, frequently applying them to model the dynamics of algal–herbivore interactions in aquatic systems. In this study, we augment a Lotka–Volterra system by introducing a bioenergetically-explicit, ecophysiological model to examine how variations in resource allocation affect zooplankton growth and subsequently phytoplankton dynamics. Ingested material within a zooplankton's gut is separated into distinct internal congener pools that are used to support physiological processes occurring in a hierarchical direction: neurological functions, energetics, osmoregulatory maintenance, waste management, and finally growth. Consistent with the predictions of the “stoichiometric knife edge” theory, our analysis suggests that a balanced algal congener composition is required to optimize zooplankton internal congener saturations, resulting in a maximal allocation of energy to growth. In examining the advantages rendered by different strategies of minimum and optimum somatic quotas when experiencing phosphorus-enrichment conditions, we show that herbivores with narrow homeostatic bounds and animals with low minimum quotas (or depletion specialists) achieve optimal performance first. Our analysis also predicts patterns of multiple stable equilibria in which the same environmental conditions can be characterized by dramatically different prey-to-predator ratios. Importantly, abrupt shifts from one state to another can be induced not only by short-term variations in food abundance but also by variations in the nutritional quality of the prey. Our predictions have profound implications for connecting microscopic processes with macroscopic patterns and offer new insights into the multitude of factors that modulate food web dynamics.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Lotka and Volterra's pioneering work to reproduce the dynamics of a predator–prey system has formed the core of ecological modelling over the last century (Elser et al., 2012; Wangersky, 1978). Theoretical ecologists have since built on variants of these equations, frequently applying them to model the dynamics of algal–herbivore interactions in aquatic systems. The trophic linkages between primary producers and consumers are arguably the most important in aquatic food webs (Brett and Muller-Navarra, 1997), as their interactions control the flow of energy to higher trophic levels. In freshwater pelagic environments, the keystone herbivores *Daphnia* (Altshuler et al., 2011) exert strong grazing impacts on phytoplankton biomass and species composition (Elser and Goldman, 1991; Sarnelle, 2005). The plethora of data available on *Daphnia*, spanning multiple levels of ecological organization (from genome to individuals to populations), make it a prime subject around which to develop models of food web dynamics (Mulder

and Bowden, 2007; Nisbet et al., 2010). Consequently, a rich history of *Daphnia*-based models have emerged over the past several decades that typically examine dynamics at the individual (McCauley et al., 1990; Mooij et al., 2003; Paloheimo et al., 1982; Rinke and Petzoldt, 2003) or population (McCauley et al., 1996; Nisbet et al., 1997) levels.

Contemporary zooplankton modelling has focused on internal dynamics (e.g., at the sub-individual level), investigating the theoretical implications of varying mass and energy on population dynamics and algal–herbivore interactions. For example, “ecological stoichiometry” integrates population dynamics with the mass balance of key nutrient elements, namely carbon, nitrogen, and phosphorus, in order to link grazer dynamics and algal nutritional status (Elser and Urabe, 1999; Sterner and Elser, 2002). In the last few decades, multiple stoichiometrically-explicit models of *Daphnia*–algal interactions have been developed (Andersen, 1997; Mulder and Bowden, 2007; Muller et al., 2001; Sterner, 1990), which have provided insights into the coupling of population dynamics and nutrient recycling. Further extensions of the stoichiometric concept have coupled chemical heterogeneity with Lotka–Volterra equations to capture the effects of food quality and nutrient recycling feedbacks (Andersen et al., 2004; Loladze et al.,

* Corresponding author.

E-mail address: georgea@utsc.utoronto.ca (G.B. Arhonditsis).

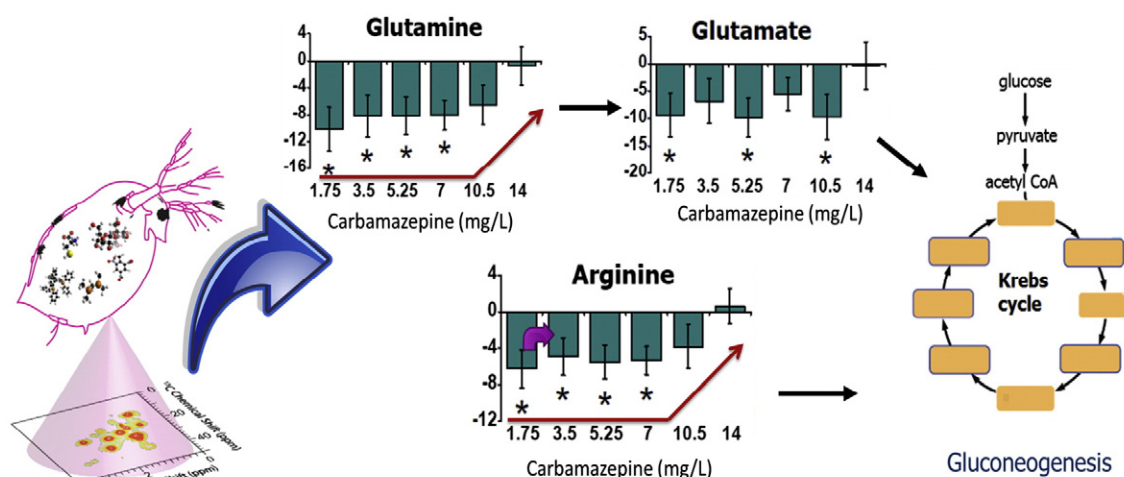


Fig. 1. Metabolomics provide metabolite-specific information regarding the perturbations of *Daphnia magna*. This illustration shows how sub-lethal carbamazepine exposure alters metabolites that participate in gluconeogenesis. Using ¹H NMR-based metabolomics, metabolite fluctuations with sub-lethal exposure can be linked to perturbations in the physiological status of *D. magna* (see Kovacevic et al., 2016 for details).

2000), while Perhar et al. (2013a) examined a zooplankton stoichiometric growth model that simulated the interplay among nitrogen, phosphorus, and highly unsaturated fatty acids (HUFAs). Stoichiometric models are now being applied to examine a phenomenon termed the “stoichiometric knife edge”, where consumer dynamics are affected by both insufficient as well as excess dietary nutrient content (Elser et al., 2012; Peace et al., 2013, 2014).

Other contemporary advances in the modelling literature have focused on energy budgets, as well as individual-based perspectives, in an attempt to introduce more realism into model dynamics. The dynamic energy budget (DEB) theory, based on a balance approach for mass and energy, seeks to capture the quantitative aspects of metabolism at the individual level for organisms of all species (Kooijman, 2010; Sousa et al., 2008). DEB models use differential equations to describe the acquisition and utilization of resources over an organism's entire life-cycle, which depend on both the state of the organism and its environment (Martin et al., 2012; Nisbet et al., 2000). For zooplankton, DEB models have successfully described growth, maturation, and reproductive processes in response to food availability (Nisbet et al., 2010), and investigated the implications of low food and starving physiology on predator-prey dynamics (Peeters et al., 2010). Individual-based models (IBMs) simulate populations composed of discrete individuals, of which each obeys a set of attributes or behaviours, such that population-level behaviours emerge from the interactions among autonomous individuals with each other and their abiotic environment (Grimm, 1999; Huston et al., 1988). This bottom-up approach can link the dynamics of individuals to higher levels of biological organization, and is thus frequently used to answer research questions that involve variations among individuals, their interactions, and individual life-cycles (DeAngelis and Grimm, 2014). Two recent studies have combined DEB theory and IBMs to predict *Daphnia* population cycles and response to toxicants (Martin et al., 2013a, 2013b).

Even though these modelling approaches collectively capture key aspects of ecosystem functioning, several limitations surrounding their use remain. For example, DEB models are attractive to ecologists because standard DEB theory is applicable across species (e.g., models differ in parameter values not mathematical structure) which offers generality, yet estimating a large number of parameters from published data to characterize the individual can be challenging (Nisbet et al., 2010; Sousa et al., 2010). Further, as the individual is the key unit of interest, extrapolating behaviour to higher levels of biological organization requires the development of additional modelling tools (Martin et al., 2012) or individual developments may not be widely applicable

to other species or ecosystem settings (DeAngelis and Grimm, 2014; but see Grimm et al., 2006, 2010). A major drawback of existing stoichiometric models is their narrow focus on nutrients as sole determinants of zooplankton growth, which does little to illuminate the broad range of daphnid internal metabolic processes. In this regard, a handful of studies have moved beyond the simple mass balance approach to incorporate separate metabolic terms for the energy and material budgets of zooplankton, in order to characterize internal homeostatic processes (Anderson et al., 2005; Arhonditsis and Brett, 2005a, 2005b; Perhar and Arhonditsis, 2012; Perhar et al., 2012, 2013b). Despite these advances, the empirical information required to properly constrain these models, as well as the sequence of physiological processes, remain poorly characterized (Perhar et al., 2013a).

An emerging field of research known as environmental metabolomics yields a promising means to depict the physiological status of zooplankton. Metabolomics is the analysis of small molecules (e.g., amino acids, proteins, carbohydrates, fats, macronutrients) within a cell, tissue, organ, biological fluid, or entire organism, in response to an external stressor (Lankadurai et al., 2013; see also our Fig. 1). Changes in organism health are manifested within the metabolome more rapidly than in the genome, proteome, and transcriptome (Viant, 2008). As a result, the field of metabolomics has emerged as a rapid, robust, and informative method for monitoring organism health (Lankadurai et al., 2013). In environmental metabolomics, nuclear magnetic resonance (NMR) is the primary platform used to identify metabolites because the non-selectivity of NMR facilitates the discovery of key metabolites that are sensitive to environmental perturbations. To date, several NMR-based metabolomic studies have successfully utilized this method to examine the response of the *Daphnia* metabolome to contaminant exposure (Li et al., 2015; Nagato et al., 2013; Poynton et al., 2011; Taylor et al., 2009, 2010; Vandenbrouck et al., 2010), although only one has examined the impact of varying nutritional sources (Wagner et al., 2015). By identifying a suite of metabolites that varied when *Daphnia* were exposed to either low food quantity, nitrogen or phosphorus limiting diets, Wagner et al. (2015) clearly demonstrated how metabolomics provide a new framework to identify the nutritional status of consumers. Combining *Daphnia* metabolomic responses into a broader modelling framework promises to rapidly accelerate our understanding of algal-grazer dynamics and unite previously discordant approaches to food web modelling.

Following this motivation, Perhar and Arhonditsis (2015) developed a bioenergetically-explicit ecophysiological model that demonstrates how variations in resource allocation affect *Daphnia* growth. This

Download English Version:

<https://daneshyari.com/en/article/4374749>

Download Persian Version:

<https://daneshyari.com/article/4374749>

[Daneshyari.com](https://daneshyari.com)