



# Development of a metabolite-driven daphnia ecophysiological model

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## ABSTRACT

One of the founding principles of modern aquatic ecology is that human-induced perturbations in the autotroph-herbivore interface have the potential to affect ecological processes at higher trophic levels. Thus, zooplankton's physiological state can be an early warning sign of broader impairments of aquatic ecosystems. Based on this reasoning, the micro-crustacean *Daphnia* is often identified as a keystone freshwater species, but its bioenergetic motivations and physiological priorities remain only partially understood. Using a bioenergetically explicit ecophysiological approach, we model how trade-offs in resource allocation can shape a daphnid's growth. Our multi-faceted hierarchical approach to metabolite utilization challenges the popular paradigm of elemental stoichiometry being the primary regulatory factor of algal food quality. We examine the post-gut bioenergetic ramifications of an unbalanced diet, showing that animal growth can be significantly compromised by the elevated energetic requirements of homeostasis. Our modeling framework offers an excellent stepping-stone to connect zooplankton physiological processes with the signals of external stressors, and subsequently evaluate the patterns of mass and energy flow at an ecosystem scale. The proposed microscopic-to-macroscopic strategy will likely offer a new prospect towards the development of early warning systems for the management of freshwater resources.

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## 1. Introduction

Freshwater ecosystems are subject to constant changes in their physical properties and water chemistry, invasion of exotic species, and over-harvesting of fisheries (Altshuler et al., 2011). To maintain the health and integrity of freshwater environments, the establishment of early warning systems has been proposed to reliably detect imminent ecosystem organizational discontinuities (or other non-linear state shifts) to react strategically ahead of time (Scheffer et al., 2001). The concept of an early warning system is comprised of three distinct phases: i) identification and collection of weak signals; ii) analysis of trends in space and time; and iii) formulation of appropriate management responses (Scheffer and Carpenter, 2003). In this context, weak signals are unstructured, fragmented, incomplete data points that require deep analysis to be articulated into valuable information (see Mendonca et al., 2015). In freshwater environments, the sheer number of signals to process makes the development of early warning systems challenging, but shifting the focus to keystone species can offer a pragmatic strategy to move forward. The keystone species concept was first introduced by Paine (1969), stating that the presence of certain species is crucial in maintaining the organization and diversity of ecological communities. Namely, this concept postulates that there are species exerting direct and indirect influences on biotic assemblages disproportionately and thus can profoundly impact the overall food web structure and functioning (Garibaldi and Turner, 2004;

Libralato et al., 2006; Paine, 1995). Nonetheless, the current monitoring methods are disconnected from the stress levels of individual organisms, and usually focus on larger-scale ecological patterns that may not be sensitive indicators of potential ecosystem regime shifts (Scheffer et al., 2012).

Herbivorous zooplankton transform plant material into animal tissue, resulting from their role as intermediaries between primary production and secondary consumption in aquatic food webs. Pelagic fish, crustaceans, mollusks, and mammals depend on zooplankton both directly and indirectly (Gajbhiye, 2002). Their large community density, relatively short life spans, high phenotypic diversity, and ability to exert grazing pressure on algae lend them to be used as indicator organisms for physical, chemical, and biological processes in aquatic ecosystems. Several studies identify zooplankton of the genus *Daphnia* as keystone herbivores (Altshuler et al., 2011; Colbourne et al., 2011; Miner et al., 2012; Persson et al., 2007; Seda and Petrusek, 2011; Sperfeld and Wacker, 2009; Straile et al., 2012; Van Doorslaer et al., 2009; Wagner and Benndorf, 2007). *Daphnia* spp. are effective filter feeders with high grazing impacts on phytoplankton biomass and species composition (Martin-Creuzburg et al., 2005). They are a preferred food choice for both vertebrate and invertebrate predators, stemming largely from their nutritious composition, relatively large size, and limited ability to evade predation (Lampert, 1987; Miner et al., 2012). Thus, daphnids are an integral link between primary production and higher trophic levels. *Daphnia* spp. populations are also very sensitive to modern toxicants in the environment, and are thus used to assess the ecological impacts of environmental change (Colbourne et al., 2011). Natural stressors include bacterial infections, predation and parasitism,

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synthetic hormones, diet variation, ultraviolet radiation, hypoxia, acidity, salinity, and low ambient calcium levels (Altschuler et al., 2011). These sensitivities are offset with *Daphnia* spp.'s high phenotypic plasticity. Specifically, they have the ability to alter diurnal vertical migration patterns and develop extensive morphological defense features to avoid predators, and can adjust hemoglobin levels in response to falling oxygen availability (Colbourne et al., 2011).

Zooplankton experimental methodologies often involve the use of micro- and mesocosms, combined with controlled changes in ambient conditions (e.g., Kurbatova, 2005; Loureiro et al., 2013; Patterson et al., 2002; Rothhaupt, 1997; Sorf et al., 2015; Wang et al., 2009). The metrics produced can be reasonable proxies of ecosystem scale dynamics, but offer limited insights into their mechanistic underpinning. For example, studies analyzing the toxicity of various metals (Biesinger and Christensen, 1972), parasites (Aalto et al., 2013), and algae (Hietala et al., 1995) on *Daphnia* spp. report survival rates, reproduction rates, and life history progression as toxicity metrics. A drawback of these studies, however, is the “black-boxed” nature of the inference drawn, in the sense that patterns are established but the physiological sequence of events driving these patterns is not. More recently, gene mapping has opened up a new avenue of investigation. Because *Daphnia* spp. ecology is fairly well understood, access to its genomic sequences allows for detailed investigation of environmental influences on gene functions (Colbourne et al., 2011). Jansen et al. (2013), for example, found distinct, time-dependent transcriptional expressions in *Daphnia magna* subject to differential stresses. In the post genomic era, methodological advances are driven by technologies allowing functions of both cells and whole organisms to be explored at the molecular level (Whitfield et al., 2004).

Changes in tissues and biological fluids are indicative of an animal's well being (Micholson and Lindon, 2008), and provide a comprehensive molecular view of cellular control mechanisms (Whitfield et al., 2004). Metabolomics is the study of naturally occurring, low molecular weight organic metabolites within cells, tissues, and biofluids (Griffiths, 2007). Metabolomic measurements can be mechanistically related to higher levels of biological organization (Bundy et al., 2009). Metabolomics provide an integrated view of biochemistry in complex organisms, as opposed to the traditional approach associated with systems biology, whereby interactions between genes, proteins, and metabolites in individual cell types are investigated (Nicholson et al., 1999). The problem with the latter approach are the different time scales at which each level of biological organization (i.e., genomics, gene expression, protein expression, and metabolism) operate, making it difficult to find causal linkages (Nicholson et al., 1999). The application of metabolomics to characterize organism interactions with their environments is called environmental metabolomics, and these interactions can be studied from individuals to populations (Bundy et al., 2009).

If the objective of a modeling exercise is to explain large scale patterns rather than describe them, the patterns need to be built up from processes (Royle and Dorazio, 2008). In zooplankton modeling, this inevitably requires consideration of physiological processes. An early example of this strategy came from Sjöberg (1980), who assumed zooplankton to vary its feeding strategy in response to gut contents. Food particles in the gut were treated as a queue, in that digestion was a service given only to the food item holding first position, and consequently the digestive process was the growth limiting factor instead of the food capture and ingestion. Dynamic Energy Budget (DEB) models are a relatively recent concept, aiming to distinguish the metabolic organization of individual organisms (Kooijman, 2001). DEB theory provides a framework to build process-based models for organism life cycles (Jager et al., 2013), and explain body-size scaling relationships of natural history parameters that can otherwise be difficult to comprehend (Kooijman, 2001). DEB models track structural and storage somatic constructs across life stages. In a similar context, Perhar et al. (2012a, 2012b) attempted to integrate zooplankton physiology into a fully functional ecosystem model. Namely, zooplankton dynamics were driven from physiological processes including molt turnover,

biomass turnover, hormone production, regulatory release, and internal nutrient and highly unsaturated fatty acid reserves. These processes were shown to heavily influence the producer-consumer interface, while fundamentally altering the nature of ecosystem feedback loops (Perhar et al., 2012c).

Perhar et al. (2012c) questioned the validity of extreme modeling results in the literature that are rarely (if ever) observed in nature. In particular, the explicit consideration of intra-organism processes into a conventional plankton model phased out the emergence of oscillatory behavior associated with the paradox of enrichment (Rosenzweig, 1971). Similarly, Fussmann and Heber (2002) argued that while very simple mathematical frameworks can display chaotic dynamics, natural food webs likely possess architectural properties that can intrinsically minimize the likelihood to observe these patterns in the real world. Thus, linking processes at the organismal level with large-scale food web patterns can maximize the utility of ecosystem models in a management context.

In this study, our key objective is to utilize *Daphnia* spp. metabolomic data to formulate a mechanistic individual-based model. By linking each metabolite (or congener) to a physiological process, internal concentrations can shed light on the individual's health. Because it can be easily linked to management-oriented ecosystem models, the overarching benefit of our individual-based physiological model is its potential to serve as a device for detecting early warning signs. Our proposed “microscopic-to-macroscopic” strategy will provide a mechanistic look into the bioenergetic motivations of daphnids, and potentially offer a new methodological tool for water resource management.

## 2. Methodology

Our zooplankton physiology framework is intended to plug into mass balance ecosystem models to enhance the realism of zooplankton dynamics. We have built on the foundation of Anderson et al. (2005), who modeled a stoichiometrically explicit nutrient regulation strategy in *Daphnia*. The authors considered the carbon (C), nitrogen (N), and phosphorus (P) contents of ingested food, with each congener playing a unique somatic role. By considering a post-gut regulation mechanism, Anderson et al. (2005) were able to illustrate the delicate balance between food quantity and food quality. Subsequent advances in the modeling literature have also illustrated this balance (Perhar et al., 2012b, 2012c). Perhar et al. (2012a) built on this approach and considered the highly unsaturated fatty acids (HUFAs) eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), in addition to N and P to quantify somatic growth in their zooplankton submodel. We continue here along a similar trajectory, with an expanded domain considering 14 congeners (see Table 1). Each congener is a proxy for a physiological process. Using congener saturation measures, we quantify the potential investment for each physiological process considered. Congeners are gathered through food intake, which is assumed to be a fixed rate (GRAZ). We employ a food quality index (FQ) in a fashion similar to Perhar et al. (2012a), whereby morphological and toxicological features are defined by a single index. The food quality index, along with parameters accounting for thermodynamic losses ( $\alpha_{C1}$  and  $\alpha_{C2}$ ; see Table 1) quantify carbon assimilation efficiency (AE). The product of assimilation efficiency and grazing rate yields assimilated carbon (AC).

$$AE = \frac{\alpha_{C1} \cdot FQ}{\alpha_{C2} + FQ} \quad (1)$$

$$AC = \text{GRAZ} \cdot AE. \quad (2)$$

Assimilated congener ( $A_{S_i:C}$ ) is calculated by multiplying AC with food congener to carbon ratios (see Table 3). Assimilated congeners are added to existing somatic pools, from where they are mobilized for physiological use.

$$A_{S_i:C} = AC \cdot \text{food}_{S_i:C} \quad (3)$$

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