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Somatic Growth Dilution of a toxicant in a predator–prey model under stoichiometric constraints

Angela Peace [a,b,*], Monica D. Poteat [c], Hao Wang [d]

[a] Department of Mathematics and Statistics, Texas Tech University, Lubbock, USA
[b] National Institute for Mathematical and Biological Synthesis, University of Tennessee, USA
[c] Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA
[d] Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB, Canada T6G 2G1

HIGHLIGHTS

- We integrated realistic ecological processes into an aquatic ecotoxicology model.
- Stoichiometric predator–prey model parameterized to Algae–Daphnia subject to MeHg.
- The ODE model investigates concurrent nutrient and toxicant stressors.
- Analytical analysis, numerical simulations, bifurcation analysis are performed.
- The model captures and explores the Somatic Growth Dilution phenomenon.

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ABSTRACT

The development of aquatic food chain models that incorporate both the effects of nutrient availability, as well as, track toxicants through trophic levels will shed light on ecotoxicological processes and ultimately help improve risk assessment efforts. Here we develop a stoichiometric aquatic food chain model of two trophic levels that investigates concurrent nutrient and toxic stressors in order to improve our understanding of the processes governing the trophic transfer for nutrients, energy, and toxicants. Analytical analysis of positive invariance, local stability of boundary equilibria, numerical simulations, and bifurcation analysis are presented. The model captures and explores a phenomenon called the Somatic Growth Dilution (SGD) effect recently observed empirically, where organisms experience a greater than proportional gain in biomass relative to toxicant concentrations when consuming food with high nutritional content vs. low quality food.

1. Introduction

Chemical contaminants are widely dispersed throughout Earth's ecosystems due to a multitude of human activities, as well as natural phenomena, and have the potential to adversely impact a diverse range of organisms (Walker et al., 2012). Bioaccumulation of toxic compounds in aquatic food chains can pose risk to ecosystem conservation as well as wildlife and human health. Accurately assessing the risks of contaminants requires more than an understanding of the effects of contaminants on individual organisms, but requires further understandings of complex ecological interactions, elemental cycling, and the interactive effects of natural stressors, such as resource limitations, and contaminant stressors.

Ecotoxicological modeling aims to predict how contaminants cycle through aquatic food systems. It is vital to understand the processes that determine the trophic transfer of toxicants to improve developed risk assessment protocols. Wang et al. (1996) developed a simple biokinetic model that has been used to predict total bioaccumulated toxicant concentrations in multiple species of aquatic organisms over that last decade (Wang and Rainbow, 2008; Wang, 2012). It models the change in toxicant concentration (v) in an organism due to uptake and loss due to efflux and growth:

$$\underbrace{\frac{dv}{dt}}_{\substack{\text{Change in toxicant conc.}\\ \text{of predator over time}}} = \underbrace{a_2 T}_{\substack{\text{uptake from}\\ \text{water}}} + \underbrace{\xi f u}_{\substack{\text{uptake from}\\ \text{consuming prey}}} - \underbrace{(\sigma_2 + g) v}_{\substack{\text{loss due to}\\ \text{efflux \& growth}}} \quad (1)$$

* Corresponding author at: Department of Mathematics and Statistics, Texas Tech University, Lubbock, USA.
E-mail address: a.peace@ttu.edu (A. Peace).

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where a_2 is the uptake rate constant from the dissolved toxicant, T is the concentration of dissolved toxicant, ξ is the toxicant assimilation efficiency, f is the predator's ingestion rate, u is the toxicant concentration in the prey, σ_2 is the toxicant efflux rate, and g is the predator's growth rate. The Biokinetic model (1) incorporates constant parameters for the predator's growth rate (g) and ingestion rate (f). It also assumes the quantity and toxicant concentration in the prey are constant.

Dynamic ecological population models can offer insight on the variability of these biokinetic parameters and their influences on the trophic transfer of toxicants. Huang et al. (2014) developed a toxicant-mediated predator–prey model that incorporates a variable prey quantity. This model tracks the prey and predator population densities, as well as the toxicant body burdens in each population. The biokinetic model (1) corresponds with the predator body burden equation from Huang et al. (2014):

$$\underbrace{\frac{dv}{dt}}_{\text{Change in toxicant conc. of predator over time}} = \underbrace{a_2 T}_{\text{uptake from water}} + \underbrace{\xi f(x) u}_{\text{uptake from consuming prey}} - \underbrace{\sigma_2 v}_{\text{loss due to efflux}} - \underbrace{e(v) f(x) v}_{\text{loss due to growth}} \tag{2}$$

where $e(v)$ is the toxicant dependent biomass conversion efficiency. The original constant ingestion rate f is replaced with function $f(x)$ and depends on prey quantity; the constant predator growth rate g is replaced with the expression $e(v)f(x)$ and depends on the prey quantity, as well as, the predator's toxicant concentration. Huang et al. (2014) parameterize their model with the toxicant mercury (Hg), a toxic contaminant that can bioaccumulate in aquatic food chains as methylmercury (MeHg) posing risk to ecosystems and humans (Mergler et al., 2007). Their toxicant-mediated predator–prey model helped shed light on the different complicated ways varying toxicant concentrations affects organisms at different trophic levels.

While this model incorporates variable food quantity, it does not consider food quality. Elemental imbalances, such as phosphorus:carbon (P:C) ratios, between trophic levels affect life-history traits such as growth and reproduction. Toxic compounds can have similar impacts on these traits. There is increasing evidence that considering resource stoichiometry and nutrient availability will improve risk assessment protocols in ecotoxicology (Ieromina et al., 2014; Sarwar et al., 2010; Lessard and Frost, 2012; Alexander et al., 2013). The interactive effects of nutrient availability and aqueous Hg concentration may play a significant role in the bioaccumulation of MeHg. Karimi et al. (2007) show stoichiometric constraints, such as food quality, can affect the accumulation of MeHg in *Daphnia*. They show empirical evidence of Somatic Growth Dilution (SGD) as *Daphnia* experience a greater than proportional gain in biomass relative to MeHg under high phosphorus concentrations (Fig. 1). They used MeHg radio-tracer to measure juvenile *Daphnia pulex* MeHg concentrations, growth rate, and ingestion rate when fed on *A. falcatus* algae of low and high quality (vary algal P:C ratio). Estimated *Daphnia* steady-state MeHg concentrations using the biokinetic model (System (1)) showed that *Daphnia* grown on high quality food had 3.5 times higher growth rates, slightly lower ingestion rates, and MeHg concentrations at steady-state a third lower than *Daphnia* grown on low quality food.

Given this empirical evidence, the interactive effects of resource limitation and contaminant stress on organisms and

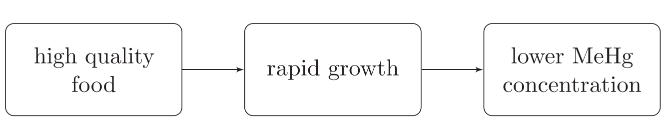

Fig. 1. Simple depiction of Somatic Growth Dilution (SGD), where an organism experiences a greater than proportional gain in biomass relative to toxicant under high food quality conditions.

ecosystems needs to be considered in toxicological risk assessment applications. Models have proven to be useful tools in ecotoxicological predictions, however current models do not consider dynamical interactive effects of contaminant stressors and stoichiometric constraints, such as nutrient/light availability and food quality.

In order to incorporate and balance multiple essential elements and contaminants, the mathematical models and the empirical experiments will be structured under the framework of the theory of Ecological Stoichiometry (Sterner and Elser, 2002). This theory considers the balance of multiple chemical elements and how the relative abundance of essential elements, such as carbon (C), nitrogen (N), and phosphorus (P), in organisms affects ecological dynamics. Ecologists have made important progress collecting large amounts of data from both lab experiments and field sites to support Ecological Stoichiometry (Andersen, 1997; Sterner and Elser, 2002; Urabe and Sterner, 1996; Elser et al., 1996; Elser and Urabe, 1999; Elser et al., 2000, 2001; Urabe et al., 2002; McCauley et al., 2008; Hessen et al., 2013). Since the development of the theory of ecological stoichiometry, a wide variety of stoichiometric food web models have been proposed and analyzed (Andersen, 1997; Loladze et al., 2000; Grover, 2004; Hall, 2004; Wang et al., 2008a; Hall, 2009; Wang et al., 2012; Peace et al., 2013, 2014). Stoichiometric models incorporate the effects of both food quantity and food quality into a single framework that produces rich dynamics. Stoichiometric models allow one to investigate the effects of nutrient stressors on population dynamics and track the trophic transfer of energy and nutrients (Peace, 2015). Empirical efforts and models developed under the theory of Ecological Stoichiometry have advanced our understanding of ecological interactions (Andersen et al., 2004; Hessen et al., 2013).

Two existing ecotoxicology models do consider a contaminant stressor along with a single stoichiometric constraint: (1) Bontje et al. (2009) developed a model that considers both nutrient stress and toxicant stress parameterized for a *N*-limited algal population and (2) Ankley et al. (1995) developed a model that considers both light availabilities and contaminant concentrations to looks at the effects of varying light intensities on a photo-activated contaminant stressor on aquatic organisms. However, unlike Ecological Stoichiometric models, these models do not allow for multiple dynamic stoichiometric constraints where the element limiting growth can change with environmental nutrient and light availabilities.

Ecological Stoichiometry has proven successful in aquatic ecological applications and has the potential to improve our understanding of the effects chemical contaminants have on organisms and ecosystems (Hansen et al., 2008). It offers a conceptual framework to investigate the impact of elemental imbalances on the response of organisms to contaminants while simultaneously considering the effects of contaminants on ecosystem processes (Danger and Maunoury-Danger, 2013).

Here, we extend System (3) under the framework of Ecological Stoichiometry (Sterner and Elser, 2002) to develop a toxicant-mediated predator–prey model that incorporates a variable food quantity as well as quality. Loladze et al. (2000) formulated a stoichiometric predator–prey Lotka–Volterra type model (LKE model) of the first two trophic levels of an aquatic food chain incorporating the fact that both the predator and prey are chemically heterogeneous organisms composed of two essential elements, carbon (C) and phosphorus (P). The model allows the phosphorus to carbon ratio (P:C) of the prey to vary above a minimum value, which brings food quality into the model. The LKE model is described in detail in Appendix A and is used as guide as we expand System (3) under the Ecological Stoichiometric framework. These modeling efforts help shed light on nutrient and chemical contaminant cycling and ultimately can improve toxicological risk assessment protocols.