



Effects of light, nutrients, and food chain length on trophic efficiencies in simple stoichiometric aquatic food chain models



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ABSTRACT

Ecological trophic transfer efficiencies can provide meaningful measures of ecosystem function. Light levels, nutrient availability, and food chain length impact ecological interactions and can cause elemental imbalances between trophic levels which may lead to stoichiometric constraints on food chain efficiencies. Despite the important role that the chemical composition of primary producers and food quality plays in determining consumer productivity, most food chain models used to evaluate trophic transfer efficiencies neglect stoichiometric constraints. This study presents simple stoichiometric models of two and three trophic levels and investigates the effects of light and nutrient availability on ecological transfer efficiencies. The models predict that food chain efficiency is reduced when consumers are nutrient limited. Nutrient levels such that the primary producer and consumer have similar stoichiometric compositions provide conditions for high food chain efficiency. In fixed low nutrient environments, food chain efficiency is highest in light level conditions such that the primary producer and consumer have similar stoichiometric compositions. In fixed high nutrient environments, food chain efficiency is highest for intermediately low light levels such that the phosphorus:carbon ratio of the primary producer is higher than the phosphorus:carbon ratio of the consumer. Food chain efficiency is lower in tritrophic food chains than ditrophic food chains and consumer efficiency is lower in the presence of predation constraints. It is essential for future models to consider light and nutrient availability and the consequential stoichiometric constraints when predicting how energy and elements transfer across trophic levels and up food chains.

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1. Introduction

Considering the impacts of environmental factors on ecosystem function and their constraints on energy and nutrient transfer through food chains is important for gaining insight on many ecological processes. Predicting amounts of fish harvested as a function of primary production in aquatic systems requires knowledge of the efficiencies of transfer between trophic levels (Kemp et al., 2001). Ecological efficiencies have proved useful in the pursuit of understanding important influences on ecosystem function and the trophic transfer of nutrients and carbon up the food chain (Lindeman, 1942; Hairston Jr and Hairston Sr, 1993; Dickman et al., 2008; Tanaka and Mano, 2012). There are various measures of efficiency useful for understanding trophic transfer and ecological processes. Hairston Jr and Hairston Sr (1993) define the consumption efficiency as the percentage of net production of one trophic

level that is consumed by the level above it. This efficiency is useful as it reflects the impact consumers have on the trophic levels they feed on. They define the assimilation efficiency as the percentage of consumed energy (carbon) that is assimilated into the trophic level. Classically, trophic transfer efficiency (also referred to as carbon use efficiency) is the rate of production of one trophic level divided by the rate of production of the trophic level immediately underneath it (Sterner and Elser, 2002). Food chain efficiency is the rate of production of the top trophic level divided by the rate of production of the lowest trophic level. Food chain efficiency can be an important indicator of ecosystem processes as it determines the productivity of the top trophic level given the amount of primary productivity (Tanaka and Mano, 2012).

Nutrient and light availability can create drastic differences between the chemical compositions of primary producers and consumers which induce stoichiometric constraints on ecological efficiencies. The constraints on predators may be less important as their stoichiometric composition is more similar to that of their prey (Andersen, 1997; Sterner and Elser, 2002). Dickman et al. (2008) provide empirical evidence that light and nutrient

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availability constrain trophic transfer efficiencies. Their study found that increased nutrient availability and/or decreased light availability improves food chain efficiency. This empirical evidence is supported by another study where zooplankton (consumer) production increased as light level decreased in a phosphorus limited lake (Urabe et al., 2002). Nutrient/light balance plays an important role in ecological interactions and influences food chain efficiencies.

Trophic transfer efficiencies depend on food quality and organo-mineral composition. Despite this fact, most food chain models that evaluate trophic transfer efficiencies focus on how a single constituent, usually carbon or energy, is transferred up the food chain. Tanaka and Mano (2012) built a minimal model of pelagic ecosystems with primary producers, consumers, and predators which predicted that the conversion efficiency of the consumer was one of the most important and general factors for determining food chain efficiencies. A major component of consumer efficiency is the stoichiometric composition of the primary producer, which is highly dependent on nutrient and light availability.

Incorporating the effects of multiple constituents and nutritional food quality into food chain models may more accurately capture population dynamics and lead to improved predictions and understandings of trophic transfer efficiencies and ecosystem processes. The theory of ecological stoichiometry, which considers the balance of energy and multiple chemical elements in ecological interactions, provides new constraints and mechanisms that can be formulated into mathematical models (Sterner and Elser, 2002; Andersen et al., 2004; Moe et al., 2005; Hessen et al., 2013). Modeling under the framework of ecological stoichiometry allows the investigation of food quantity, as well as, food quality on food web population dynamics. Many models that incorporate stoichiometric constraints have produced rich dynamics, making qualitatively different predictions on population dynamics, community structure, and the effects of environmental perturbations compared to nonstoichiometric models (Andersen, 1997; Loladze et al., 2000; Muller et al., 2001; Grover, 2004; Andersen et al., 2004; Hall et al., 2007; Elser et al., 2012; Peace et al., 2013; Hessen et al., 2013). A stoichiometric food chain model can incorporate the consequences of elemental imbalances between trophic levels when determining ecological efficiencies.

This study considers simple stoichiometric models of two and three trophic levels to investigate the impacts of environmental factors on ecosystem function. The models use ecological trophic transfer efficiencies as important gauges of ecosystem function in order to determine the effects of nutrient enrichment, light availability, and food chain length. The models are used to test two hypotheses: (1) food chain efficiency is highest under light and nutrient conditions such that the stoichiometric composition of the primary producer is near that of the consumer; and (2) transfer efficiency from primary producer to consumer is lower in chains of three trophic levels than in chains of only two trophic levels due to predation constraints.

2. Methodology

2.1. Mathematical models

Loladze et al. (2000) formulated a producer–consumer Lotka–Volterra type model (LKE model) of the first two trophic levels of an aquatic food chain (algae–*Daphnia*) incorporating the fact that both producers and consumers 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 producer to vary above a minimum value. This variable P:C ratio of the producer, denoted as Q , brings food

quality into the model. Below is the LKE model from Loladze et al. (2000):

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{\min\{K, (P - \theta y)/q\}} \right) - f(x)y \quad (1a)$$

$$\frac{dy}{dt} = \hat{e} \min \left\{ 1, \frac{Q}{\theta} \right\} f(x)y - dy \quad (1b)$$

where

$$Q = \frac{P - \theta y}{x}.$$

$x(t)$ and $y(t)$ are the biomass of the producer and consumer respectively, measured in terms of C. b is the maximum growth rate of producer, K is the light dependent producer carrying capacity in terms of C, P is the total phosphorus in the system, θ is the consumer's constant P:C, Q is the producer's variable P:C ratio, q is the producer's minimal P:C, \hat{e} is the maximum production efficiency, and d is the consumer loss rate. The consumer's ingestion rate, $f(x)$ is taken to be a monotonic increasing and differentiable function, $f(x) \geq 0$, $f(0) = 0$. $f(x)$ is saturating with $\lim_{x \rightarrow \infty} f(x) = \hat{f}$. The model makes the following three assumptions.

- A1: The total mass of phosphorus in the entire system is fixed, i.e., the system is closed for phosphorus with a total of P (mg P/L).
- A2: P:C ratio in the producer varies, but it never falls below a minimum q (mg P/mg C); the consumer maintains a constant P:C, θ (mg P/mg C).
- A3: All phosphorus in the system is divided into two pools: phosphorus in the consumer and phosphorus in the producer.

Here, a minimum function is used to describe the producer carrying capacity, $\min\{K, (P - \theta y)/q\}$. The first input, K , is the carrying capacity determined by light availability. The second input, $(P - \theta y)/q$ is the carrying capacity determined by phosphorus availability. Another minimum function is used to describe the consumer growth rate, $\min\{1, Q/\theta\}$. The first input, 1, is used when consumer growth is limited by carbon. The second input, Q/θ is used when consumer growth is limited by phosphorus.

2.1.1. Ditrophic model

In order to investigate the effects of light and nutrients on systems of two trophic levels this study uses the LKE model (1) with a slight modification. A portion of the ingested carbon is used for the consumer's metabolic costs, such as respiration. Let e_y be the consumer's maximal production efficiency in terms of carbon. Then Q/e_y is the P:C ratio of the post-ingested producer representing the amount of P and C available for consumer growth. Let θ_y be the constant P:C ratio of the consumer and $g(x, y)$ the consumer growth rate. When $(Q/e_y) > \theta_y$, the growth of the consumer is limited by carbon and satisfies $g(x, y) = f(x)e_y$. However when $(Q/e_y) < \theta_y$, the growth of the consumer is limited by phosphorus and satisfies $g(x, y)\theta_y = f(x)Q$. Modifying the consumer's growth yields the following ditrophic model:

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{\min\{K, (P - \theta_y y)/q\}} \right) - f(x)y \quad (2a)$$

$$\frac{dy}{dt} = \min \left\{ e_y, \frac{Q}{\theta_y} \right\} f(x)y - d_y y \quad (2b)$$

where

$$Q = \frac{P - \theta_y y}{x},$$

e_y is the consumer maximal production efficiency in terms of carbon, d_y is the consumer loss rate, and θ_y is the consumer's constant P:C ratio. Its important to note that this ditrophic model is simply

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