



Functional traits of herbivores and food chain efficiency in a simple aquatic community model

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ABSTRACT

Large-bodied zooplankton play important roles in the flow of nutrients and energy along the food chain in freshwater ecosystems. However, the importance of functional traits of zooplankton in trophic flow is not well understood. We used the minimal food-chain model, which includes producers (algae), first-order consumers (grazer zooplankton), and secondary consumers (fish), to reveal which functional traits of phyto- or zooplankton affect one of the most important ecosystem processes for functioning, the trophic transfer efficiency (TTE) across three trophic levels. Numerical simulations indicated that, regardless of the level of nutrient loading and the fish density, the conversion coefficient of grazer zooplankton was one of the most important and general factors for determining TTE. The antipredator defense and maximum grazing rate of zooplankton greatly affected TTE, but the effect depended on the level of nutrient loading and the fish density. For an ecosystem that had high nutrient loading and high fish density and in which the zooplankton density was regulated by the top-down effect, antipredator defense and maximum grazing enhanced TTE. Opposite relationships were observed for other states of the ecosystem. In general, those functional traits of the first-order consumers that affected vertical ecological interaction were important for trophic flow in the ecosystem, whereas the sensitivity of trophic flow to these traits depended largely on whether the zooplankton were regulated by the bottom-up or the top-down effect.

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1. Introduction

Evaluation of the impact of environmental factors on ecosystem function is a challenging task in ecosystem risk assessment. For this purpose, we need a measure of communities that is relevant for predicting how ecosystem function is influenced by environmental driving factors. The ecological or functional traits of composite species may be a good candidate of such a measure. If a functional trait is appropriately chosen such that a particular ecosystem function is decided by the functional trait, changes in the functional trait in a community can indicate responses by the community in terms of functioning (Lavelle and Garnier, 2002; Hooper et al., 2005; McGill et al., 2006; Schmitz et al., 2008). Here, we consider trophic transfer efficiency (TTE) across three trophic levels (i.e. food chain efficiency) as one of the most important indicators for ecosystem functioning (Lindeman, 1942; Hairston and Hairston, 1993; Cebrian, 2004; Dickman et al., 2008; Gascuel et al., 2008), and we investigate how particular functional properties or traits of individual species are related to TTE.

TTE across three trophic levels was measured here as the fraction of primary production by phytoplankton that is converted to fish biomass via the fishes' predation on grazer zooplankton. We assumed that TTE was an important indicator of ecosystem processes in aquatic ecosystems, because it determines the productivity of fish (i.e. secondary and higher consumers) with a particular amount of primary productivity and it restrains the organic matter produced by algae from entering the detritus pool. If the flow rate from algal biomass to detritus pool exceeds the recycling capacity of the ecosystem, this flow may result in perturbation of the system-specific balance between the grazing food chain (herbivory) and decomposition (Cebrian and Lartigue, 2004), causing environmental problems such as hypoxia and loss of biodiversity, in lakes and ponds (Brönmark and Hansson, 2002).

The aims of this study were to identify those functional traits of species at a particular trophic level that were important in determining food chain efficiency and to infer how the relationships between the functional traits and TTE depended on the trophic state of the ecosystem (eutrophic or oligotrophic) and the strength of ecological interaction (i.e. the predation pressure of fish on zooplankton). We made two hypotheses: (1) the functional traits of grazer zooplankton are more important than any of the traits of phytoplankton, because zooplankton mediate between producer and predator as the intermediate consumer; and (2) maximum

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grazing rate and edibility (i.e., low tolerance to fish predation) in zooplankton enhance TTE, because they facilitate trophic transfer from algae to fish per unit biomass of zooplankton. To examine these predictions, we used a simple community model to simulate freshwater pelagic ecosystems, the main components of which are phytoplankton (the producers), grazer zooplankton (the first-order consumers), and planktivorous fish (the secondary consumers).

TTE is affected by two ecological factors: (1) the energetic or metabolic properties of composite species; and (2) the community trophic structure (i.e., the relative biomass abundance at each trophic level). The former factor includes feeding ecology, assimilation rate, metabolic efficiency, and any other physiological and life-history traits that affect the energy flow per unit biomass at a particular trophic level. The latter factor is governed by the numerical responses of composite species to vertical ecological interactions. The effect of trophic structure may predominate over the energetic effect per unit biomass for determining trophic transfer in aquatic ecosystems (Hairston and Hairston, 1993). The intermediate trophic level (the herbivore), a key component for regulating the trophic flow from producers to higher consumers, is especially prone to numerical changes due to both bottom-up and top-down effects (Hairston and Hairston, 1993; Scheffer et al., 2000; Kemp et al., 2001; Gascuel, 2005). Nutrient and energy flow in the ecosystem should depend largely on whether the herbivore level is maintained at a high density or regulated to a low density by predation. Predation pressure is determined by combinations of the species traits of the herbivore and the predator.

Use of a simple community model can elucidate which functional traits of species at a particular trophic level affect TTE in a complex system where the components (i.e. trophic levels) interact with each other and the effect to be examined (i.e., the TTE) can be mediated by this interaction. We used the minimal model developed by Scheffer (1990, 1991), because such simple community models can describe the essential features of pelagic ecosystems, which are compatible with actual observations, with the least number of model parameters. The parsimonious structure of the model in terms of the number of interacting variables helps with our mechanistic understanding of the derived results.

Some recent studies have indicated that the detritus food chain and pelagic–benthic coupling by omnivorous fish are important for sustaining aquatic ecosystems (Covich et al., 1999; Vadeboncoeur et al., 2003; Darwall et al., 2010). The benthic pathway from primary production by algae to omnivorous fish via detritivores that feed on detritus originating from the algal biomass may supplement TTE based on the pelagic food web. For the sake of simplicity of the model, we additionally examined the effect of the detritus loop in maintaining TTE in an extended version of the model.

2. Methodology

2.1. The minimal grazer model

The present model depicts an aquatic ecosystem in a shallow and unstratified lake. We propose two versions of the model, the minimal grazer (MG) model and the grazer–detritivore (GD) model.

The MG model incorporates the pelagic part of lakes and includes three trophic levels (algae, zooplankton, and fish) and three variables (nutrient concentration, algal density, and zooplankton density). The three variables do not correspond to the three trophic levels, because we treat fish density as a constant for the following reason.

Generally, the tri-trophic community model can be regarded as a system which consists of coupling of two 2-species subsystems (the algae–zooplankton system and the zooplankton–fish system) (Hastings and Powell, 1991). If the two systems have very different

process rates, the slow dynamics (the zooplankton–fish system) can be approximately fixed in order to investigate the dynamic property of the entire system. This treatment is analogous in concept to the singular perturbation analysis (Muratori and Rinaldi, 1992). The pelagic ecosystem may be regarded as a such case, because fish and zooplankton have very large body mass ratio (fish is much larger than zooplankton), and fish has much slower dynamics than algae and zooplankton.

In order to examine the effect of the detritus food web on the relationships between functional traits of species and TTE, the GD model includes two additional components, detritus and detritivore. Thus, the GD model partly incorporates the benthic component of lakes in addition to the pelagic component.

We examined the numerical relationships between model parameters and TTE along stable equilibrium solutions of the model, and we attempted to identify important trophic levels and the functional traits that determine TTE.

We include total phosphorus as the nutrient, because phosphorus is one of the most important nutrients and is the limiting factor for algal growth in oligotrophic lakes (Seip, 1991) of temperate regions (Dillon and Rigler, 1974; Elser et al., 1990), whereas nitrogen is often the limiting factor in tropical regions (Vincent et al., 1984; Wurtsbaugh et al., 1985) and eutrophic lakes (McCauley et al., 1989). Changes in nutrient concentration N ($\mu\text{g/L}$) with time t , are calculated by using the following equation:

$$\frac{dN}{dt} = (Q - N)\phi - U_{\max}u(N)A, \quad (1)$$

in which inflows from the source of nutrient are denoted by $(Q - N)\phi$ and uptake by algae (phytoplankton) is denoted by $U_{\max}u(N)A$, where Q is the nutrient concentration ($\mu\text{g/L}$) in the source, ϕ is the flow rate per day, A is algal density measured as chlorophyll a density ($\mu\text{g Chla/L}$), $u(N)$ is the response of nutrient uptake by algae to nutrient concentration, and U_{\max} is the maximum uptake rate. The inflow increases with the nutrient concentration in the source and the flow rate if $Q > N$. The nutrient uptake rate by a unit biomass of algae follows the Michaelis–Menten equation, $u(N) = N/(h_a + N)$, where h_a is the half-satiation coefficient of nutrient uptake by the algae.

We assumed that nutrient concentration was the predominant factor limiting algal growth, which is a linear function of nutrient uptake per unit biomass, with a constant value of the coefficient of conversion from nutrient to algal biomass, c_n , in Eq. (2):

$$\frac{dA}{dt} = c_n U_{\max} u(N) A - \beta_a A^2 - G_{\max} g(A) Z - d_a A, \quad (2)$$

where β_a is the intraspecific competition coefficient of algae, G_{\max} is the maximum grazing rate of algae by zooplankton, $g(A)$ is the response of zooplankton grazing to algal density, Z is zooplankton density (mg/L), and d_a is the mortality rate of algae. The population growth of algae is checked by the density effect (β_a), the mortality (d_a), and the loss of algae because of grazing by zooplankton; this last factor is denoted by the third term in the right side of Eq. (2). We postulate that the density effect occurs because of competition for a limited physical resource other than the nutrient (e.g., light) and sets the carrying capacity of algae (K_A) as the algal asymptotic biomass, even if the uptake of nutrient is satiated and grazing by zooplankton is absent: $K_A = (c_n U_{\max} - d_a) / \beta_a$.

The rate of zooplankton grazing of algae is assumed to follow the Holling Type III functional response to algal density, which is satiated at the maximum grazing rate per zooplankton biomass (G_{\max}) at the rate of $g(A) = A^2 / (h_g^2 + A^2)$, in which h_g is the half-satiation coefficient of zooplankton grazing. We define grazing efficiency as $\log(1/h_g)$, which indicates the efficiency of grazing when the algal density is very low.

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