Grazer-mediated coexistence and the Kill-the-Winner Functional Response

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Introduction

One of the central challenges of pelagic ecology has been resolving the apparent conflict between the observed high diversity of phytoplankton species and the assumed principles of competitive exclusion that should limit coexistence – a problem which was termed the 'paradox of the plankton' by G. Evelyn Hutchinson. One mechanism that supports the high diversity that is observed in phytoplankton communities is grazing pressure by zooplankton. Grazing promotes diversity by allowing coexistence between competitors in situations which would otherwise lead to competitive exclusion and extinction of all but the most fit species. We used the "Kill-the-Winner" functional response to show how preference and switching behaviors by zooplankton can increase diversity in a size-structured nutrient-phytoplankton-zooplankton (NPZ) model (Fig. 1). We also identified how interactions between the preference and switching parameters in the Kill-the-Winner functional response can lead to unintuitive dynamics that may be an undesirable characteristic of the functional response.

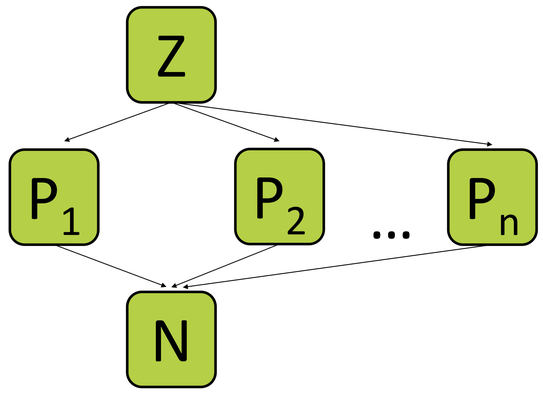

Figure 1: Model structure showing the trophic relationships between nutrients (N), phytoplankton (P_i), and zooplankton (Z).

$$\frac{dN}{dt} = D(N_0 - N) - \sum_{i=1}^{n} \mu_i P_i \frac{N}{k_i + N}$$

$$\frac{dP_i}{dt} = \mu_i P_i \frac{N}{k_i + N} - G_i(P_1, P_2, \ldots P_n)Z - m_p P_i - DP_i \text{ , for } i = 1{:}\,n$$

$$\frac{dZ}{dt} = \gamma \sum_{i=1}^{n} G_i(P_1, P_2, \ldots P_n)Z - m_z Z$$

Preference and switching

A zooplankton exhibits a **preference** (ρ) for a phytoplankton type when the proportion of that phytoplankton in its diet differs from that in the environment (Fig. 2). Preference may occur because of differential searching rates or rejection of some phytoplankton types. Preferences are fixed and independent of changes in the phytoplankton community.

A zooplankton exhibits **switching** (α) when the proportion of a phytoplankton type in its diet changes from less than expected to greater than expected as the proportion of that phytoplankton in the environment increases (Fig. 2). Switching may result from a change in behavior, such as switching feeding strategies in response to changes in the phytoplankton community.

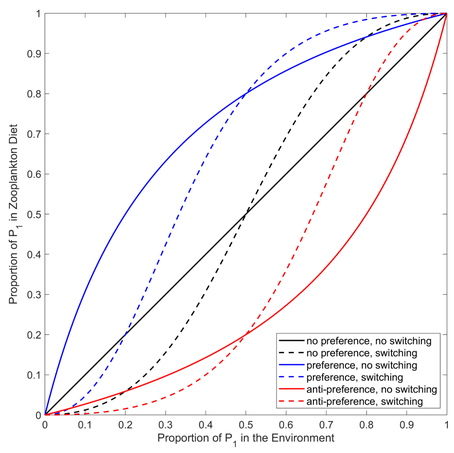

Figure 2: Proportion of P_1 in the zooplankton's diet as a function of the proportion of P_1 in the environment. For this example, n=2.

The Kill-the-Winner functional response:

$$G_i = g_{max} \frac{\rho_i P_i^{\alpha}}{\sum_{j=1}^{n} \rho_j P_{ij}^{\alpha}} \frac{\sum_{j=1}^{n} \rho_j P_j}{k_{sat} + \sum_{j=1}^{n} \rho_j P_j}$$

No preference or switching: α = 1 and ρ_i = constant
Preference for P_1: $\rho_1 > \rho_i$, for i≠1
Switching: α > 1

Preference and switching both increase phytoplankton diversity.

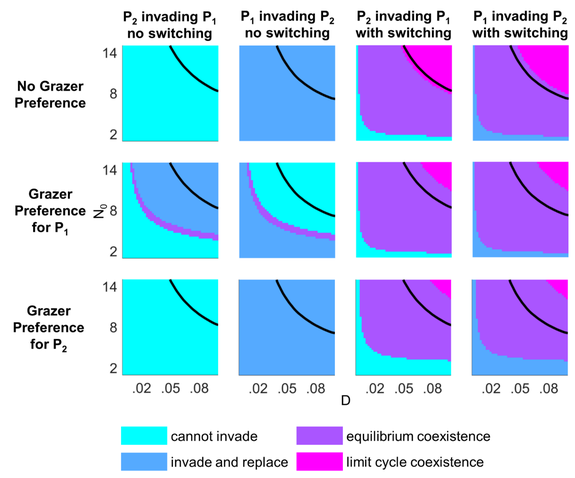

Figure 3: Dynamics of the model when n=2 as a function of nutrient input (N_0) and mixing (D) under different scenarios of preference and switching. Each point is color coded to show the steady-state result of either P_1 or P_2 invading a system with the other phytoplankton existing at a stable equilibrium. The Hopf bifurcation point for the linear food chain model is plotted in black.

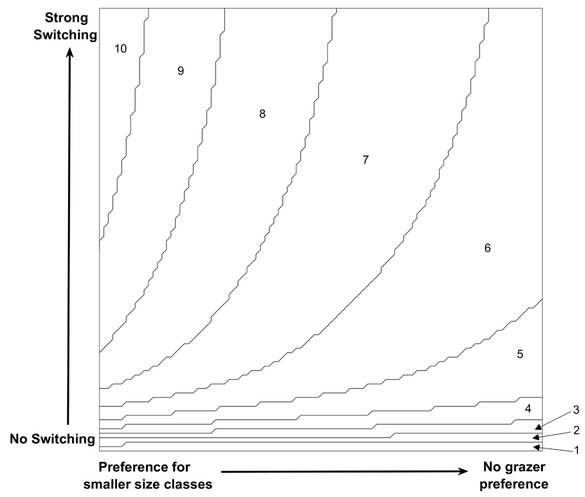

Figure 4: Phytoplankton species richness at steady state in a model with 10 size classes as a function of grazer preference and switching strength. The values of ρ are distributed such that the slope is always negative, indicating a preference for smaller size classes, but moves left to right from a strong preference for smaller size classes to no preference (even distribution of ρ across size classes).

"Synergistic grazing" in the Kill-the-Winner functional response

Synergistic Grazing occurs when the grazing rate on one phytoplankton type increases as the density of an alternative phytoplankton type increases ($dG_i/dP_j > 1$, $i \neq j$). In some cases, synergistic grazing can make it easier for a phytoplankton size class to invade the system when the zooplankton has a stronger preference for it (Fig. 5).

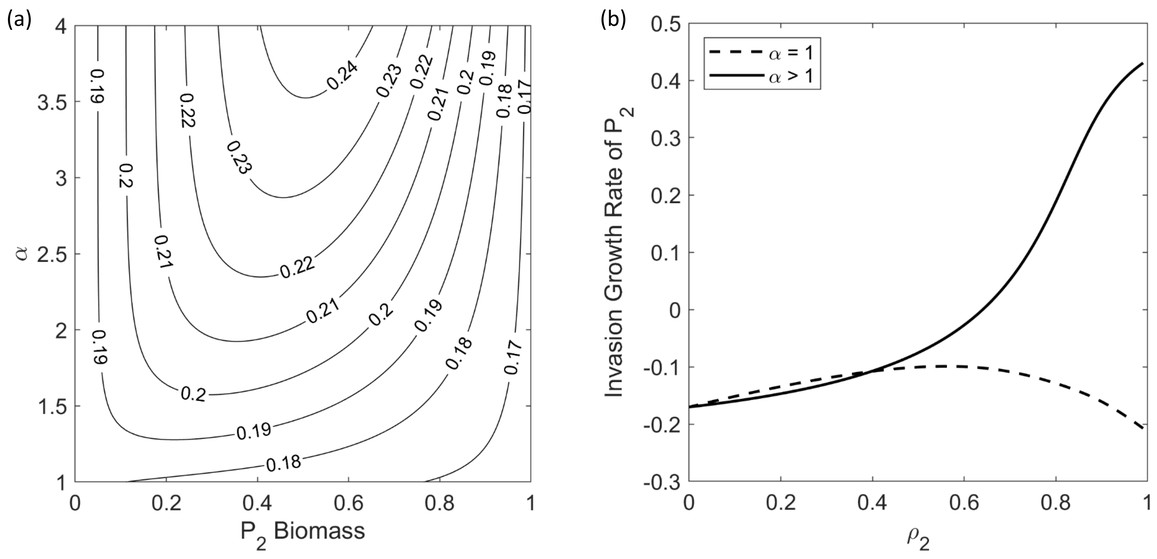

Figure 5: (a) Grazing rate on P_1 as a function of α and P_2 and (b) the invasion growth rate of P_2 as function of ρ_2. For (b), $\rho_1 = 1 - \rho_2$. In this example, n=2.

Conclusions

- Coexistence between competing phytoplankton in the model could be achieved through either zooplankton preference for smaller phytoplankton size classes or through switching.
- Switching is a robust mechanism for promoting coexistence between competing phytoplankton, while coexistence mediated by preference alone requires a delicate balance between zooplankton preference and the competitive ability of the phytoplankton types.
- The Kill-the-Winner functional response is useful for representing preference and switching behaviors, but displays synergistic grazing, which may be undesirable.