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.

Preference and switching

A zooplankton exhibits a preference (p) 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 (a) 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.

Preference and switching both increase phytoplankton diversity.

“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 ≠ 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).

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.