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Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages.

Steady state phytoplankton assemblages during thermal stratification in deep alpine lakes. Do they occur?

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Abstract

Phytoplankton seasonal and long-term succession can be described and functionally classified by associations similar as in terrestrial vegetation studies. Such a concept has to include 'climax' into pelagic succession which in turn leads to the question to what extent steady state assemblages occur and if during periods of dynamic equilibrium can be identified. Here we explore the situation with respect to the above question for deep, nutrient poor, alpine lakes in Austria. We first track the long-term development of phytoplankton biomass, their taxonomic structure and their relation to total phosphorus and chlorophyll-*a* as predictors of trophic state over the past 35 years. We then analyse this data set for coherent algal associations which can be ascribed to trait separated functional groups according to Reynolds et al. (2002). A three year period of stable environmental conditions has then be extracted from the progression of trophic state indices, having similar dominating species each year. These years were finally analysed for steady state conditions according to definitions given in Sommer et al. (1993). During thermal stratification, achievement of an equilibrium could be ruled out although coexistence of several dominating species lasted for several weeks. Habitat templates were constructed from environmental variables prior to biomass peaks for two species important in summer assemblages, the dinoflagellate *Ceratium hirundinella* and the diatom *Fragilaria crotonensis*. In summary, functional groups proved to be a valid and useful concept to describe species succession of phytoplankton in deep alpine lakes while pelagic climax is much less clear and steady state conditions were never met.

Introduction

The seasonality of freshwater phytoplankton has attracted considerable attention during the limnological venue of last century summarised in e.g. Munawar & Talling (1986). Much of the periodicity in the wax and wane of the phytoplankton taxa has been gathered through, often long-time, serial investigations in a wide variety of lake types and reservoirs. Although additional, essential information has been generated by controlled laboratory experiments, interpretation of field results has been hampered by the difficulty to test hypotheses properly. Whole lake experiments and the advent of aquatic enclosures offered an alternative and generated a brake-through in the testing of ecological hypotheses in freshwaters (e.g. Reynolds, 1986). Detailed information has been accumulated since then by experimental manipulations and field observations on adaptive strategies of phytoplankton, importance of their functional morphology and species selection across trophic gradients summarised in e.g. Álvarez-Cobelas et al. (1998), Reynolds et al. (2000) and Hamilton et al. (2000). These and other results had influential impacts on the progressive development of a coherent theory of dynamic processes in the pelagic (Reynolds, 1997). This topic was further developed towards functional classification and prediction of freshwater phytoplankton (Reynolds & Irish, 1997; Reynolds at al., 2002). In essence, the theory hypothesizes succession leading to a climax in the pelagic similar to terrestrial vegetation (Grime, 1979).

If this concept has relevance, we must hypothesize that phytoplankton assemblages or associations sensu Reynolds et al. (2002) shall achieve steady state