

Response of phytoplankton and bacteria to nutrients and zooplankton: a mesocosm experiment

Kathryn L. Cottingham^{1,3,4}, Susan E. Knight¹, Stephen R. Carpenter¹, Jonathan J. Cole², Michael L. Pace² and Amy E. Wagner¹

¹Center for Limnology, University of Wisconsin, Madison, WI 53706 and

²Institute of Ecosystem Studies, Box AB, Route 44A, Millbrook, NY 12545, USA

³Present address: National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93109, USA

⁴To whom correspondence should be addressed at: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93109, USA

Abstract. Although both nutrient inputs and zooplankton grazing are important to phytoplankton and bacteria in lakes, controversy surrounds the relative importance of grazing pressure for these two groups of organisms. For phytoplankton, the controversy revolves around whether zooplankton grazers, especially large cladocerans like *Daphnia*, can effectively reduce phytoplankton populations regardless of nutrient conditions. For bacteria, little is known about the balance between possible direct and indirect effects of both nutrients and zooplankton grazing. However, there is evidence that bacteria may affect phytoplankton responses to nutrients or zooplankton grazing through direct or apparent competition. We performed a mesocosm experiment to evaluate the relative importance of the effects of nutrients and zooplankton grazing for phytoplankton and bacteria, and to determine whether bacteria mediate phytoplankton responses to these factors. The factorial design crossed two zooplankton treatments (unsieved and sieved) with four nutrient treatments (0, 0.5, 1.0 and 2.0 μg phosphorus (P) L^{-1} day⁻¹, together with nitrogen (N) at a N:P ratio of 20:1 by weight). Weekly sieving with 300 μm mesh reduced the average size of crustacean zooplankton in the mesocosms, decreased the numbers and biomass of *Daphnia*, and increased the biomass of adult copepods. Nutrient enrichment caused significant increases in phytoplankton chlorophyll *a* (4–5 \times), bacterial abundance and production (1.3 \times and 1.6 \times , respectively), *Daphnia* (3 \times) and total zooplankton biomass (2 \times). Although both total phytoplankton chlorophyll *a* and chlorophyll *a* in the <35 μm size fraction were significantly lower in unsieved mesocosms than in sieved mesocosms, sieving had no significant effect on bacterial abundance or production. There was no statistical interaction between nutrient and zooplankton treatments for total phytoplankton biomass or bacterial abundance, although there were marginally significant interactions for phytoplankton biomass <35 μm and bacterial production. Our results do not support the hypothesis that large cladocerans become less effective grazers with enrichment; rather, the difference between phytoplankton biomass in sieved versus unsieved zooplankton treatments increased across the gradient of nutrient additions. Furthermore, there was no evidence that bacteria buffered phytoplankton responses to enrichment by either sequestering P or affecting the growth of zooplankton.
