

TROPHIC CASCADES, NUTRIENTS, AND LAKE PRODUCTIVITY: WHOLE-LAKE EXPERIMENTS

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Abstract. Responses of zooplankton, pelagic primary producers, planktonic bacteria, and CO₂ exchange with the atmosphere were measured in four lakes with contrasting food webs under a range of nutrient enrichments during a seven-year period. Prior to enrichment, food webs were manipulated to create contrasts between piscivore dominance and planktivore dominance. Nutrient enrichments of inorganic nitrogen and phosphorus exhibited ratios of N:P > 17:1, by atoms, to maintain P limitation. An unmanipulated reference lake, Paul Lake, revealed baseline variability but showed no trends that could confound the interpretation of changes in the nearby manipulated lakes. Herbivorous zooplankton of West Long Lake (piscivorous fishes) were large-bodied *Daphnia* spp., in contrast to the small-bodied grazers that predominated in Peter Lake (planktivorous fishes). At comparable levels of nutrient enrichment, Peter Lake's areal chlorophyll and areal primary production rates exceeded those of West Long Lake by factors of approximately three and six, respectively. Grazers suppressed pelagic primary producers in West Long Lake, relative to Peter Lake, even when nutrient input rates were so high that soluble reactive phosphorus accumulated in the epilimnions of both lakes during summer. Peter Lake also had higher bacterial production (but not biomass) than West Long Lake. Hydrologic changes that accompanied manipulation of East Long Lake caused concentrations of colored dissolved organic carbon to increase, leading to considerable variability in fish and zooplankton populations. Both trophic cascades and water color appeared to inhibit the response of primary producers to nutrients in East Long Lake. Carbon dioxide was discharged to the atmosphere by Paul Lake in all years and by the other lakes prior to nutrient addition. During nutrient addition, only Peter Lake consistently absorbed CO₂ from the atmosphere, due to high rates of carbon fixation by primary producers. In contrast, CO₂ concentrations of West Long Lake shifted to near-atmospheric levels, and net fluxes were near zero, while East Long Lake continued to discharge CO₂ to the atmosphere.

Key words: bacteria; carbon dioxide flux; chlorophyll; lake ecosystem; fish; food web; nutrient effects; Paul Lake, Peter Lake, East and West Long Lakes; phosphorus input; trophic cascades; zooplankton.