

# Nutrient recycling by fish versus zooplankton grazing as drivers of the trophic cascade in alpine lakes

Orlando Sarnelle<sup>1</sup>

Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, 48824

Roland A. Knapp

Sierra Nevada Aquatic Research Laboratory, University of California, HCR 79, Box 198, Crowley Lake, California 93546

## Abstract

In a multilake experiment, we found little effect of nutrient excretion by zooplanktivorous fish, but a large effect of herbivorous zooplankton, on phytoplankton biomass and phosphorus (P) limitation. Whole-lake removal of fish from small alpine lakes resulted in little change in phytoplankton biomass or the intensity of P limitation during 1–6 postremoval years, over which herbivorous zooplankton did not change. In contrast, significant decreases in phytoplankton biomass and the intensity of phytoplankton P limitation were observed after *Daphnia* became reestablished. Fish removal also caused large increases in the biomass of benthic macroinvertebrates, but the timing of these increases suggested that P recycling by the benthos did not confound our attempt to measure the effects of P recycling by fish. Estimates of the amount of P recycled by fish and zooplankton and estimates of P demand by the phytoplankton also supported the conclusion that fish recycling was not a major source of P to the phytoplankton in these lakes. Relative to *Daphnia* grazing, fish recycling of P appears to be relatively unimportant as a driver of trophic cascades in these alpine lakes.

The cascading response of phytoplankton biomass to fish manipulation in lakes represents a major piece of evidence in support of food-web theory (Strong 1992; Brett and Goldman 1996; Shurin et al. 2002), but uncertainty remains with respect to the mechanisms driving the phytoplankton response to fish removal. It has been commonly assumed that the decrease in phytoplankton biomass after zooplanktivorous fish removal results from an increase in grazing pressure from herbivorous zooplankton (Vanni and Layne 1997). However, there is also evidence to suggest that a reduction in the supply of inorganic nutrients, as a result of the loss of fish excretion, may be at least partly responsible for the decrease in phytoplankton (Carpenter et al. 1992; Schindler 1992; Vanni and Layne 1997). Although experimental evidence supports the role of nutrient excretion by fish, Kalff (2002) has noted, “Whether the cause (of reduced phytoplankton) is reduced fish predation on the zooplankton, as generally believed, or is at least in part attributable to a reduction in nutrient recycling by fish, is not well resolved.”

Evidence for the role of nutrient recycling by fish derives from two types of studies (Vanni 2002). The first calculates the total nutrient recycling rate of fish populations and compares this to other sources of nutrient supply or to total nutrient uptake rate by phytoplankton. The conclusions of such studies are mixed with respect to whether recycling by zoo-

planktivorous fish is a major nutrient source for the phytoplankton (Nakashima and Leggett 1980; Carpenter et al. 1992; Schindler et al. 1993). At best, these studies provide only indirect evidence for the role of fish recycling in the trophic cascade response, because it is not a simple matter to translate calculated changes in nutrient supply into estimates of long-term change in total phytoplankton biomass after fish manipulation, the primary currency of trophic cascade studies (Brett and Goldman 1996).

Alternatively, a few studies have experimentally isolated the influence of nutrient recycling by fish from that of zooplankton grazing by using mesocosms or in situ enclosures, accomplishing this by caging either the fish or the phytoplankton away from the zooplankton (Schindler 1992; Vanni and Layne 1997; Attayde and Hansson 2001). These studies tend to support the view that nutrient recycling by fish is an important mechanism driving the response of phytoplankton biomass to fish manipulation. Ideally, enclosure/mesocosm results should be compared to manipulations at the whole-lake scale to rule out enclosure artifacts (Mazumder et al. 1990; Carpenter 1996), but the experimental separation of zooplankton grazing effects from the effects of nutrient recycling by fish seems logistically impossible at the whole-lake scale. In previous whole-lake fish manipulations, changes in zooplankton biomass and composition have typically been large and immediate (i.e., within a single growth season) after fish manipulation (Carpenter et al. 1987). Consequently, the confounded mechanisms of recycling and grazing have not been separated at the whole-lake scale.

A unique opportunity to disentangle the effects of fish removal from the effects of changes in zooplankton biomass and composition at the whole-lake scale arose in the context of a multilake fish manipulation study. We compared the dynamics of phytoplankton biomass and phosphorus (P) limitation before and after complete fish removal in two exper-

<sup>1</sup> Corresponding author (sarnelle@msu.edu).

## Acknowledgments

We thank A. Kramer, C. Archer, M. Crowder, J. Garton, P. Kirchner, W. Kuhn, S. Roll, A. Selters, M. Sheehy, and L. Wilkinson for assistance in the field and laboratory; J. Bence for statistical advice; and S. Hamilton, S. Peacor, J. Bence, and anonymous reviewers for critical comments.

Financial support was provided by the National Science Foundation (grants DEB-9629473 and DEB-0075509 to R.K. and O.S.).

Table 1. Limnological characteristics of the experimental and control lakes averaged over all years. Temperatures are means of readings taken at 1 m depth every 30 min from 11 July–31 August. TP concentrations are means for the ice-free period. Phytoplankton productivity was measured twice per year in August and September.

Lake	Elevation (m)	Mean (max) depth (m)	Surface area (km <sup>2</sup> )	Temperature (°C)	TP (mg m <sup>-3</sup> )	Productivity (mg C m <sup>-3</sup> d <sup>-1</sup> )
Experimental lakes						
Knob	3,358	1.8 (5.5)	0.034	14.4	8.3	33
Square	3,443	1.9 (3.5)	0.017	14.7	7.3	13
No Good	3,516	1.9 (5.0)	0.017	13.2	5.7	17
Control lakes						
Lower Desolation	3,413	1.7 (5.0)	0.131	14.0	6.6	27
Mesa	3,437	3.0 (6.0)	0.112	13.7	6.2	18

imental alpine lakes (Knob Lake, No Good Lake), relative to two unmanipulated control lakes (Mesa Lake, Lower Desolation Lake). There was no immediate increase in zooplankton biomass or shift in species composition after whole-lake fish removal in the experimental lakes, so we assumed that any immediate decrease in phytoplankton biomass that was associated with an increase in the intensity of phytoplankton P limitation would be attributable to the loss of P recycling by fish. In a fifth lake that reverted to a fishless condition at the beginning of the study (Square Lake), the reestablishment of a large *Daphnia* population after fish disappearance was used to (1) estimate the effect of *Daphnia* herbivory on phytoplankton biomass and P limitation in a fishless alpine lake, and (2) compare *Daphnia*'s effect with that of nutrient recycling by fish in the experimental lakes. The latter comparison was crucial because strong trophic cascades in lakes are generally restricted to systems in which *Daphnia* is abundant in the fish-removal treatment (Leibold 1989).

## Methods

**Study sites**—All five lakes were historically fishless and are located in Humphrey's Basin, John Muir Wilderness, Sierra National Forest, California (Table 1). Lakes ranged from 3350–3520 m in elevation and 0.02–0.13 km<sup>2</sup> in area, and are separated by 0.4–5.6 km (Sarnelle and Knapp 2004). Across the five lakes, mean molar total nitrogen:total P (TN:TP) and sestonic carbon (C):P varied from 37–53 and 213–280, respectively. These ranges, coupled with high levels of phosphatase activity in lake water (see Results), indicated that phytoplankton production was likely P limited.

Before the start of the study, four of the five lakes (Knob, Square, Mesa, Lower Desolation) contained populations of golden trout (*Oncorhynchus mykiss aquabonita*) maintained by natural reproduction and biennial stocking of fingerlings. No Good Lake contained a brook trout population (*Salvelinus fontinalis*) maintained by natural reproduction (no stocking). Stocking in Knob and Square Lakes was discontinued after 1994 but continued in the control lakes (Mesa and Lower Desolation) for the duration of the present study.

**Experimental procedures**—Whole-lake fish removals via intensive gill-netting (Knapp and Matthews 1998) were initiated in Knob Lake and No Good Lake in late September 1997 and 2000, respectively. Fish removal in both lakes was

essentially complete before the start of the next summer. We removed a total of 599 golden trout from Knob Lake and 485 brook trout from No Good Lake. All fish removed from each lake were disposed of outside of each lake's watershed to avoid fertilizing the lakes with P from decomposing fish carcasses. We also initiated fish removal in Square Lake in 1997, but we collected only two fish despite intensive efforts (trout were last stocked into Square Lake in 1994 and were common in the lake when sampled in 1995, but they apparently died out during 1995 and 1996). Thus, we considered Square Lake to be fishless, with respect to any conceivable impacts of nutrient recycling by fish, from 1997 onward.

**Sampling**—All the lakes were sampled for nutrients, phytoplankton, and zooplankton between 1996 and 2003 (except for No Good Lake, which was sampled from 1999–2001) two or three times per summer on the same seasonal schedule. All planktonic samples were collected from a float tube that slowly drifted over the deepest part of each lake. For phytoplankton and nutrients, lake water was collected at a depth of 2.5 m by using a closing bottle. Lake water was transported in coolers to the laboratory for same-day determinations of chlorophyll *a* (Chl *a*), productivity (as <sup>14</sup>C uptake rate), and P limitation (as phosphatase enzyme activity). Phytoplankton samples for microscope counting were preserved with Lugol's in the field. Samples for TP and TN concentrations in the water column were frozen on delivery at the laboratory. Samples for particulate P and particulate organic C were collected on Gelman A/E filters in the field and were dried in the laboratory. Zooplankton were sampled with vertical hauls of a 30-cm (diameter), 64- $\mu$ m mesh net. Two replicate hauls were composited into each sample, and two samples were collected on each date. One sample was preserved in 95% ethanol for crustaceans, the other was preserved in 2% glutaraldehyde for rotifers.

Benthic macroinvertebrates were sampled twice per summer from the littoral zone of each lake by using a D-net with a mesh size of 0.5 mm (Knob and Square Lakes: 1996–2003; Mesa and Lower Desolation Lakes: 1997–2003; No Good Lake: 1999–2003). The goal of benthic sampling was to estimate the relative abundance of taxa that are typically consumed by trout. These taxa tend to be epibenthic and conspicuous (Englund et al. 1999; Knapp et al. 2001), so the sampling technique was deemed suitable. At each lake, we made 15 standard sweeps, with a standard sweep being de-

fined as a 1-m sweep in one direction followed immediately by a 1-m sweep across the same area in the opposite direction. D-net sweeps followed bottom contours and sampled epibenthic, water column, and surficial sediment habitats in portions of each lake that were <1.2 m deep. All littoral habitats along the north shore of each lake were sampled, and each common habitat was sampled approximately in proportion to its availability. Benthic macroinvertebrates were separated from detritus and sediment in the field and were preserved in 95% ethanol.

The number of amphibians at each water body was determined by using visual encounter surveys (Crump and Scott 1994) of the entire shoreline conducted once per summer. During the summer, tadpoles occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes by shoreline searches (Knapp 2005). At each lake, we used electronic loggers to record water temperature every 30 min at a depth of 1 m in the center of each lake.

**Sample analyses**—Chl *a* was determined via fluorometric measurement of ethanol-extracted pigment with acid correction (Nusch 1980). The fluorometer was calibrated against a commercial Chl *a* standard (*Anacystis*). Phytoplankton were counted via the inverted microscope technique (Sarnelle 1993). Across lakes and years, Chl *a* concentrations were strongly correlated with phytoplankton biomass estimates from microscope counts ( $r = 0.82$ ,  $p < 0.00001$ ,  $n = 41$ ), so Chl *a* was used as an index of total phytoplankton biomass. Phosphatase activity, an index of P deficiency, was determined via fluorometric measurement of the liberation of methylumbelliferone in lake water by using saturating levels of 4-methylumbelliferyl- $\text{PO}_4^{3-}$  as substrate (Pettersson 1980). Phosphatase activity was expressed on a Chl *a*-specific basis ( $\text{nmol PO}_4^{3-}$  released  $\mu\text{g-Chl } a^{-1} \text{ h}^{-1}$ ). We validated this measure of P limitation by comparing Chl *a*-specific phosphatase activities of Square Lake water incubated in situ for 5 d with and without added  $\text{PO}_4^{3-}$ . Chl *a*-specific phosphatase activity decreased after 5 d in the presence of added  $\text{PO}_4^{3-}$  (45% decrease,  $t$ -test,  $p < 0.01$ ), indicating the validity of the index in this study. Annual mean Chl *a* and P limitation for each lake and year were calculated from two samplings conducted between mid-August and early September. No Chl *a* or phosphatase data were obtained from the lakes in 2002, because of instrument failure, or from No Good Lake in 2003, because of budget limitations.

Phytoplankton primary productivity was measured in four of the five lakes from 1997–2001, and in No Good Lake from 1999–2001. Samples of lake water were incubated on the day of collection in 75-mL glass jars under a 400-W metal halide light source (Hill and Boston 1991) in a walk-in incubator. Light levels were varied between 250 and 1500  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  to mimic the range of typical midday irradiances through the water column in the study lakes on a clear midsummer day ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ : 0.5 m, 1500; 1.5 m, 1000; 2.5 m, 750; 3.5 m, 500; 4.5, 350; 5.5 m, 250). Incubation temperature was maintained at  $15 \pm 1^\circ\text{C}$ , which was representative of midday water temperatures in the study lakes. Dark controls were incubated simultaneously. Samples were acclimated under the light source for 1 h before adding

isotope ( $\sim 185$  kBq of  $^{14}\text{C}$ -labeled bicarbonate) and then incubated for 4 h. Isotope addition increased the alkalinity of lake water by no more than 5%. Radioactivities of phytoplankton collected on Whatman GF/F filters, and radioactivities of lake water were measured via liquid scintillation counting with quench correction. Productivity estimates were corrected for dark  $^{14}\text{C}$  uptake and averaged across light levels to estimate average productivity for the water column. Hourly rates were multiplied by 10 to estimate daily productivity rates (Thomas et al. 1991). Specific growth rates ( $\text{d}^{-1}$ ) of the phytoplankton were estimated from Chl *a* and productivity measurements assuming a carbon:Chl *a* ratio of 30 (Reinertsen et al. 1990).

Total and particulate P were analyzed via persulfate digestion followed by ascorbic acid-molybdate colorimetry (Murphy and Riley 1962; Menzel and Corwin 1965). Total N was analyzed via second-derivative spectroscopy (Crump et al. 1992) by using a Perkin-Elmer Lambda 20 scanning spectrophotometer. Particulate organic C was determined with a CHN analyzer (Control Equipment, model 240XA). P demand by the phytoplankton ( $\mu\text{g P m}^{-3} \text{ d}^{-1}$ ) was estimated by dividing daily productivity rates ( $\text{mg C m}^{-3} \text{ d}^{-1}$ ) by phytoplankton C:P (Schindler et al. 1993; Shostell and Bukaveckas 2004). In contrast to previous studies, we estimated phytoplankton C:P by using field measurements of sestonic C:P rather than applying the Redfield Ratio. This method should result in relatively conservative estimates of P demand because C:P ratios in the lakes were always above Redfield.

Crustacean zooplankton were identified, counted, and measured under a stereomicroscope at  $40\times$ . Rotifers were generally a negligible fraction of total zooplankton biomass (percentage of total biomass across lakes and years: mean = 6%, SD = 11%) and so are not further considered in the present study. Biomass ( $\text{mg L}^{-1}$ ) of the two dominant crustaceans, *Leptodiptomus signicauda* and *Daphnia middendorffiana*, was determined from densities and length distributions by using length-dry mass regression equations for the congeners *L. siciloides* and *D. pulicaria* in Zaca Lake, California (Sarnelle 1999). Grazing mortalities ( $\text{d}^{-1}$ ) inflicted by these two populations were estimated from densities and length distributions by using a length-grazing rate regression equation for *L. siciloides* in Zaca Lake (Sarnelle 1993) and equation 2 of Knoechel and Holtby (1986). P excretion by the entire zooplankton assemblage was estimated by multiplying total zooplankton biomass by a mass-specific P excretion rate taken from the literature. To be conservative, we chose a low value ( $2.4 \mu\text{g mg}^{-1} \text{ d}^{-1}$ ) of mass-specific P excretion rate from the review in Carrillo et al. (1996). Annual means for zooplankton biomass, grazing, and excretion for each lake and year were based on three samples collected in late July, mid-August, and late-August–early September (one sample per date). Standard errors of these annual means represent the combined influence of spatial and seasonal variation. Total wet mass of benthic macroinvertebrates was determined by weighing entire preserved samples.

To estimate P excretion rates by the fish populations in each study lake, we first estimated fish biomass in each lake. Fish biomass in Knob and No Good Lakes was determined directly from the fish removal manipulation. All fish were

removed and counted, so there was essentially no error in the density determinations for these two lakes. All fish collected during removals were measured, and at least the first 100 were weighed. Biomass ( $\text{kg km}^{-2}$ ) was then calculated by using length-wet mass regression equations derived for each lake. To estimate fish biomass in Square Lake and the two control lakes, we set a single, variable mesh size gill net in each lake for 8–12 h, and converted the resulting catch per unit effort (CPUE) into fish density ( $\text{No. km}^{-2}$ ) using the following equation: fish density =  $55 + 8.8\text{CPUE}$  ( $R^2 = 0.99$ ,  $n = 3$ ), taken from Schindler et al. (2001). Fish density was multiplied by average weight of gill-netted fish to estimate fish biomass. Fish biomass estimates for the control lakes were based on catches from gill-net sets conducted in three separate years (Lower Desolation Lake: 1996, 1999, 2001; Mesa Lake: 1995, 2000, 2001), whereas that for Square Lake was based on the catch from a single gill-net set (1995). Although the latter three estimates were based on gill-net sampling rather than counting and measuring every fish, they were very similar in magnitude to the estimates from Knob and No Good Lakes, lakes of comparable depth, elevation, and productivity in which sampling error was negligible.

P excretion by each fish population,  $E$ , ( $\mu\text{g P m}^{-3} \text{d}^{-1}$ ) was estimated from fish biomass,  $B$ , ( $\text{kg km}^{-2}$ ), by using an empirical relationship ( $E = 4.08 + 0.72B$ ,  $R^2 = 0.74$ ) that was developed for trout in alpine lakes of the Sierra Nevada (Schindler et al. 2001). The range of fish biomass in the study lakes fell within the range of fish biomass in the empirical relationship. Use of this relationship assumes that trout size distributions in the study lakes were similar to those in the lakes from which the equation was derived, because P excretion rates of fish vary allometrically (Post 1990; Kraft 1992). Trout in the study lakes (mean length = 203 mm) were somewhat larger than were trout in the lakes from which the relationship was derived (mean length = 186 mm). Our use of a relationship based on smaller fish should result in overestimates of P excretion by fish in the study lakes, given that mass-specific excretion rates are greater for smaller fish (Post 1990; Kraft 1992). Standard errors for P excretion rates of fish populations were calculated by using the delta method (Seber 1982) as:  $\sqrt{s_{E,B}^2 + s_B^2\beta^2}$ , where  $s_{E,B}^2$  is the variance of  $E$  values predicted from the regression of  $E$  on  $B$  (Sokal and Rohlf 1981),  $s_B^2$  is the variance of fish biomass estimates (based on multiple gill-net samplings in the control lakes) and  $\beta$  is the slope of the regression of  $E$  on  $B$  (0.72). For Knob and No Good Lakes,  $s_B^2$  was essentially zero because all fish were counted and measured; for Square Lake, we assumed that  $s_B^2$  was equal to that for Lower Desolation Lake ( $13.7 \text{ kg km}^{-2}$ ), the control lake with the higher sampling variance.

**Statistical analysis**—To assess the separate influences of fish removal and *Daphnia* reestablishment on phytoplankton biomass and P limitation, we adjusted values of each response variable in the experimental lakes for temporal dynamics in the control lakes (Schmitt and Osenberg 1996) by calculating the ratio  $\bar{X}_e/\bar{X}_c$ , where  $\bar{X}_e$  is the annual mean for an experimental lake and  $\bar{X}_c$  is the average of the annual means of the two control lakes. We also ran a parallel set of

statistical analyses on arithmetic differences between experimental and control means, but these analyses led to exactly the same conclusions as the analyses based on ratios. We present ratios in the present study. The statistical significance of temporal changes in adjusted means in response to fish removal or *Daphnia* reestablishment was assessed via two-tailed  $t$ -tests that allowed for unequal variances. In these tests, years were considered replicate observations. Log transformation tended to increase heterogeneity of variances in some cases and so was not applied in these tests. If P recycling by fish is an important mechanism driving the cascading response of phytoplankton biomass to fish removal, we would expect a significant decrease in phytoplankton biomass, coupled with a significant increase in the severity of P limitation, beginning immediately after fish removal (i.e., during the summer after fish removal), in the absence of any increase in zooplankton biomass or grazing pressure.

## Results

Mean water temperatures from 11 July–1 August were strongly correlated among the five lakes, with 1998 as an unusually cold year (Fig. 1). Large interannual variation in water temperatures between 1997 and 2000 coincided with both the fish-removal treatment in Knob Lake and the reestablishment of *Daphnia* in Square Lake. In the control lakes across all years, water temperature had a strong positive influence on Chl  $a$  concentration (linear regression,  $p < 0.001$ ; Fig. 1) but no influence on Chl  $a$ -specific phosphatase activity (linear regression,  $p > 0.50$ ). Given the potential for strong climatic effects on phytoplankton in these and other alpine lakes (Goldman et al. 1989; Sickman and Melack 1992), adjusting responses in the experimental lakes for changes in the control lakes was crucial.

The dominant zooplankton in all study lakes when fish were present was *L. signicauda*, a species that, on average, made up 93% of total zooplankton biomass across lakes when fish were present. This small herbivorous copepod commonly coexists with introduced trout in Sierra Nevada lakes (Knapp et al. 2001) and was only rarely found in the stomachs of trout sampled from our study lakes. In Knob Lake, there was no change in the adjusted biomass (experimental/control) of *L. signicauda* in response to fish removal, and although *Daphnia* (*D. middendorffiana*) reappeared in 2002, it remained rare in 2002 and 2003 (Fig. 2). Consequently, any changes in phytoplankton biomass and P limitation between fish (1996–1997) and no-fish (1998–2003) periods should constitute a response to the loss of P recycling by fish.

There were no significant differences in adjusted Chl  $a$  or phosphatase activity in Knob Lake between fish and no fish periods (Figs. 3, 4), suggesting that there was little or no effect of the complete elimination of P recycling by fish. In this particular case, adjusting responses in the experimental system for dynamics in the controls was immaterial because the same general lack of response was apparent in both the raw and the adjusted data (Figs. 3, 4). The results from the second fish-removal lake, No Good Lake, were similar to those in Knob Lake. There was little change in adjusted Chl

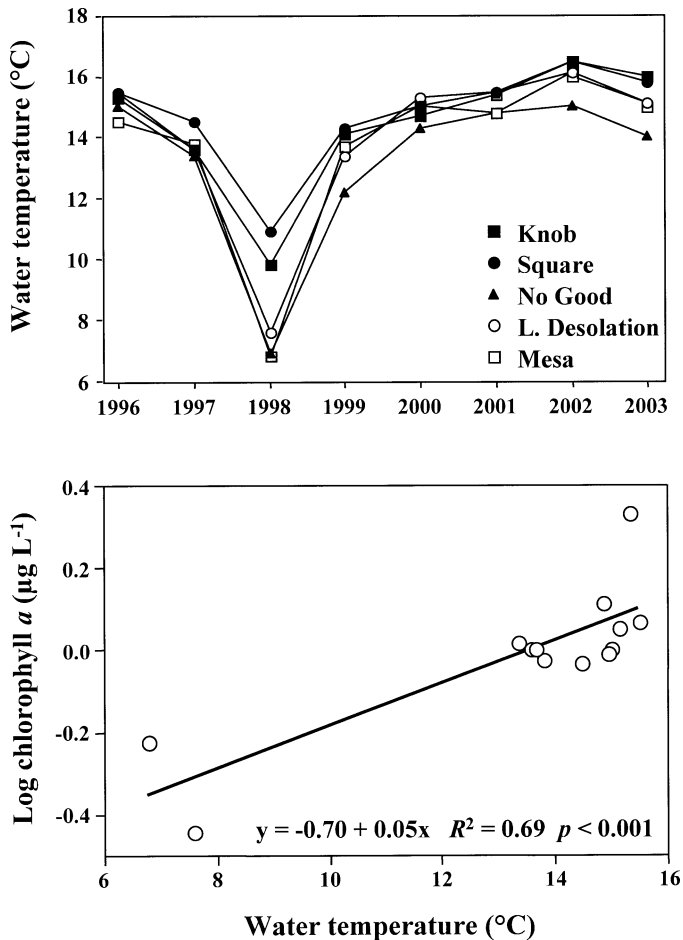


Fig. 1. Average annual water temperature at 1-m depth between 11 July and 31 August in the five study lakes (upper panel), and the influence of average annual water temperature on average annual Chl *a* concentration (lower panel) in the control lakes (Mesa and Lower Desolation Lakes).

*a* or phosphatase activity in No Good Lake in the first summer after fish removal (Fig. 5), the only postmanipulation year in which *D. middendorffiana* was not abundant.

In contrast to the above results, phytoplankton biomass responded significantly to the reestablishment of *Daphnia* in fishless Square Lake in a manner consistent with the classical trophic-cascade model (Carpenter et al. 1985). Adjusted Chl *a* was consistently and significantly lower in Square Lake after *Daphnia* reestablishment (Fig. 6). In essence, Chl *a* concentrations in Square Lake changed from being higher than the controls before *Daphnia* to being lower than the controls after *Daphnia* (Fig. 6). Adjusted Chl *a* was also negatively correlated with *Daphnia* biomass across all years in Square Lake (log-log relationship,  $n = 6$ ,  $r = -0.75$ ,  $p = 0.05$ ). Adjusting the response of the experimental system for the dynamics in the controls was crucial because water temperatures and Chl *a* concentrations increased strongly in the control lakes (unadjusted Chl *a* more than doubled between 1998 and 2000) at the same time that *Daphnia* was increasing in Square Lake (Figs. 1, 6).

We observed a reduction in adjusted Chl *a* in Square Lake

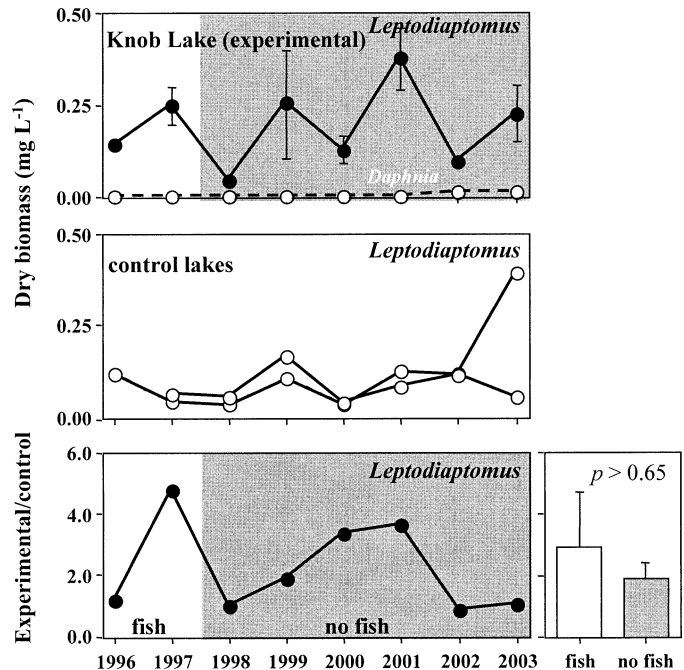


Fig. 2. Biomass dynamics ( $\pm 1$  SE) of the dominant zooplankton, *Leptodiatomus signicauda*, in Knob Lake before and after complete fish removal, and in two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin. *Daphnia* biomass in Knob Lake was undetectable until 2002. The bottom panel shows the dynamics of adjusted *L. signicauda* biomass, the ratio of biomass in Knob Lake to mean biomass in the control lakes. Panel to the right indicates that there was no significant difference in mean adjusted *L. signicauda* biomass ( $\pm 1$  SE) between fish (1996–1997) and no-fish (1998–2003) periods in Knob Lake.

(Fig. 6) despite indications that the phytoplankton were less severely P limited after *Daphnia* reestablishment. Phosphatase activities in Square Lake were about double the levels in the control lakes before *Daphnia* reestablishment and decreased to levels similar to the controls after *Daphnia* reestablishment (Fig. 7). In this case, adjusting responses for control dynamics was not crucial simply because phosphatase activity showed little interannual variation in the controls.

Changes in the abundance of nonplanktonic consumers after fish removal constitute a potential confounding factor that could influence the response of the phytoplankton to fish manipulation. Previous studies have indicated that introduced trout have major negative impacts on frogs and benthic macroinvertebrates in alpine lakes of the Sierra Nevada (Bradford et al. 1998; Knapp and Matthews 2000; Knapp et al. 2001). Thus, it is possible that increases in tadpoles and/or benthic invertebrates could have resulted in enough of an increase in P recycling from benthic sources to make up for the loss of P supply from fish. This might have prevented both a decrease in phytoplankton biomass and an increase in P limitation in response to fish removal in Knob and No Good Lakes. This mechanism cannot account for the lack of response in Knob Lake (Fig. 3, 4) because (1) no tadpoles were observed in Knob Lake until 2002, 5 yr after fish removal, and (2) benthic invertebrate biomass did not increase

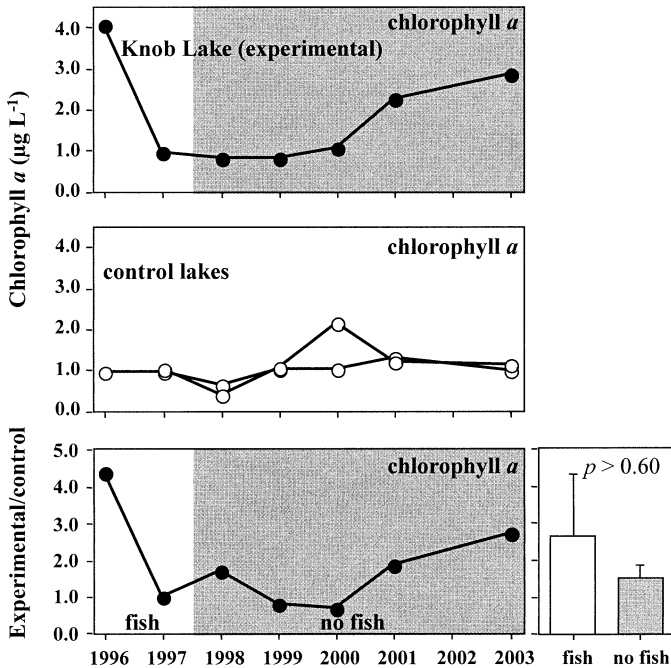


Fig. 3. Dynamics of Chl *a* in Knob Lake before and after complete fish removal, and in two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin. The bottom panel shows the dynamics of adjusted Chl *a*, the ratio of Chl *a* in Knob Lake to mean Chl *a* in the control lakes. Panel to the right indicates that there was no significant difference in mean adjusted Chl *a* ( $\pm 1$  SE) between fish (1996–1997) and no-fish (1998–2003) periods in Knob Lake.

in Knob Lake until 2001, 4 yr after fish removal (Fig. 8). In No Good Lake, no tadpoles were ever observed, but benthic invertebrate biomass increased substantially in the first year after fish were removed (mean adjusted biomass: 1999–2000 = 0.13, SD = 0.12; 2001 = 2.29). As a result, in No Good Lake, we cannot rule out the possibility that increased rates of nutrient excretion by benthic invertebrates prevented a decrease in P availability after fish removal (but see additional evidence regarding estimates of P excretion by fish, below). In Square Lake, the declines in adjusted Chl *a* that occurred concomitant with the rise of *Daphnia* persisted from 1999–2003 (Fig. 6), despite apparent increases in adjusted benthic invertebrate biomass after 2000 (Fig. 8).

To complete our assessment of the importance of P recycling by fish in these lakes, we compared estimates of P excretion by fish in each lake to estimates of the P demand of the phytoplankton and to estimates of P excretion by the zooplankton. Estimates of P excretion by fish populations ranged from a minimum of  $7 \mu\text{g P m}^{-3} \text{d}^{-1}$  in Square Lake to a maximum of  $18 \mu\text{g P m}^{-3} \text{d}^{-1}$  in No Good Lake. Across all five lakes, P excretion by fish was only 3–10% of the median P demand of the phytoplankton (Fig. 9), supporting the general conclusion that P excretion by fish populations provided only a very small fraction of the phosphate needed by the phytoplankton to sustain measured productivity rates. This result can be considered conservative because our methods probably overestimated fish excretion and underestimated phytoplankton demand. Our conservative esti-

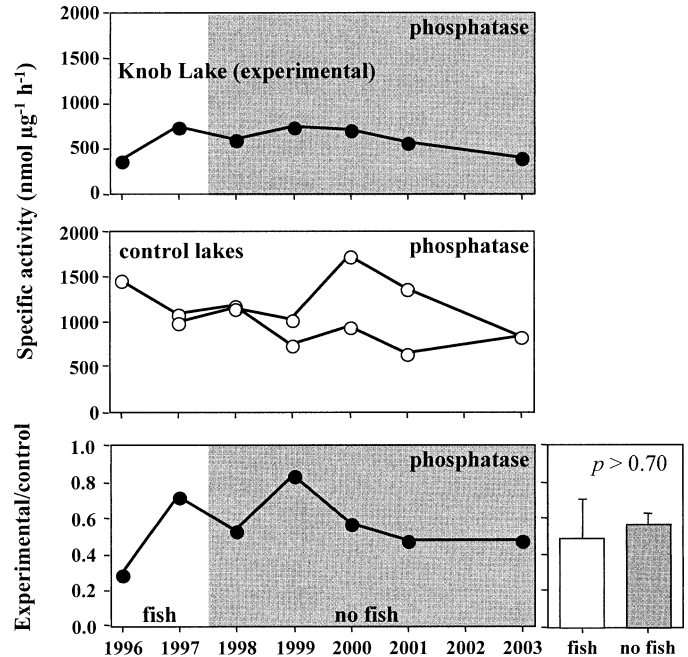


Fig. 4. Dynamics of Chl *a*-specific phosphatase activity in Knob Lake before and after complete fish removal, and in two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin. The bottom panel shows the dynamics of adjusted phosphatase activity, the ratio of phosphatase activity in Knob Lake to mean phosphatase activity in the control lakes. Panel to the right indicates that there was no significant difference in mean adjusted phosphatase activity ( $\pm 1$  SE) between fish (1996–1997) and no-fish (1998–2003) periods in Knob Lake.

mates of median P excretion by the zooplankton ranged from  $215\text{--}710 \mu\text{g P m}^{-3} \text{d}^{-1}$  across the five lakes, values that were more than order of magnitude higher than P excretion by fish and seemingly sufficient to meet the P demands of the phytoplankton (Fig. 9).

Discussion

The delayed response of *Daphnia* to fish removal in Knob Lake (Fig. 2) relative to Square Lake (Fig. 6) may have been

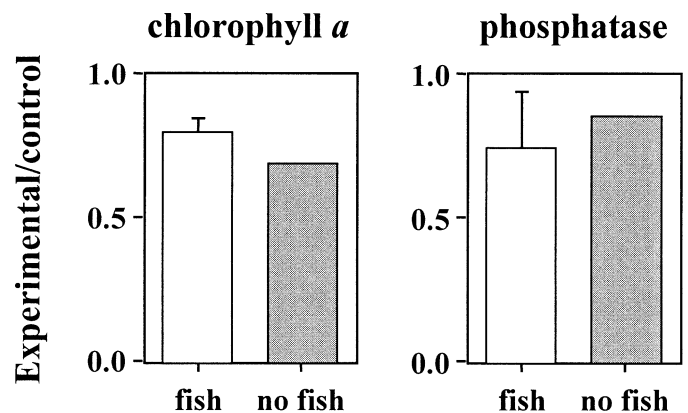


Fig. 5. Mean adjusted Chl *a* and Chl *a*-specific phosphatase activity for fish (1999–2000,  $\pm 1$  SE) and no-fish (2001) years in No Good Lake.

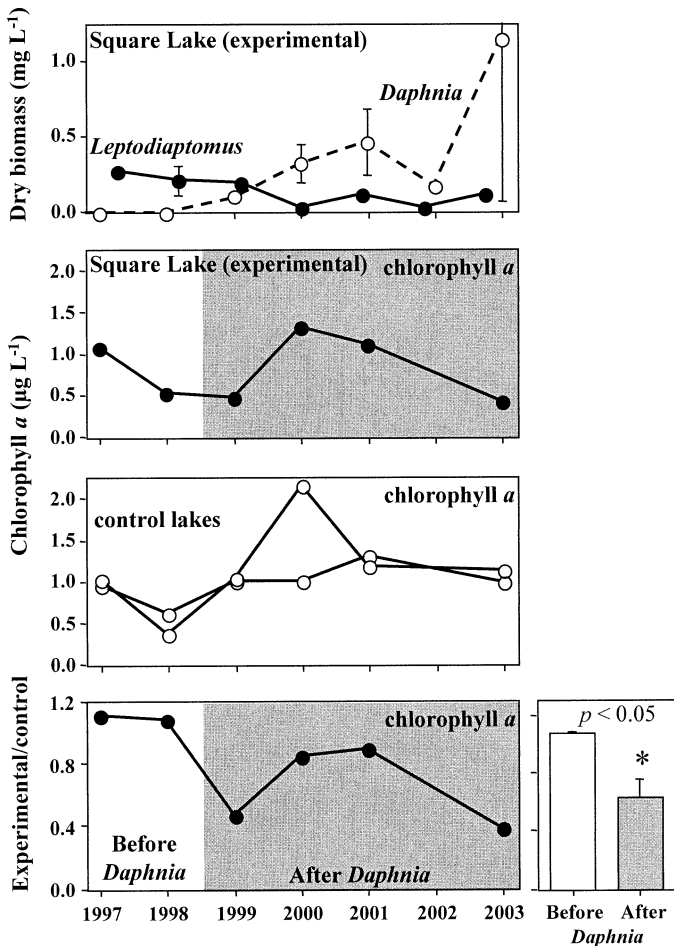


Fig. 6. Dynamics of Chl *a* and *Daphnia middendorffiana* biomass ( $\pm 1$  SE) during the recovery of the *Daphnia* population in fishless Square Lake, and the dynamics of Chl *a* in two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin. The bottom panel shows the dynamics of adjusted Chl *a*, the ratio of Chl *a* in Square Lake to mean Chl *a* in the control lakes. Panel to the right indicates that there was a significant change in mean adjusted Chl *a* ( $\pm 1$  SE) after *Daphnia* reestablishment in Square Lake.

a function of a smaller egg bank in Knob Lake (Sarnelle and Knapp 2004). Regardless of the cause, the difference in *Daphnia* response among the experimental lakes enabled a comparison of the effects of nutrient recycling by fish and grazing by *Daphnia* at the whole-lake scale. The lack of phytoplankton response to fish removal in both Knob and No Good Lakes in the absence of increases in zooplankton grazing, coupled with the negative response of both Chl *a* and phosphatase activity to the reestablishment of *Daphnia* in Square Lake (Figs. 6, 7), suggest that *Daphnia*'s ability to influence phytoplankton biomass and alleviate phytoplankton P limitation was considerably stronger than that of fish in these lakes. This conclusion must be tempered by the fact that there was high variance in both response variables during the 2-yr premanipulation period in Knob Lake (Figs. 3, 4). Thus, it is important to also examine the specific dynamics of Chl *a* and phosphatase activity in Knob Lake to

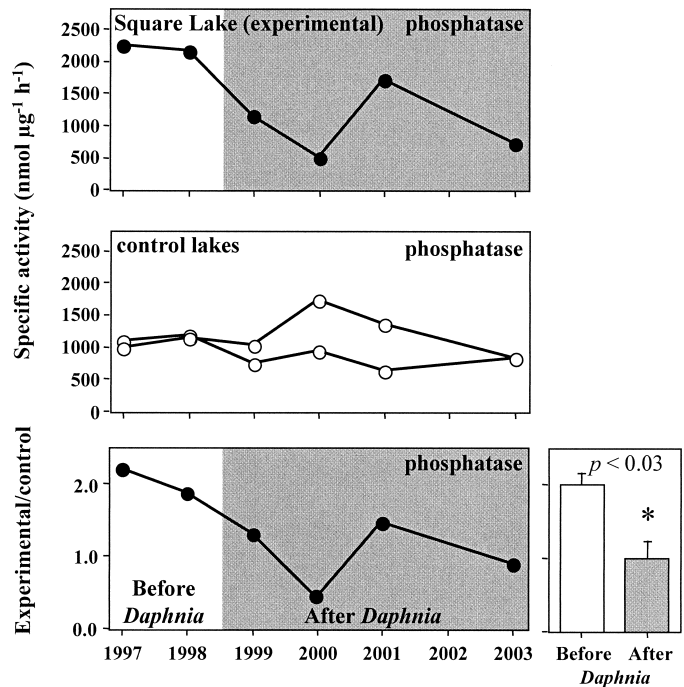


Fig. 7. Dynamics of Chl *a*-specific phosphatase activity during the recovery of the *Daphnia* population in fishless Square Lake, and the dynamics of Chl *a*-specific phosphatase activity in two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin. The bottom panel shows the dynamics of adjusted phosphatase activity, the ratio of phosphatase activity in Square Lake to mean phosphatase activity in the control lakes. Panel to the right indicates that there was a significant change in mean adjusted phosphatase activity ( $\pm 1$  SE) after *Daphnia* reestablishment in Square Lake.

assess whether high premanipulation variance could be responsible for the apparent lack of response to fish removal in this lake. It is reasonable to expect that the complete elimination of a major source of P (e.g., fish excretion) would cause an immediate (i.e., during the next growth season) increase in P deficiency and decrease in phytoplankton biomass. Instead, phosphatase activity declined slightly in the first summer after fish removal in Knob Lake (Fig. 4). Likewise, there was a 75% increase in adjusted Chl *a*, as well as essentially no change in unadjusted Chl *a*, in the first summer after fish removal (Fig. 3). These results provide no indication that the complete loss of P supply from fish excretion had an impact on the phytoplankton. This conclusion is further supported by estimates of P excretion by each fish population (7 and 18 µg P m<sup>-3</sup> d<sup>-1</sup>), which were only a small fraction of phytoplankton P demand and zooplankton excretion (Fig. 9).

We found no evidence for effects of P recycling by fish on phytoplankton biomass or P limitation despite several factors that predispose our experiment toward finding an effect of the complete loss of P excretion by fish. First, the study lakes are all low in P (Table 1) and have high light penetration, so phytoplankton growth should be highly sensitive to changes in P supply (Sterner et al. 1997). Second, zooplanktivorous fish abundance was not low in the fish-

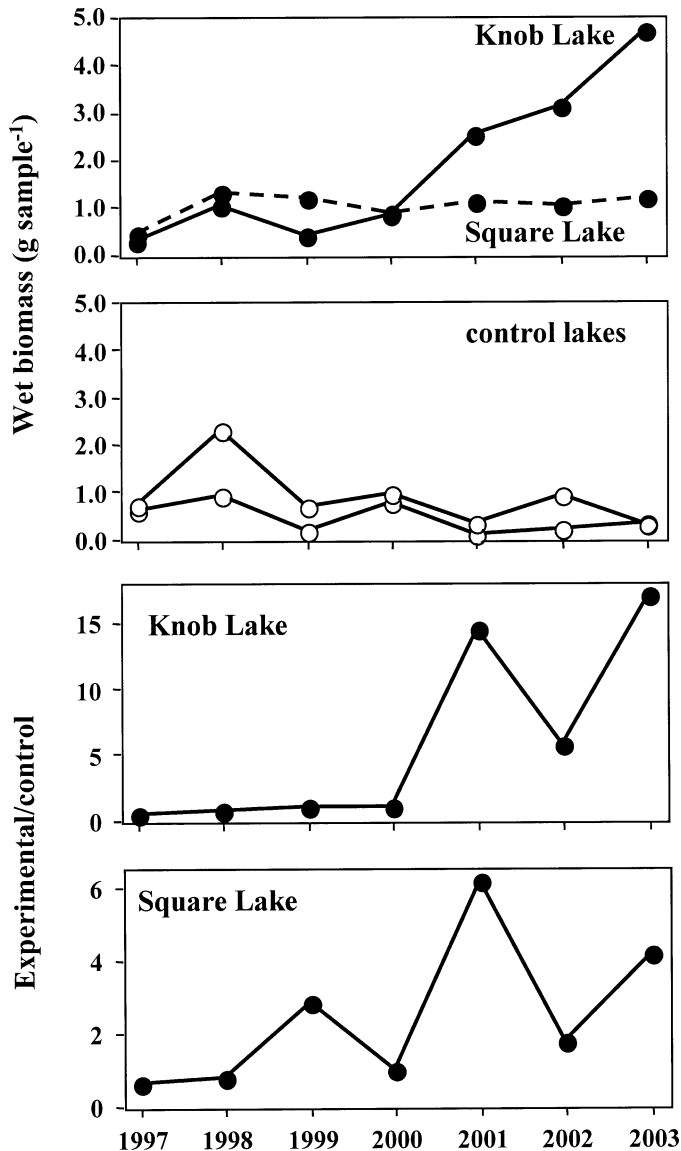


Fig. 8. Dynamics of total benthic macroinvertebrate biomass in Knob Lake, Square Lake, and two control lakes (Mesa and Lower Desolation Lakes) located in the same drainage basin (upper panels), and the ratios of benthic macroinvertebrate biomass in Knob Lake and Square Lake to mean benthic macroinvertebrate biomass in the control lakes (lower panels).

removal lakes at the initiation of the manipulation relative to similar alpine lakes in the Sierra Nevada (Schindler et al. 2001). Fish biomass was  $0.10 \text{ kg km}^{-2}$  in Knob Lake and  $0.19 \text{ kg km}^{-2}$  in No Good Lake at the time of fish removal. These values are somewhat lower than what would be predicted for temperate lakes with the same TP concentrations ( $0.20\text{--}0.26 \text{ kg km}^{-2}$ ) (Hanson and Leggett 1981), but even in the unlikely case that alpine lakes can support the same fish biomass as temperate lakes at the same nutrient levels, excretion by such higher fish stocks ( $18\text{--}23 \mu\text{g P m}^{-3} \text{ d}^{-1}$ , using the equation in Schindler et al. 2001) would still not constitute a substantial fraction of the P demand of the phytoplankton in these lakes (Fig. 9). Zooplanktivorous fish

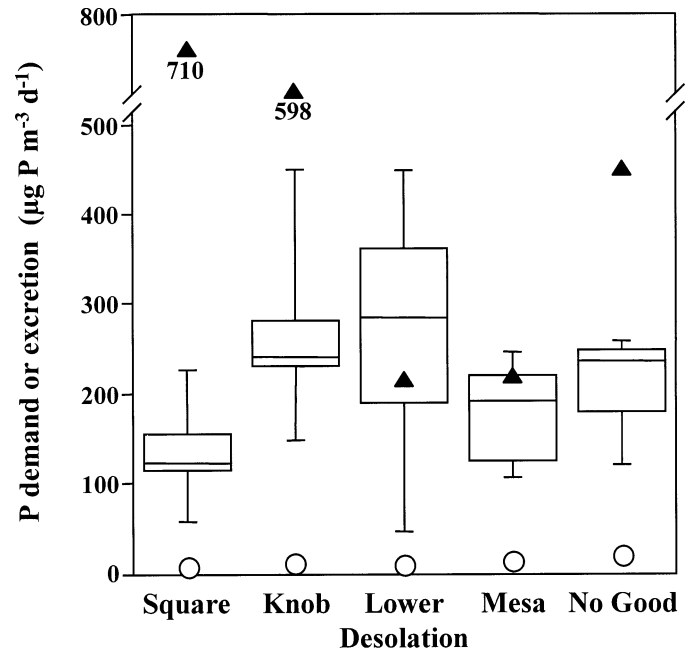


Fig. 9. Distributions of phytoplankton P demand (box plots), median P excretion estimates for zooplankton assemblages (triangles), and P excretion estimates for fish populations (circles,  $\pm 1$  SE) in each lake. Boxes delineate upper and lower quartiles of the P demand data, bars within the boxes are medians, and bars extending above and below the boxes are maxima and minima. Standard errors of fish excretion estimates are within the symbols. Numbers below triangles denote actual estimates of zooplankton P excretion for Square and Knob Lakes.

abundance in these lakes was also high enough to cause the complete extinction of large zooplankton species after fish stocking (Sarnelle and Knapp 2004). Third, during fish removals we prevented the experimental lakes from being fertilized with P, via the decomposition of fish carcasses, which might have muted any increases in P limitation. Fourth, the fish in these lakes feed primarily on benthic and terrestrial invertebrates (Schindler et al. 2001) when large zooplankton have been completely eliminated, so a large fraction of the P they recycle is in the form of “new” P from nonplanktonic sources (note that in Sierra Nevada lakes deeper than 8 m and with low fish densities, in which introduced trout and large zooplankton sometimes coexist, trout are zooplanktivorous/benthivorous) (Schindler et al. 2001). This again should make it more likely to find effects of fish recycling on the phytoplankton (Carpenter et al. 1992; Schindler et al. 2001). Despite these factors, we observed little or no effect of P recycling by fish on phytoplankton biomass or P limitation.

A strong reduction in Chl *a* after the reappearance of *Daphnia* in Square Lake (Fig. 6) was somewhat surprising given that *Daphnia* effects on phytoplankton biomass tend to be relatively small in low-productivity lakes (Sarnelle 1992). This appears to be the first experimental evidence at the whole-lake scale of a cascading effect of fish manipulation on phytoplankton biomass in alpine lakes. In support of this conclusion, estimates of mortality rates inflicted on the phytoplankton by zooplankton grazing in Square Lake

(sum of *L. signicauda* and *D. middendorffiana* grazing, mean = 0.47 d<sup>-1</sup>) were comparable to estimates of phytoplankton specific growth rate (mean = 0.56 d<sup>-1</sup>). There was no significant increase in zooplankton grazing after *Daphnia* re-appearing (mean = 0.40 d<sup>-1</sup> before *Daphnia*, mean = 0.50 d<sup>-1</sup> after *Daphnia*), leading us to suspect that *Daphnia*'s ability to consume a wider range of particles may have been the primary mechanism leading to the reduction in total phytoplankton biomass.

A decrease in the severity of P limitation after *Daphnia* reestablishment in Square Lake (Fig. 7) was also somewhat surprising, in light of species-specific stoichiometry of nutrient recycling by zooplankton, and the fact that *Daphnia* replaced *Leptodiatomus* as the dominant herbivore (Fig. 6). Stoichiometric considerations would suggest that replacement of a diaptomid copepod, which should have a relatively low need for P, by *Daphnia*, which has a relatively high need for P (Hessen and Lyche 1991), would lead to relatively less P excretion by the zooplankton (all else being equal), and so greater P deficiency in the phytoplankton, after *Daphnia* reestablishment (Brett et al. 1994). However, we note that the literature is equivocal as to whether cladocerans have significantly lower mass-specific P excretion rates than do copepods (Carrillo et al. 1996), and that zooplankton biomass was higher after *Daphnia* reestablishment (mean total biomass: 0.24 mg L<sup>-1</sup> before *Daphnia*, 0.54 mg L<sup>-1</sup> after *Daphnia*) in Square Lake, although this difference was not statistically significant ( $p > 0.18$ ). We suggest that reduced phytoplankton P limitation after *Daphnia* reestablishment in Square Lake may have resulted from little net change in P recycling by zooplankton coupled with reduced demand by phytoplankton (Fig. 6) and perhaps bacteria. We did not measure the latter, but it is well-known that *Daphnia* are much more efficient consumers of bacteria than are diaptomid copepods (Sterner 1989), so a decline in bacterial biomass after *Daphnia* reestablishment is possible (Zöllner et al. 2003).

Our aim was to test the hypothesis that recycling by zooplanktivorous fish is a major factor, relative to zooplankton grazing, influencing total phytoplankton biomass in trophic cascade experiments. We do not claim that fish recycling is negligible under all circumstances. We explicitly compared fish recycling effects to the effects of *Daphnia* grazing because changes in *Daphnia* are considered to be a prerequisite for strong trophic cascades (Leibold 1989). In systems that lack *Daphnia*, the effect of zooplankton grazing may be small or nonexistent, such that a small effect of fish recycling may appear large by comparison. We were unable to statistically demonstrate any effect of fish recycling (in contrast to significant effects of *Daphnia*), but smaller-scale experiments are more likely to reveal effects of small magnitude given lower residual error and greater replication (Schindler 1992; Vanni and Layne 1997; Attayde and Hansson 2001). In addition, recycling by fish that feed on benthic detritus has the potential to supply much larger amounts of nutrients to the phytoplankton relative to carnivorous fish, via either direct excretion or disturbance of the sediment (Brabrand et al. 1990; Schaus and Vanni 2000), because such fish feed at a lower trophic level in addition to being a conduit for the transfer of nutrients from the benthic zone to the

pelagic zone. We also recognize that there may be subtle effects of fish recycling on phytoplankton species composition (Schindler 1992; Vanni and Layne 1997; Attayde and Hansson 2001) that were beyond the scope of the present study. The trophic cascade, however, is typically defined in terms of effects on the total biomass of primary producers, the currency that we employed.

We recognize that whole-lake experiments have limitations, most notably with respect to the strength of inferences that can be made based on observations before and after manipulation (Carpenter 1990). We presented the results of statistical tests to provide a basis for judging whether changes subsequent to fish removal or *Daphnia* reestablishment (relative to controls) were large compared with typical inter-annual variation. That is, we asked whether the changes we observed were likely to be larger than were those expected by chance alone. These tests are subject to well-known limitations (Schmitt and Osenberg 1996) and, consequently, should be viewed only as part of the evidence underlying our inferences about the relative importance of P excretion by fish versus *Daphnia* grazing. Our conclusion that the phytoplankton were not appreciably influenced by the complete loss of P excretion from fish is based on multiple lines of evidence: (1) in Knob and No Good Lakes, there was no significant change in Chl *a* and phosphatase activity in response to complete fish removal (Figs. 3–5); (2) in Knob Lake, the timing of changes in benthic consumers indicated that increased recycling by the benthos was not compensating for the loss of P supply from fish in the first 3 yr after manipulation (Fig. 8); and (3) estimates of P excretion by fish were small relative to the P demands of the phytoplankton and P excretion by zooplankton (Fig. 9). Our results are congruent with some studies that compare P recycling by zooplanktivorous fish to phytoplankton demand or other sources of P supply (Kitchell et al. 1975; Nakashima and Leggett 1980; Boers et al. 1991), and provide more definitive answers to the questions posed by Schindler et al. (2001) about the role of nutrient recycling by fish in alpine lakes. In contrast, our conclusions are at odds with the results of several enclosure experiments (Schindler 1992; Vanni and Layne 1997; Attayde and Hansson 2001). The latter disparity may stem from differences in the magnitude of fish excretion across lakes, but the possibility also exists that the disparity is a consequence of differences in experimental scale or methodology. The present study provides the only experimental assessment of the effects of P excretion by fish at the whole-lake scale.

## References

- ATTAYDE, J. L., AND L. A. HANSSON. 2001. The relative importance of fish predation and excretion effects on planktonic communities. *Limnol. Oceanogr.* **46**: 1001–1012.
- BOERS, P., L. V. BALLEGOOIJEN, AND J. UUNK. 1991. Changes in phosphorus cycling in a shallow lake due to food web manipulation. *Freshw. Biol.* **25**: 9–20.
- BRABRAND, A., B. A. FAAFENG, AND J. P. M. NILSSEN. 1990. Relative importance of phosphorus supply to phytoplankton production: Fish excretion versus external loading. *Can. J. Fish. Aquat. Sci.* **47**: 364–372.
- BRADFORD, D. F., S. D. COOPER, T. M. J. JENKINS, K. W. KRATZ,

- O. SARNELLE, AND A. D. BROWN. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. *Can. J. Fish. Aquat. Sci.* **55**: 2478–2491.
- BRETT, M. T., AND C. R. GOLDMAN. 1996. A meta-analysis of the freshwater trophic cascade. *Proc. Natl. Acad. Sci. USA* **93**: 7723–7726.
- BRETT, M. T., K. WIACKOWSKI, F. S. LUBNOW, A. MUELLER SOLGER, J. J. ELSER, AND C. R. GOLDMAN. 1994. Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. *Ecology* **75**: 2243–2254.
- CARPENTER, S. R. 1990. Large-scale perturbations: Opportunities for innovation. *Ecology* **71**: 2038–2043.
- . 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**: 677–680.
- CARPENTER, S. R., J. R. HODGSON, AND J. F. KITCHELL. 1985. Cascading trophic interactions and lake productivity. *Bioscience* **35**: 634–639.
- CARPENTER, S. R. AND OTHERS 1987. Regulation of lake primary productivity by food web structure. *Ecology* **68**: 1863–1876.
- CARPENTER, S. R., X. HE, J. R. HODGSON, C. E. KRAFT, P. A. SORRANO, AND R. WRIGHT. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *Am. Nat.* **140**: 781–798.
- CARRILLO, P., I. RECHE, AND L. CRUZ-PIZARRO. 1996. Intraspecific stoichiometric variability and the ratio of nitrogen to phosphorus resupplied by zooplankton. *Freshw. Biol.* **36**: 363–374.
- CRUMP, M. L., AND N. J. SCOTT, JR. 1994. Visual encounter surveys, p. 84–91. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek and M. S. Foster [eds.], *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian.
- CRUMPTON, W. G., T. M. ISENHART, AND P. D. MITCHELL. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. *Limnol. Oceanogr.* **37**: 907–913.
- ENGLUND, G., O. SARNELLE, AND S. D. COOPER. 1999. The importance of data-selection criteria: meta-analysis of stream predation experiments. *Ecology* **80**: 1132–1141.
- GOLDMAN, C. R., A. JASSBY, AND T. POWELL. 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. *Limnol. Oceanogr.* **34**: 310–323.
- HANSON, J. M., AND W. C. LEGGETT. 1981. Empirical prediction of fish biomass and yield. *Can. J. Fish. Aquat. Sci.* **39**: 257–263.
- HESSEN, D. O., AND A. LYCHE. 1991. Inter- and intra-specific variations in zooplankton element composition. *Arch. Hydrobiol.* **121**: 343–353.
- HILL, W. R., AND H. L. BOSTON. 1991. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnol. Oceanogr.* **36**: 1375–1389.
- KALFF, J. 2002. *Limnology: Inland water ecosystems*. Prentice-Hall.
- KITCHELL, J. F., J. F. KOONCE, AND P. S. TENNIS. 1975. Phosphorus flux through fishes. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **19**: 2478–2484.
- KNAPP, R. A. 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. *Biol. Conserv.* **121**: 265–279.
- KNAPP, R. A., AND K. R. MATTHEWS. 1998. Eradication of nonnative fish by gill-netting from a small mountain lake in California. *Restoration Ecol.* **6**: 207–213.
- KNAPP, R. A., K. R. MATTHEWS, AND O. SARNELLE. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecol. Monogr.* **71**: 401–421.
- KNOEHEL, R., AND L. B. HOLTBY. 1986. Construction and validation of a body-length-based model for the prediction of cladoceran filtering rates. *Limnol. Oceanogr.* **31**: 1–16.
- KRAFT, C. E. 1992. Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. *Can. J. Fish. Aquat. Sci.* **49**: 2596–2604.
- LEIBOLD, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* **134**: 922–949.
- MAZUMDER, A., W. D. TAYLOR, D. J. MCQUEEN, D. R. S. LEAN, AND N. R. LAFONTAINE. 1990. A comparison of lakes and lake enclosures with contrasting abundances of planktivorous fish. *J. Plankton Res.* **12**: 109–124.
- MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.* **10**: 280–282.
- MURPHY, J., AND L. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* **27**: 31–36.
- NAKASHIMA, B. S., AND W. C. LEGGETT. 1980. The role of fishes in the regulation of phosphorus availability in lakes. *Can. J. Fish. Aquat. Sci.* **37**: 1540–1549.
- NUSCH, E. A. 1980. Comparison of different methods for chlorophyll and phaeopigment determination. *Arch. Hydrobiol. Beih.-Erf. Ergebnisse der Limnologie* **14**: 14–36.
- PETTERSSON, K. 1980. Alkaline phosphatase activity and algal surplus phosphorus as phosphorus-deficiency indicators in Lake Erken. *Arch. Hydrobiol.* **89**: 54–87.
- POST, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* **47**: 554–560.
- REINERTSEN, H., A. JENSEN, J. I. KOKSVIK, A. LANGELAND, AND Y. OLSEN. 1990. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. *Can. J. Fish. Aquat. Sci.* **47**: 166–173.
- SARNELLE, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* **73**: 551–560.
- . 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. *Ecol. Monogr.* **63**: 129–149.
- . 1999. Zooplankton effects on vertical particulate flux: Testable models and experimental results. *Limnol. Oceanogr.* **44**: 357–370.
- SARNELLE, O., AND R. A. KNAPP. 2004. Zooplankton recovery after fish removal: Limitations of the egg bank. *Limnol. Oceanogr.* **49**: 1382–1392.
- SCHAUS, M. H., AND M. J. VANNI. 2000. Effects of gizzard shad on phytoplankton and nutrient dynamics: Role of sediment feeding and fish size. *Ecology* **81**: 1701–1719.
- SCHINDLER, D. E. 1992. Nutrient regeneration by sockeye salmon (*Oncorhynchus nerka*) and subsequent effects on zooplankton and phytoplankton. *Can. J. Fish. Aquat. Sci.* **49**: 2498–2506.
- SCHINDLER, D. E., J. F. KITCHELL, X. HE, S. R. CARPENTER, J. R. HODGSON, AND K. L. COTTINGHAM. 1993. Food-web structure and phosphorus cycling in lakes. *Trans. Am. Fish. Soc.* **122**: 756–772.
- SCHINDLER, D. E., R. A. KNAPP, AND P. R. LEAVITT. 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. *Ecosystems* **4**: 308–321.
- SCHMITT, R. J., AND C. W. OSENBURG. 1996. *Detecting ecological impacts: Concepts and applications in coastal habitats*. Academic Press.
- SEBER, G. A. F. 1982. *The estimation of animal abundance and related parameters*, 2nd ed. Macmillan.
- SHOSTELL, J., AND P. A. BUKAVECKAS. 2004. Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. *Aquatic Ecol.* **38**: 359–373.
- SHURIN, J. B. AND OTHERS. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* **5**: 785–791.
- SICKMAN, J. O., AND J. M. MELACK. 1992. Photosynthetic activity

- of phytoplankton in a high altitude lake (Emerald lake, Sierra Nevada, California). *Hydrobiologia* **230**: 37–48.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*, 2nd ed. W. H. Freeman.
- STERNER, R. W. 1989. The role of grazers in phytoplankton succession, p. 107–170. *In* U. Sommer [ed.], *Plankton ecology: succession in plankton communities*. Springer-Verlag.
- STERNER, R. W., J. J. ELSER, E. J. FEE, S. J. GUILDFORD, AND T. H. CHRZANOWSKI. 1997. The light-nutrient ratio in lakes: The balance of energy and materials affects ecosystem structure and process. *Am. Nat.* **150**: 663–684.
- STRONG, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**: 747–754.
- THOMAS, W. H., B. C. CHO, AND F. AZAM. 1991. Phytoplankton and bacterial production and biomass in subalpine Eastern Brook Lake, Sierra Nevada, California, II: Comparison with other high-elevation lakes. *Arctic Alpine Res.* **23**: 296–302.
- VANNI, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annu. Rev. Ecol. Syst.* **33**: 341–370.
- VANNI, M. J., AND C. D. LAYNE. 1997. Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. *Ecology* **78**: 21–40.
- ZÖLLNER, E., B. SANTER, M. BOERSMA, H.-G. HOPPE, AND K. JÜRGENS. 2003. Cascading predation effects of *Daphnia* and copepods on microbial food web components. *Freshw. Biol.* **48**: 2174–2193.

*Received: 11 March 2005*

*Accepted: 19 July 2005*

*Amended: 2 August 2005*