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Importance of zooplankton for the persistence of a deep chlorophyll layer: A limnocorral experiment

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Abstract

A variety of interacting physical, chemical, and biological hypotheses have been proposed to explain the formation of deep chlorophyll layers (DCL). We used an experiment to test the importance of zooplankton grazing and nutrient transport as factors maintaining the DCL. In oligotrophic Yellow Belly Lake (Sawtooth Mountains, central Idaho), which has a DCL, we compared changes in the chlorophyll profiles in 17-m-deep limnocorrals with and without crustacean zooplankton. ^{15}N ammonia and rhodamine dye were added to the epilimnion or metalimnion of the corrals to measure nutrient transport and diffusivity. In the limnocorrals with zooplankton, epilimnetic macrozooplankton biomass was 2× higher and estimated grazing rates were 1.8× higher than those in the metalimnion. After 11 d, chlorophyll levels in the zooplankton treatment declined 72% in the epilimnion but only 53% in the metalimnion, leading to the maintenance of the DCL. In the treatment without zooplankton, the epilimnetic chlorophyll increased 11% and the metalimnetic algal levels decreased 41%, resulting in the formation of an epilimnetic chlorophyll maxima. Biologically mediated movement of ^{15}N from the epilimnion and metalimnion was downward, into either the metalimnion or the hypolimnion. Turbulent movement measured with rhodamine was high in the limnocorrals, and presumably ^{15}N also moved into adjoining strata through this process. Grazing, however, coupled with a downward movement of nutrients via sedimentation into the lower strata appears to explain the persistence of the DCL.

In oligotrophic lakes and oceans, large algal populations frequently develop below the surface mixed layer, either in a sharp peak (deep chlorophyll maxima) or in a broad deep chlorophyll layer (DCL). Even though net primary production in these layers can account for up to 72% of the productivity on an areal basis (Moll and Stoermer 1982), we do not understand why these layers form. DCLs occur in thermally stratified waters where there is sufficient light and nutrients for net algal growth (Longhurst and Harrison 1989), and they are frequently composed of mobile species specialized to live in low-light regimes. In oligotrophic lakes, sufficient light penetrates into the metalimnion, but the source of the ''new'' nutrients (Dugdale and Goering 1967) that supply elements for algal growth in the DCLs is unclear. The predominant hypothesis, at least for the oceans, is that phytoplankton grow in DCLs because diffusive processes provide nutrients to the photic zone from the underlying nutrient-rich stratum (Fasham et al. 1985). It is not clear, however, whether diffusive processes provide sufficient nutrients to DCLs in the oceans (Carter et al. 1986; Planas et al. 1999) or in lakes (Fee et al. 1977; Pick et al. 1984). Many other alternative hypotheses have been proposed to explain the formation of DCLs (Venrick et al. 1972; Cullen 1982; Gasol et al. 1992). These include (1) an increase in the chlorophyll : cell ratio in the deep low-light environment, (2) passive sedimentation of epilimnetic phytoplankton that accumulate in the DCL because of slower sedimentation rates there, (3) accumulation of mobile flagellates that are avoiding predation in the epilimnion, (4) mixotrophy of phytoplankton in the DCLs, and (5) low respiratory and grazing losses in the DCL coupled with low but positive algal growth. Several processes may interact to control the distribution and magnitude of the DCL (Richerson et al. 1978).

Macrozooplankton grazing and excretion may also affect nutrient movements and influence the formation of DCLs. Fee (1976) and St. Amand (1990) suggested that even when metalimnetic algae are light limited and have low production, the DCL can develop because of lower grazing losses, respiration, and sedimentation rates than those of phytoplankton in the epilimnion. Fee et al. (1977) suggested that nutrient supply for the DCL comes from metalimnetic mineralization of sedimenting epilimnetic particles, but they did not specify whether algal sedimentation or fecal materials derived from grazing dominates this process.

The seasonal sequence of nutrient import and distribution into lakes may also interact with zooplankton grazing to pro-

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Table 1. Summer limnological conditions in Yellow Belly Lake, Idaho.

Parameter	Epilimnion	Metalimnion
Chlorophyll *a* (μg L^{-1})	0.5	3–5
Total P (μmol L^{-1})	0.3	0.3
Total N (μmol L^{-1})	4.0	9.8
Dissolved inorganic N (μmol L^{-1})	<2.0	<4.2
Soluble reactive P (μmol L^{-1})	<0.06	<0.09
Dissolved inorganic C (mmol L^{-1})	0.1	
Phytoplankton biovolume (μm^3 ml^{-1})	50,000	100,000

Data are taken primarily from Steinhart et al. (1994).

mote DCLs. New nutrients are particularly important for the spring algal bloom that takes place after spring runoff and lake mixing bring nutrients to the epilimnion. Subsequently, an epilimnetic depletion of nutrients driven by high zooplankton densities leads to a clear-water phase (Lampert 1978), with zooplankton causing a downward movement of nutrients (Dini et al. 1987; Angeli et al. 1995; Hays et al. 1997). Zooplankton may feed on the phytoplankton-rich epilimnetic layers during the night and then migrate to the hypolimnion during the day, where trapped excretion products and egesta enrich hypolimnetic waters and increase the primary productivity (Fee 1976). However, in systems with DCLs in the meta- and hypolimnion, this same argument would suggest that zooplankton that feed and live in the deep waters during the day might move nutrients upward when they migrate to the surface at night. In spite of these speculations on how zooplankton distribution may influence the formation of a DCL through grazing and nutrient transport, no experiments have been done to study these processes in lakes.

Here, we describe a mesocosm experiment performed to test the importance of zooplankton in the maintenance of a DCL in an oligotrophic mountain lake. We used epilimnetic and metalimnetic ^{15}N and ^{13}C injections in 17-m-deep mesocosms with and without macrozooplankton to determine how zooplankton grazing, diel vertical migration (DVM), and zooplankton-mediated changes in nutrient sedimentation rates affected the vertical transport of nutrients and favored the persistence of a DCL.

Study site

Yellow Belly Lake is a small (0.73 km^2), dimictic, oligotrophic lake formed by glaciers in the granitic Sawtooth Mountains of Idaho at 44°0′N, 114°53′W and 2,157 m above sea level. The lake is normally ice free from late May through November. Mean and maximum depths are 14 and 26 m, respectively. The mean summer epilimnetic chlorophyll *a* level is near 0.5 μg L^{-1}, and nutrient concentrations are low (Table 1). In summer, both the epilimnion (0–6 m) and metalimnion (6–14 m) are colimited by nitrogen and phosphorus (Wurtsbaugh et al. 1997, 2001). In the summer, the photic zone extends into the hypolimnion (22 m; W. Wurtsbaugh unpubl. data), and a DCL is present in the meta- and hypolimnion (Budy et al. 1995*a*) where summer chlorophyll levels are elevated 3–4-fold. During our experiment, the weather was primarily sunny, and mean (±SD) solar radiation was 20,700 ± 3,900 kJ m^{-2} d^{-1}.

The biotic community in Yellow Belly Lake is typical of lakes in the Sawtooth Mountains and in many Rocky Mountain lakes. The summer phytoplankton community in the lake is usually dominated by Cryptophyceae, Chrysophyceae (*Dinobryon* sp.), and cyanobacterial picoplankton (*Synechococcus* sp.). The zooplankton community is dominated by the cladocerans *Daphnia rosea* followed by *Holopedium gibberum* and *Polyphemus pediculus* and the copepod *Leptodiaptomus tyrelli* (Budy et al. 1995*a*). There are also summer blooms of the colonial rotifer *Conochilus unicornis.* The main fish species are brook trout (*Salvelinus fontinalis*), cutthroat trout (*Oncorhynchus clarki*), and redside shiners (*Richardsonius balteatus*), but they are not abundant (Beauchamp et al. 1997).

Methods

We used eight limnocorrals and a factorial design to measure how the presence or absence of macrozooplankton affected the DCL and nutrient transport. The experiment was not designed to exactly duplicate conditions in Yellow Belly Lake but rather to establish a DCL and zooplankton community characteristic of lakes in the region. The experimental factors were zooplankton and injection depth. The levels (or treatments) for zooplankton were presence (+Z) and absence (−Z), with four limnocorrals for each. The levels for injection depth were epilimnetic or metalimnetic injection of nutrient and water mass tracers. For each zooplankton treatment, we injected a ^{15}N and rhodamine mixture into the epilimnion of two limnocorrals and into the metalimnion of the other two limnocorrals, thus providing two replicates for each combination among levels. The tracers helped us assess the vertical spread of the nitrogen due to zooplankton migration (upward and downward), sedimentation (downward), and physical factors (eddy diffusivity).

Limnocorral characteristics and phytoplankton—The limnocorrals were made with 200-μm-thick impermeable polyethylene tubes, 1 m in diameter and 18 m long, and contained 13 m^3 when deployed. They had three external rings at 5-m intervals to keep the corral walls straight and foam-filled flotation collars made of 0.20-m-diameter polyethylene pipe. They were tied off at 17 m, and a 30-kg weight was attached to the bottom. Prior to the experiment, the limno-

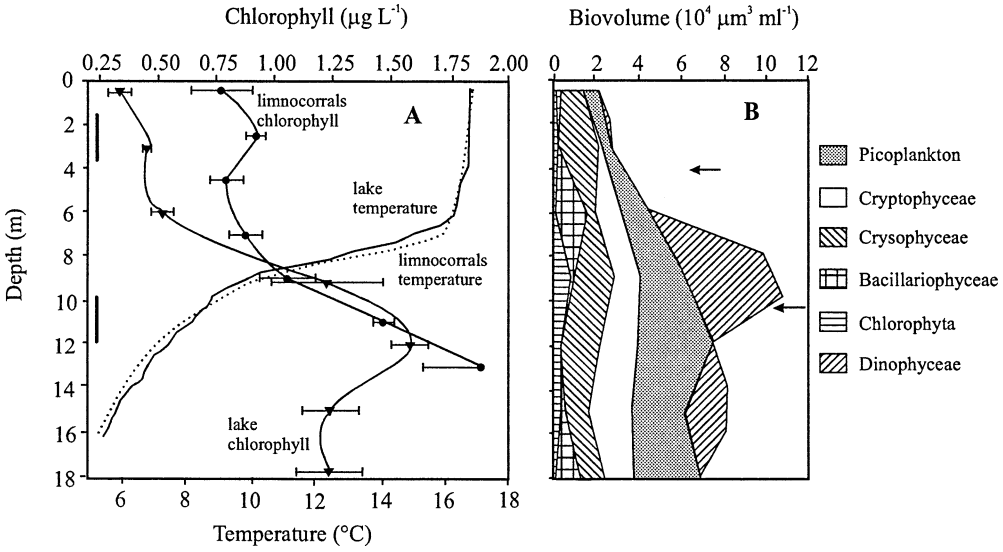

Fig. 1. (A) Mean initial limnocorral chlorophyll (μg chlorophyll *a* L^{-1}) and temperature (°C) in the −Z treatment, a temperature profile in Yellow Belly at the beginning of the experiment (15 August 1999), and a lake chlorophyll profile (5 August) near the time limnocorrals were filled. Vertical bars show the depths where stable isotopes and rhodamine tracers were injected in either the epilimnetic or the metalimnetic treatments. Error bars show the SD of two replicates from the lake. (B) Biovolumes of phytoplankton in Yellow Belly Lake calculated as the time-weighted average of samples taken on 5 July and 19 August 1999. Arrows mark the depth from which water was pumped to fill the limnocorrals.

corrals were soaked for 2 d in the lake to remove toxic substances, as suggested by O'Brien et al. (1992). The limnocorrals were then removed and washed with a high-pressure pump to remove any periphyton growth.

The limnocorrals were sealed and filled on 12 August 1999 when a DCL was present below 6 m in the lake. The limnocorrals were deployed into the lake and filled with a rotary pump by pumping water from 10 m for 10 min and then from 4 m for 6 min to create DCLs in the mesocosms. This filling procedure and the subsequent thermal equilibration with the lake established a 6-m-deep epilimnion, an 8-m-thick metalimnion, and a 3-m-thick hypolimnion (Fig. 1A). All limnocorrals were initially filled with water without macrozooplankton by filtering the pumped water consecutively through 153-μm and then 80-μm mesh. The corrals were tied together in an east–west line to ensure equal illumination of each corral. The terminal corrals in the line were moored from the flotation collars to the bottom (20 m depth).

Biomass estimates of lake phytoplankton were made from Lugol's-preserved samples that were concentrated in 100-ml Utermöhl chambers and counted at 1000X magnification. At least 100 individuals of dominant taxa were counted. Cyanobacteria picoplankton biomass estimates were made by filtering 10–15 ml aliquots on black, 0.2 μm polycarbonate filters, covering them with low-fluorescence immersion oil and a cover slip, and freezing at −20°C. They were enumerated with fluorescent microscopy at ×1,000 using a green (510–550 nm) excitation filter. Biovolumes of phytoplankton were estimated using geometric shapes (Hillebrand et al. 1999).

Chlorophyll, temperature, light, and Secchi depths were measured on 14 August. Profiles of in vivo chlorophyll and temperature were measured in each limnocorral and in the lake at midday with a Wetstar fluorometer mounted on a SeaBird model 25 CTD. Water transparency was measured using a 20-cm Secchi disc. Irradiance (photosynthetic active radiation [PAR]) at the bottom of the metalimnion (14 m) was estimated from Secchi depths for both treatments using regressions made for Sawtooth Valley lakes (Budy et al. 1995*a*). We used this measure rather than direct PAR measurements to describe water column light responses because the direct PAR was influenced by light passing through the lake water and then obliquely entering the limnocorrals.

Chlorophyll *a* was analyzed in the limnocorrals at the beginning (15 August) and at the end (26 August) of the experiment for samples collected with a diaphragm pump at depths of 0.5, 2.5, 4.5, 7, 9, 11, 13, and 16 m. Given the thermal stratification, sampling at these depths provided adequate representation of epilimnetic and metalimnetic characteristics. The sampling hose was allowed to clear for 1 min between samples to avoid contamination between sampling depths. Two replicate 50-ml aliquots from each depth were filtered on 0.45-μm cellulose acetate filters and frozen. Pigments were subsequently extracted for 24 h with 100% methanol, and chlorophyll *a* concentrations were determined with a Turner 10AU fluorometer (Welschmeyer 1994). The first three samples in the profile were averaged to represent the epilimnetic chlorophyll concentration. Metalimnetic chlorophyll levels were presented as the average of concentrations from 7 to 13 m. The last depth (16 m) was not included in the analysis because chlorophyll levels were unusually high. These high levels could have been the result of samples comprising not only seston but also sediments or

periphyton because of the funnel-shaped bottom of the limnocorral.

Zooplankton treatments and measurements—Zooplankton were added to the +Z treatment on 12 August, and their densities were measured at the end of the experiment. After thermal equilibrium between the lake and limnocorrals had been established, zooplankton were collected from the lake by an oblique tow with a 153-μm net from approximately 10 m to the surface, and aliquots of the sample were placed in every other corral in the line. We did not use a randomized design because the potential bias caused by an even placement is less than when all or most of the replicates of one treatment are in adjacent locations, as can happen when small numbers of units are assigned randomly (Hurlbert 1984). We added somewhat higher zooplankton biomasses than were present in the lake to accelerate any responses because we did not want a long experiment that would allow environmental conditions to diverge in replicate limnocorrals. To compare zooplankton biomasses in the lake and in all limnocorrals, 15-m-long vertical tows with a 0.16-m diameter net were taken at the end of the experiment. Zooplankton were counted and measured at $\times$20 magnification, and biomass was estimated using length–weight relationships (McCauley 1984). Mean ($\pm$SD) macrozooplankton biomass in the +Z treatments at the end of the experiment was 148 $\pm$ 39 μg L^{-1}, that was 60% daphnids and 40% copepods. The biomass in Yellow Belly Lake at this time was 87 $\pm$ 6 μg L^{-1}, which was 82% daphnids and 18% copepods. In the −Z limnocorrals, macrozooplankton biomass at the end of the experiment was 4 $\pm$ 4 μg L^{-1}. Although zooplankton biomasses in the +Z treatments were higher than those in the lake, they were close to those observed previously (130 μg L^{-1}; Budy et al. 1995*b*). Furthermore, the ratio of zooplankton biomass to in vivo chlorophyll *a* measured at the start of the experiment was similar in the +Z treatments and in the lake (159 : 1 and 150 : 1, respectively), suggesting that the relative trophic proportions in the treatment were close to the normal range of the lake.

Because macrozooplankton in Yellow Belly Lake often lack a strong DVM and they generally show a peak at 2 m (N. Brindza unpubl. data), we promoted their migration by caging three small fish (brook trout and redside shiners) with a mean biomass of 25 $\pm$ 5 g in every corral to keep a constant kairomone production (Loose et al. 1993). These fish were held in 20- $\times$ 15-cm cages with 0.5-cm mesh at a depth of 2.5 m.

Zooplankton DVM in each of the +Z limnocorrals was analyzed on 14 August, 1 d before the start of the experiment, and on 26 August (at the end). DVM was not measured during the experiment to avoid mixing of the tracers that were injected into the epi- or metalimnion. Zooplankton samples were collected at 1200 and 2400 h at 0.5, 2.5, 4.5, 7, 9, 11, 13, and 16 m with a 21-liter Schindler–Patalas trap with a 153-μm net and were preserved in Lugol's solution for subsequent counting and measuring. To calculate mean zooplankton biomass in the epilimnion, we averaged data from 0.5–4.5 m, and for the metalimnion we averaged biomasses from 7–13 m. To complement the DVM information, daily field observations of zooplankton abundance in the surface 2 m of the water column were recorded.

Zooplankton clearance rates (CR) were estimated using a multiple linear regression model developed for Yellow Belly Lake using the Haney trap technique (Haney 1973; N. Brindza unpubl. data):

$$\begin{aligned}\text{CR } (\text{d}^{-1}) = {} & 0.00146(\text{temperature}) + 0.00053(\textit{Holopedium}) \\ & + 0.00069(\text{calanoid}) + 0.00060(\textit{Daphnia}) \\ & + 0.00469(\textit{Conochilus})\end{aligned}$$

where CR is expressed as the volume of water cleared of algae by the macrozooplankton present in 1 liter per day (liter L^{-1} d^{-1} or d^{-1}), temperature is in degrees Celsius, and biomasses of each taxon are in micrograms per liter. Zooplankton biomasses were estimated following McCauley's (1984) length–weight relationships. In our limnocorrals, there were no *Holopedium*, and rotifers from the genus *Conochilus* were not caught because of the mesh size used, so the multiple regression was reduced to temperature, with the biomasses of *Daphnia* and calanoid copepods as independent variables. This approach may have caused an underestimation in the CR because *Conochilus* was later found to be an important grazer, particularly in the epilimnion of this ecosystem (Armengol et al. 2001).

To account for zooplankton DVM in the CR estimation, we used the estimates of zooplankton biomass in each stratum at the end of the experiment (26 August), and we assumed that the day distribution occurred for 10 h and the night distribution for 14 h. We used the DVM measured at the end of the experiment because field notes indicated that at the first sampling (14 August, 1 d after fish addition) the zooplankton did not have a normal migration. On 14 August, zooplankton biomass during the day was located mainly in the epilimnion (83% of the total), but during the night the epilimnion biomass decreased to 43% of the total. Similar daytime peaks in abundance were found in the lake (N. Brindza unpubl. data). However, visual observations indicated that zooplankton began avoiding the top 2 m in the limnocorrals during the day from 15 August until the end of the experiment. Field observations also indicated that during the night zooplankton were horizontally well distributed but during the day they congregated near the limnocorral walls. This behavior likely affected the zooplankton biomass estimates because tows were done in the middle of the limnocorrals, and thus may have missed a portion of the zooplankton. Zooplankton biomass estimates during the day were consequently only 50% of those taken at night. To correct for this bias, daytime biomass measurements were doubled when we estimated grazing rates. Despite this large correction factor, the most important aspect of the zooplankton biomass data was the relative difference between the epilimnion and metalimnion, and the correction factor did not influence this difference.

^{15}N, ^{13}C, and rhodamine tracer analysis—Biologically mediated nutrient transport was analyzed with ^{15}N and ^{13}C, and physical transport was measured with rhodamine dye. Epilimnetic or metalimnetic tracer additions were assigned randomly to each zooplankton treatment. We injected a total

of 0.57 mmol L^{-1} of ^{15}N per limnocorral (99 atom-percent $^{15}NH_4Cl$) every 20 cm through 2-m-thick strata on 15 August. These injections were done in the middle of the epilimnion (1.5–3.5 m) or in the middle of the metalimnion (10–12 m) depending on the limnocorral. This addition should have increased the total nitrogen concentration by 0.35 μmol L^{-1}, or 3–9% over background levels. To assess the amount of epilimnetic carbon reaching the metalimnion, a secondary epilimnetic ^{13}C injection (99 atom-percent $NaH^{13}CO_3$) at a rate of 7 μmol of ^{13}C per corral was done in the limnocorrals where ^{15}N was injected in the metalimnion. Rhodamine (15 mg $corral^{-1}$) was simultaneously added with the nitrogen and carbon tracers as a water-mass tracer to detect whether nutrient transport was due to eddy diffusion.

The distribution of the tracers was measured in the seston and in sediment traps. Seston samples were collected with the diaphragm pump from the same depths as the chlorophyll samples were taken before the injection (14 August) to measure background levels of tracers, 1 d after the injection (16 August), and at the end of the experiment (26 August). To measure the sedimentation of carbon and nitrogen, two cylindrical sediment traps (6 cm diameter and 25 cm long) were suspended in each limnocorral (16 August), one at the base of the epilimnion (6 m) and the other at the base of the metalimnion (14 m). The bottom 18 cm of each trap was filled with a solution of 5% NaCl and 2% formaldehyde to collect and preserve sedimenting materials. Salt and formalin have little or no effect on isotopic enrichments (Arrington and Winemiller 2002). At the end of the experiment, the solution in the traps was filtered with a 153-μm mesh to remove macrozooplanktonic ''swimmers'' overcome by the formalin, carapaces, and other large particles from the smaller algal and fecal sediments (Sarnelle 1999). The data for the metalimnetic traps were corrected to express the metalimnion export only. Analysis of the epilimnetic ^{15}N and ^{13}C injection indicated that an mean of 48% ± 8% of epilimnetic tracers reached the metalimnetic traps in a 10-d period. Consequently, nitrogen and carbon rates from each metalimnetic trap were reduced by 48%.

Seston samples and material from the sediment traps were filtered on 47-mm precombusted Whatman GF/F filters, dried for 24 h at 60°C, and analyzed for particulate organic nitrogen (PON), particulate organic carbon (POC), and ^{15}N and ^{13}C with a Europa Scientific ANCA 2020 mass spectrometer linked with a CN analyzer. All ^{15}N data are expressed as micrograms of ^{15}N in excess. Computations were done following general fraction and ratio equations of Boutton (1991). The fractional abundance of the sample (F_{sample}) was calculated as

$$F_{sample} = [(1/R_{sample}) + 1]^{-1} = R_{sample}(1 + R_{sample})^{-1}$$

$$F_{excess} = F_{sample} - F_{background}$$

$$\mu g\ ^{15}N_{excess} = F_{excess} \times \text{nitrogen mass}$$

where R_{sample} is the $^{15}N:{}^{14}N$ ratio of the analyzed sample.

Vertical diffusion rates were estimated by measuring the distribution of rhodamine. Samples from the seston filtrate were frozen, and rhodamine was subsequently measured with a Turner 10AU fluorometer. Because rhodamine degrades with light, we used relationships between rhodamine degradation and depth from a 10-d experiment run simultaneously in the lake (W. Fleenor pers. comm.). Estimated rhodamine degradation during the 11-d experiment varied from 22% at 0.1 m to <1% at 11 m. We followed the equation of Quay et al. (1980) to estimate rhodamine vertical diffusion rates (K_z) in both the lake and the limnocorrals. Diffusive transport in the metalimnion of Yellow Belly Lake was estimated from a whole-lake rhodamine injection during 1998 (W. Fleenor unpubl. data).

The relative movement of nutrients via biological processes (^{15}N transport) was compared with the movement via physical processes (rhodamine transport) during the 11-d experiment. We first integrated the amount of each tracer in the epilimnion (0–6 m), metalimnion (6–14 m), and hypolimnion (14–16 m) and then normalized both values as the percentage of the total amount of tracer recovered (seston + sediment traps) on 26 August (end of the experiment). Thus, the final profiles show the relative distribution in the water column.

Analytical approach and statistics—Sediment trap data were used to calculate the rate of nutrient loss from each stratum. To estimate the amount of nitrogen being exported from the epilimnion and the metalimnion, we first calculated the average amount of sestonic PON present in each stratum. For the −Z treatment, this amount was calculated as the average of initial (16 August) and final (26 August) nitrogen levels. For the +Z treatment, seston PON was calculated by averaging the initial value for the −Z treatment and the final value for the +Z treatment to avoid biases that may have occurred because zooplankton were in the limnocorrals for 2 d before the initial seston samples were collected.

The influences of zooplankton addition and strata (epilimnion, metalimnion, and hypolimnion) on chlorophyll profiles were assessed using a two-way ANOVA in a split-plot design (PROC MIXED, SAS release 7.0). The whole plot unit was a limnocorral, and the whole plot variable was the presence or absence of zooplankton. The subplot variables were repeated measures on limnocorrals (sampling depths). We first determined that the $^{15}NH_4Cl$ additions did not significantly stimulate chlorophyll levels ($F_{6,6} = 0.31$, $P = 0.912$). This analysis was done for just the corrals without zooplankton to avoid the possible masking effect of grazing. Consequently, to test whether the presence or absence of zooplankton influenced the chlorophyll profiles, limnocorrals were pooled by treatment (+Z or −Z) without regard to the injection depth. Then, the effect of zooplankton on the vertical distribution of chlorophyll was assessed using the mean chlorophyll concentrations in the epilimnion and metalimnion as the subplot variabbles.

To test whether seston ^{15}N and rhodamine profiles differed between the +Z and −Z treatments for the epilimnetic or metalimnetic injections, we determined whether there was a treatment × stratum interaction using a split-plot design with the subplot variables of integrated seston ^{15}N or rhodamine for the three strata (epilimnion, metalimnion, and hypolimnion). We then applied Tukey–Kramer *t*-tests for selected pairs of interaction means.

The statistical model for nutrient sedimentation rates was

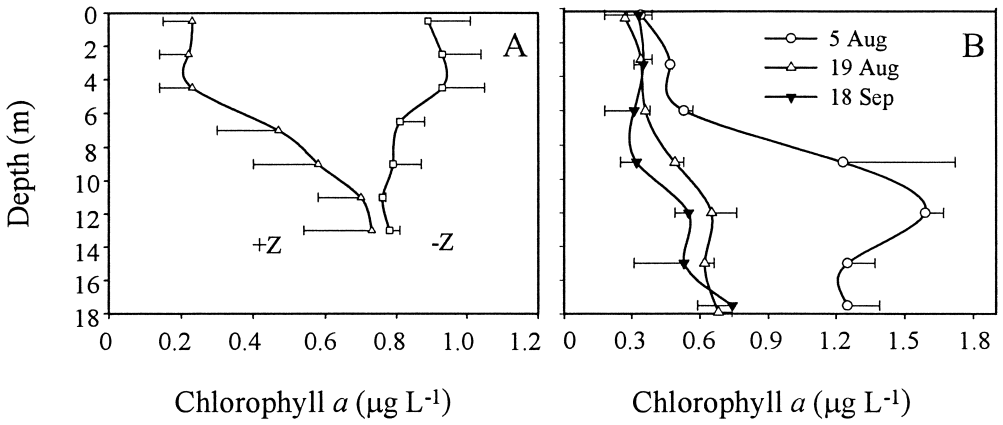

Fig. 2. (A) Chlorophyll *a* concentrations in the limnocorrals at the end of the 11-d experiment for treatments with (+Z) and without (−Z) macrozooplankton. (B) Chlorophyll *a* profiles (mean ± SD) in Yellow Belly Lake showing the demise of the DCL between 5 August and 18 September 1999.

a two-way ANOVA in a split-plot design, and the subplot variable was the trap depth (epilimnion and metalimnion). PON and POC in sedimenting material (μmol L^{-1} m^{-2} d^{-1}) were compared for different strata between different treatments (+Z and −Z). The total amount of ^{15}N recovered (seston + sediment traps) from each limnocorral varied. Consequently, to test whether the presence of zooplankton influenced the ^{15}N flux into different layers, we compared the relative contribution of ^{15}N in sediment traps to the total amount of isotope recovered from each corral. Two days after the experiment began, one of the treatments (−Z, metalimnetic ^{15}N injection) had to be discarded because of a duck-induced eutrophication process. Subsequently, all limnocorrals were covered with chicken wire to keep the duck from using them. The elimination of one limnocorral resulted in an unbalanced but still complete experimental design.

During analysis, we considered the extent to which the data met the statistical model assumptions of normality, homogeneity of variance, and covariance structure for the repeated measurements. Unfortunately, there were too few data for a robust assessment of assumptions. However, an analysis of residuals produced no evidence of a violation of normality. There appeared to be some heterogeneity of variance between treatments and among levels, which may have had some effect on results. Several covariance structures for the repeated measures were assessed. Of those covariance structures that could be estimated, the compound symmetry covariance structure provided the best fit. In addition, the *P*-values for the tests of variable, level, and interaction tended to be fairly extreme—either quite small or quite large—and qualitative conclusions were identical across variations of the statistical model. Interpretation is limited by the spatial and temporal extent of the data and by the small data set.

Results

The limnocorrals and lake were strongly thermally stratified, and small or motile phytoplankton dominated the lake's DCL at the start of the experiment (Fig. 1A). The chlorophyll distribution in the limnocorrals was similar to that in the lake, but concentrations in the limnocorrals were higher. Small flagellates and cyanobacterial picoplankton (<2 μm) of the genus *Synechococcus* dominated the lake phytoplankton community. *Chromulina* sp. and *Dinobryon* sp. were the dominant chrysophytes, and *Cryptomonas* sp. was the dominant cryptophyte. The dominant diatom was *Fragilaria ulna*, and the dominant green algae were *Oocystis* sp. and *Quadrigula lacustris* (Fig. 1B).

In the treatments with zooplankton, the DCL was maintained, but it disappeared when macrozooplankton were absent (Fig. 2A). In the corrals with zooplankton, initial epilimnetic chlorophyll levels declined 72%, whereas metalimnetic concentrations decreased only 53%, thus accentuating the magnitude of the DCL. In the epilimnion, final chlorophyll *a* levels in the +Z limnocorrals were only 0.2 μg L^{-1}. In the −Z treatment, the epilimnetic chlorophyll increased 11%, and the metalimnetic algal levels decreased 41%, resulting in the formation of a slight epilimnetic chlorophyll layer. At the end of the experiment, mean areal chlorophyll *a* levels in the +Z treatments were significantly lower than those in the −Z treatments ($F_{1,4} = 16.79$, $P = 0.015$). Mean epilimnetic and metalimnetic chlorophyll *a* concentrations for the same treatments also differed ($F_{1,4} = 20.45$, $P < 0.000$). In Yellow Belly Lake, the DCL declined and nearly disappeared by the end of the experiment (Fig. 2B).

The analysis of macrozooplankton vertical distribution and CR indicated that grazing impacts were greater in the epilimnion than in the metalimnion. Even though there was a strong DVM (Fig. 3), with both daphnids and copepods moving from deeper strata into the epilimnion at night, there was still a moderate biomass of zooplankton in the epilimnion during both day and night. Mean (±SD) time-weighted zooplankton biomasses in the epilimnion and metalimnion were 346 ± 75 μg L^{-1} and 174 ± 80 μg L^{-1}, respectively. Mean lengths of *Daphnia* and calanoid copepods in the epilimnion were 0.89 ± 0.11 mm and 0.96 ± 0.02 mm, and their densities were 29 and 27 individuals L^{-1} ($n = 24$), respectively. Larger *Daphnia* and calanoid copepods were present in the metalimnion (1.01 ± 0.08 mm and 1.08 ± 0.09 mm, respectively), but their densities were around 3×

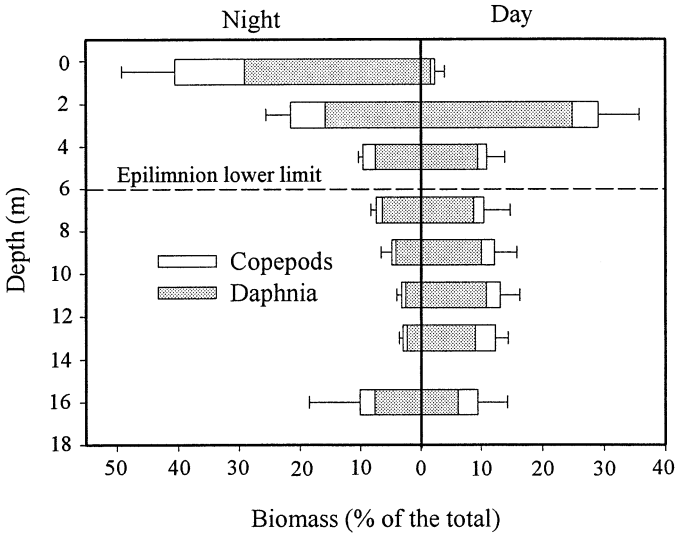

Fig. 3. DVM of zooplankton within the +Z limnocorrals at the end of the experiment (26 August 1999). Each histogram shows the mean (±SD) percentage of total biomass found in the limnocorral during the night (2400 h) and day (1200 h). The mean biomass was 260 mg L^{-1}.

lower (15 and 7 individuals L^{-1}; $n = 32$) than those in the epilimnion. Consequently, the estimated community CR was 1.8× higher in the epilimnion (240 ml L^{-1} d^{-1}) than in the metalimnion (130 ml L^{-1} d^{-1}).

Macrozooplankton also had a large impact on water transparency and light intensity. At the end of the experiment, Secchi disc depths were 7.5 ± 0.6 m ($n = 3$) in the −Z treatments and 11.7 ± 1 m ($n = 4$) in the +Z treatment. Estimated light intensities at the bottom of the metalimnion (14 m) for the −Z and +Z treatments were 2% and 6% of surface intensity, respectively.

Diffusive transport was much higher in the limnocorrals ($K_z = 7.7 \times 10^{-2}$ cm^2 s^{-1}) than has been measured in the lake ($K_z = 6.8 \times 10^{-4}$ cm^2 s^{-1}). After 11 d, 37% of the rhodamine injected into the epilimnion had moved down to the meta- or hypolimnion (Fig. 4B,C). Transport of rhodamine from the metalimnion injections was relatively even into adjacent strata, and approximately 36% moved out from the metalimnion (Fig. 4D,F). As expected, zooplankton did not influence the final rhodamine distribution in corrals with either epilimnetic or metalimnetic tracer injections ($F_{2,4} = 1.49$, $P = 0.329$ and $F_{2,2} = 4.05$, $P = 0.198$, respectively). Wave-induced pumping of the limnocorrals likely increased turbulence, that in turn increased turbulent movement of both rhodamine and ^{15}N between strata. In contrast, Bloesch et al. (1988) suggested that limnocorrals limit eddy diffusion by reducing shearing currents. The walls of our limnocorrals, however, were relatively slack, which may have allowed wave action to ''pump'' them.

Zooplankton had a marked effect on nutrient movement and tracer recovery in the limnocorrals. The presence of zooplankton significantly increased the movement of the nitrogen tracer into the metalimnion (Fig. 4B,C; $t = -2.97$, df $= 4$, $P = 0.041$). This movement was greater than the rhodamine movement, suggesting that zooplankton-mediated sedimentation and/or nitrogen excretion transported the isotope. Biological transport was low in the −Z treatment, resulting in significantly different final seston ^{15}N profiles between the two treatments ($F_{2,4} = 11.25$, $P = 0.023$). In the −Z treatment, ^{15}N and rhodamine distributions at the end of the experiment were not different, suggesting that turbulence, and not algal sedimentation, dominated nutrient transport when zooplankton were absent. In contrast, the presence or absence of zooplankton did not significantly affect the normalized distribution of ^{15}N injected into the metalimnion ($F_{2,2} = 0.94$, $P = 0.515$). The transport from the metalim-

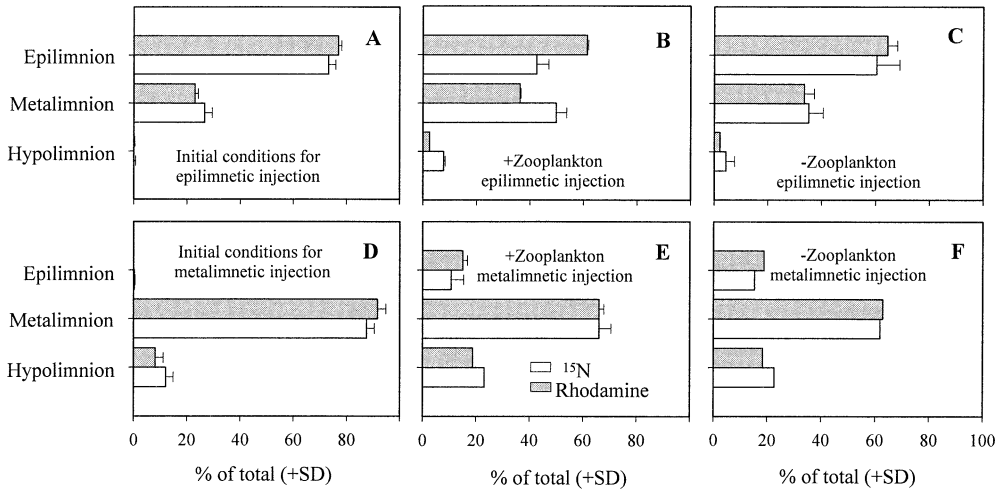

Fig. 4. Distribution of seston ^{15}N (atom-excess; open bars) and rhodamine (shaded bars) on 16 August 1999, 1 d after these substances were injected into the epilimnion (A) or metalimnion (D) of the limnocorrals. Final distribution is also shown for the same tracers (26 August) in limnocorrals with and without zooplankton and with these tracers injected into the epilimnion (B,C) or the metalimnion (E,F). Values are expressed as the mean (±SD) percentage of the total amount found at the beginning or end of the experiment ($n = 2$, except in F, were one replicate was lost).

nion into adjacent strata was nearly identical for ^{15}N and for rhodamine (Fig. 4E,F), suggesting that turbulent transport was the dominant mechanism moving nutrients from that stratum. Zooplankton also decreased the amount of ^{15}N recovered in the limnocorrals. In the −Z treatments 60% ± 15% of the tracer was recovered, but only 34% ± 8.5% was recovered from the +Z treatments, and these differences were significant (t = 2.9, df = 3, P = 0.032).

The macrozooplankton increased sedimentary losses and the relative distribution of $PO^{15}N$ in the limnocorrals. For the epilimnetic injections, the relative amount of ^{15}N in the epilimnetic sediment traps was 3× higher in the +Z than in the −Z treatment, and the difference was significant (t = −3.17, df = 4, P = 0.034). Zooplankton also increased the amount of isotope moving into the metalimnetic traps (~4×), but this difference was not significant (t = −2.48, df = 4, P = 0.068). In treatments where ^{15}N was injected into the metalimnion, zooplankton increased mean sedimentation rates into both epilimnetic (~4×) and metalimnetic (~2×) traps, but these differences were not significant ($F_{1,3}$ = 8.30, P = 0.102). The zooplankton-mediated differences in export resulted in different relative concentrations of $PO^{15}N$ in the different strata (Fig. 4). Final $PO^{15}N$ in the epilimnion was depleted ca. 20% by zooplankton grazing in comparison to the zooplankton-free treatment. Although zooplankton decreased epilimnetic $PO^{15}N$, they increased the relative amount in the metalimnion ca. 10% relative to the −Z treatments (Fig. 4B).

Chemical analysis of sedimented material also indicated that zooplankton increased sedimentation rates, particularly out of the epilimnion (Fig. 5). POC and PON sedimentation rates were around 2× higher in the limnocorrals with zooplankton than in those without zooplankton, and these differences were significant ($F_{1,5}$ = 6.83, P = 0.047 and $F_{1,5}$ = 17.72, P = 0.008, respectively). In the limnocorrals with zooplankton, mean carbon and nitrogen sedimentation rates out of the epilimnion were 2× and 5× higher than the sedimentary loss rate out of the metalimnion (t = 5.82, df = 5, P = 0.002 and t = 8.37, df = 5, P < 0.000). In treatments without zooplankton, epilimnetic carbon and nitrogen sedimentation were similar to those in the metalimnion (t = 1.76, df = 5, P = 0.134 and t = 2.17, df = 5, P = 0.083, respectively).

Zooplankton increased nitrogen and carbon export from the epi- and metalimnetic PON and POC standing stock (Table 2). The highest nitrogen daily export was observed in the epilimnion of the +Z treatment (8.4% d^{-1}), whereas in the −Z treatment export was 4× lower (2.1% d^{-1}). Nitrogen export from the metalimnion was similar in the +Z and −Z treatments (1.1% d^{-1} and 0.9% d^{-1}, respectively). Similar patterns were also observed with the daily carbon export (Table 2), but export from the epilimnion of the +Z treatment was only 2.5× greater than that from the epilimnion of the −Z treatment.

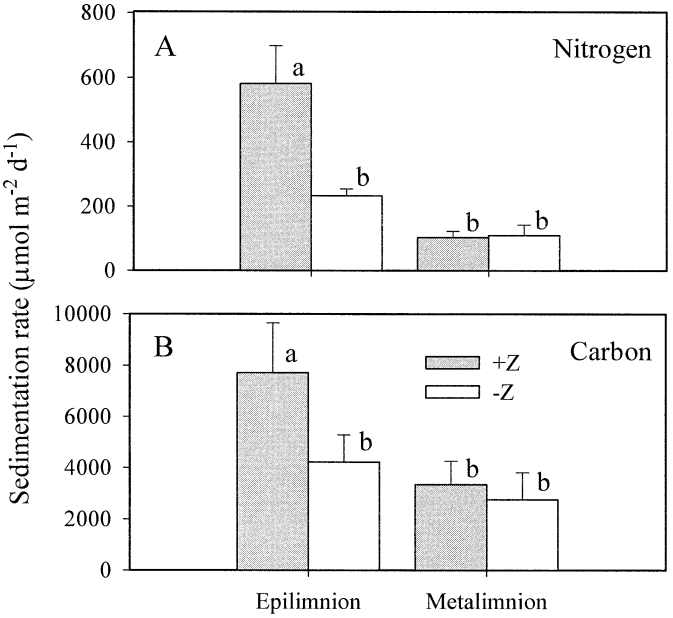

Fig. 5. Mean (±SD) nitrogen (A) and carbon (B) sedimentation rates into traps at the bottom of the epilimnion (6 m) and metalimnion (14 m) over the 11-d experiment in limnocorral treatments with (+Z) and without (−Z) zooplankton. Different letters within a frame indicate significant differences among histograms based on pairwise t-tests within each stratum (P < 0.05; n = 4 in +Z treatment, n = 3 in −Z treatment).

Discussion

The limnocorral experiment demonstrated that the term epilimnetic chlorophyll minimum might be a better term than deep chlorophyll maximum to describe algal distribution in this lake. Algal removal from the epilimnion by zooplankton, sedimentation processes, and consequently an increased export of nutrients from the surface waters into the meta- and hypolimnion may be dominant factors allowing the persistence of higher chlorophyll concentrations in the metalimnion than in the epilimnion (Table 2). However, if macrozooplankton are absent, the lack of grazing pressure, lower light penetration, and low epilimnetic export of nutrients may favor the development of a shallow chlorophyll peak.

Bloesch et al. (1988) found that zooplankton grazing in epilimnetic limnocorrals depressed seston concentrations when compared with zooplankton-free limnocorrals. In their experiment, however, the closed corrals prevented the zooplankton from migrating out of the epilimnion, forcing them to graze 24 h on the surface. In our experiment, grazing impact was higher in the epilimnion because the daily average biomass was 2.5× greater and temperatures were higher than those in the metalimnion. The estimated macrozooplankton grazing rate with these biomasses was 24% d^{-1} in the epilimnion but only 13% d^{-1} in the metalimnion. Algal growth rates in these oligotrophic lakes are low (Gross et al. 1997), and moderate grazing rates such as we calculated can control or reduce phytoplankton populations in this lake (N. Brindza unpubl. data).

In addition to removing phytoplankton from the epilimnion, heavy zooplankton grazing in the surface stratum moved nutrients downward into the metalimnion. In mesotrophic and eutrophic lakes, zooplankton increase sedimen-

Table 2. Mean (±SD) amount of sestonic N and C (mmol m^{-2}) present in the epilimnion (Epi) and metalimnion (Meta), rate of N and C flux into sediment traps (mmol m^{-2} d^{-1}), and the daily percentage of these nutrients exported from each stratum in limnocorrals with (+Z) and without (−Z) zooplankton. N and C seston concentrations are the average of initial and final concentrations in the limnocorrals. Areal concentrations of seston were calculated for a 6-m-thick epilimnion and an 8-m-thick metalimnion. Nutrient flux into the metalimnetic traps was corrected to avoid accounting for epilimnetic material sedimenting into them.

	Nitrogen				Carbon			
	+Z		−Z		+Z		−Z	
	Epi	Meta	Epi	Meta	Epi	Meta	Epi	Meta
Seston (mmol m^{-2})	7.09±1.04	9.64±1.07	11.28±1.45	12.03±0.18	71.31±8.90	97.78±5.80	100.54±16.91	128.18±8.18
Sediment trap (mmol m^{-2} d^{-1})	0.59±0.14	0.10±0.02	0.23±0.02	0.11±0.03	7.71±1.94	3.35±0.92	4.23±1.05	2.77±1.04
% exported per day	8.4±2.3**	1.1±0.08	2.1±0.3*	0.9±0.3	11.0±3.3**	3.1±1.0	4.4±1.6	2.2±0.9

Significantly higher export rates from the epilimnion than from the metalimnion: * $P<0.05$; *** $P<0.01$.

tation rates (Uehlinger and Bloesch 1987; Bloesch et al. 1988; Bloesch and Bürgi 1989), and a model by Morales (1999) suggested that in the ocean, the POC and PON export from the photic zone is greater when diel migrating zooplankton are present. In the oceans, this export is mainly via sinking fecal pellets (Turner and Ferrante 1979). Pellet size influences sinking rates and consequently remineralization by coprophagy and bacterial activity (e.g., Lampitt et al. 1990). In the ocean, copepod fecal pellets may disintegrate in the euphotic zone within hours (Lampitt et al. 1990; Beaumont et al. 2001), but in our limnocorrals the rapid sedimentation rate of copepod fecal pellets (10–150 m d^{-1}; Paffenhöfer and Knowles 1979; Small et al. 1979; Haberyan 1998) would have carried them to the bottom before significant mineralization could have occurred. The sedimentation rate of *Daphnia* feces has not been studied, but because these animals dominated the biomass in the limnocorrals, their grazing and fecal sedimentation may have contributed significantly to the export of nutrients from the epilimnion. *Daphnia* are coprophageous (A. Pilati unpubl. data), so mineralization of their sedimenting feces by excretion may have contributed to the nutrient pool for algae in the DCL. Recently, Sarnelle (1999) added a novel point of view of the effects of zooplankton grazing on both vertical particulate flux by fecal production and on modifications of algal sedimentation rates. Results of his model suggest that zooplankton grazing will increase total sedimentation in oligotrophic systems because fecal production and sedimentation will exceed the low sedimentation rate of the small phytoplankton present. Our results showing increased levels of sedimentation when zooplankton were present in an oligotrophic system provide empirical support for Sarnelle's model.

Although macrozooplankton had a large influence on nutrient transport out of the epilimnion, the ^{15}N tracer results indicate that they had little effect on movement of metalimnetic nutrients. Consequently, the net effect of the macrozooplankton was to move nutrients from the epilimnion to the metalimnion, where some accumulated. The analysis of nitrogen movement in the water column was, however, complicated by the different ^{15}N recovery between +Z and −Z treatments and by different movement rates in different strata. The lower recovery in the +Z than in the −Z treatment may have been due to zooplankton in the +Z treatments congregating near the periphery of the limnocorrals, whereas the sediment traps collected feces near the center, so that sedimenting material may have been lost. Additionally, we did not measure ^{15}N in the dissolved pool, and zooplankton may have promoted tracer movement into the dissolved organic and inorganic nitrogen pools. Loss of tracer from the limnocorrals was negligible; 100% of the rhodamine was recovered (after correction for photodegradation).

The high epilimnetic grazing pressure in the zooplankton treatment may have also stimulated the persistance of a DCL by increasing light penetration, a mechanism suggested previously by Christensen et al. (1995). Phytoplankton in the Sawtooth Mountain lakes are light limited at levels below 500 μmol quanta m^{-2} s^{-1} (Gross et al. 1997). Zooplankton grazing in the limnocorrals increased estimated midday light intensities at 14 m from 21 μmol quanta m^{-2} s^{-1} to 62 μmol quanta m^{-2} s^{-1}. If zooplankton grazing increased light trans-

mission, they should have increased photosynthetic rates and perhaps growth rates in the metalimnion. A model by Gross et al. (1997) indicated that adding nutrients to the epilimnion of an oligotrophic mountain lake would decrease the DCL. Conversely, when zooplankton grazing removes phytoplankton (and nutrients) from the epilimnion, light penetration and thus photosynthesis in deep layers should increase.

The difference in chlorophyll distribution between the limnocorrals with and without zooplankton was pronounced (Fig. 2A). In the +Z treatments, macrozooplankton grazing and the consequent nutrient flux can explain why a DCL was maintained. However, in the −Z treatments the DCL actually disappeared and chlorophyll levels in the epilimnion increased from the initial levels. The reasons for this difference are not clear, but mobile phytoplankton may have left the DCL and moved into the epilimnion once macrozooplankton grazing was reduced. Others have found that phytoplankton migrate between strata (Tilzer 1973; Gasol et al. 1992), and our limnocorrals contained many flagellated species capable of movement (chrysophytes, cryptophytes, and dinophytes). Removal of macrozooplankton from the limnocorrals may also have allowed microzooplankton to proliferate and graze heavily on the picoplankton that were most abundant in the DCL (Adrian et al. 2001).

Many zooplankton in the limnocorrals resided in the epilimnion during the day, and increased densities in this strata at night, even though seston ''food'' levels were higher in the metalimnion than in the surface stratum. Williamson et al. (1996) also noted that zooplankton moved from or through DCLs of lakes at night to graze in the epilimnion where chlorophyll levels were low. Cool temperatures in the meta- and hypolimnion may slow the filtration rates (Lampert 1987) and/or digestion rates of zooplankton, thereby reducing the net benefit of the higher food resources there. Additionally, in a concurrent experiment, Cole et al. (2002) found that *Daphnia rosea* fed epilimnetic seston from Yellow Belly Lake grew better than those fed metalimnetic food regardless of temperature, thus suggesting that food quality in the metalimnion was poor. Regardless of the reason(s) for the nocturnal migration into the epilimnion, the result was increased grazing in that stratum and the removal of phytoplankton (and nutrients) there.

The pattern of chlorophyll development in the +Z limnocorrals was in some ways similar to that in the Yellow Belly Lake. Chlorophyll levels in the limnocorrals at the start of the experiment (15 August) were, however, higher than those in the lake, particularly in the epilimnion. The higher levels in the limnocorrals may have resulted from phytoplankton growth between the date of filling (9 August) and the date zooplankton were added (12 August) and when the experiment was initiated (15 August). By the end of the experiment, however, the profiles in Yellow Belly Lake and in the limnocorrals with zooplankton were similar. In the lake, this change in pattern was due to *Daphnia* shifting from grazing primarily in the epilimnion in July and early August to heavy grazing in the metalimnion later in August (N. Brindza unpubl. data). In the +Z limnocorrals, the loss of chlorophyll was pronounced in both the epilimnion and the upper part of the metalimnion.

Although our limnocorral results are generally consistent with chlorophyll development in Yellow Belly Lake, additional experiments will be necessary to determine the generality of these results. In mesotrophic plankton towers, W. Lampert (pers. comm.) found that *Daphnia* grazing removed epilimnetic phytoplankton, causing epilimnetic chlorophyll minima to form. However, in his experiment and ours, the impact of grazing on the formation of an epilimnetic chlorophyll minimum may have been favored because zooplankton DVM was not extensive. In our experiment, zooplankton migration was delayed at least 1.5 d after fish were introduced, as was observed by DeMeester (1993). Even at the end of the study the highest biomass during the day was found in the epilimnion between 2 and 3 m (Fig. 3). The dominant zooplankton in the corrals, *D. rosea,* is highly resistant to ultraviolet radiation and has only a minimal DVM in response to potentially damaging light (Rhode et al. 2001). In systems dominated by light-sensitive zooplankton or in systems with more intense fish predation, DVM would likely be enhanced, and the relative amount of grazing pressure in the epilimnion would be reduced. Future work on the importance of zooplankton on the development of DCLs will consequently need to address the distribution of the grazers and to provide a more comprehensive analysis of how different taxa (e.g., cladocerans vs. copepods vs. microzooplankton) remove phytoplankton and influence nutrient transport.

Experimental manipulation clearly indicated that macrozooplankton were an important factor influencing the DCL in an oligotrophic lake. Not only were epilimnetic grazing losses important, but zooplankton also increased transport of nutrients to the metalimnion. The metalimnetic accumulation of nutrients in particulate matter may have been due to transported nutrients that were mineralized and subsequently taken up by the plankton. Whether these processes also determine algal distribution in mesotrophic lakes and oligotrophic oceans needs to be addressed.

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