

**Pelagic Responses to Changes in Dissolved Organic Carbon Following
Division of a Seepage Lake**



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Pelagic responses to changes in dissolved organic carbon following division of a seepage lake

Abstract—Within 2 yr of dividing a multibasin lake into discrete lakes for experimentation, dissolved organic carbon (DOC) concentrations and water color (absorption coefficient g at 440 nm, g_{440}) increased in the east basin and decreased slightly in the west basin. These changes were not explainable by watershed vegetation or groundwater chemical composition. However, g_{440} increased from 0.7 to 4.2 m⁻¹ for water moving through the sediment-water interface in the east basin. In the west basin, g_{440} of groundwater (0.6 m⁻¹), in-seeping water (0.7 m⁻¹), and lake water (0.7 m⁻¹) were all similar. Patterns of DOC distribution matched time trends in the surface waters. In the east basin, DOC concentration doubled and g_{440} increased 3-fold from 1990 to 1993. Trends in the west basin were more complex, but in general, there was a decrease in DOC and g_{440} over the same period. Changes in the light regime affected phytoplankton vertical distribution, but total areal chlorophyll

and epilimnetic chlorophyll concentrations were not altered. The depth of oxygenation was changed by altered mixing characteristics and phytoplankton distribution. Changes in light-attenuating DOC affected pelagic responses to nutrient inputs.

Dissolved organic carbon (DOC) plays multiple and pivotal roles in lake ecosystems (Wetzel 1992; Schindler et al. 1992). Allochthonous DOC is rich in colored, relatively refractory components (Thurman 1985) that have significant effects on physical and chemical processes and ecosystem structure (Jones 1992). This refractory DOC alters light penetration, pH, and trace metal and nutrient availability (Jackson and Hecky 1980; Jones 1992). Staining by DOC decreases phytoplankton production (Jack-

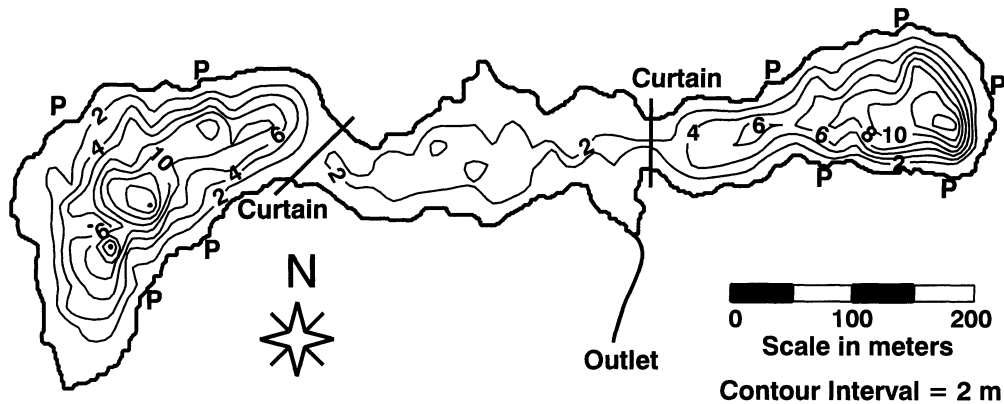


Fig. 1. Map of Long Lake. The lake is ~8.9 ha in size with a maximum depth of 17.7 m. Impermeable curtains were placed as shown on the map. The only surface-water connection is an outflow in the central portion of the divided lake. The nine piezometer sites (P) are marked. At each site we installed one piezometer at 1 m and one at 2 m below the sediment surface.

son and Hecky 1980) and alters phytoplankton community structure (Wall and Briand 1979).

Although refractory DOC can strongly affect pelagic communities, little of it originates in the pelagic zone in lakes (Jones 1992; Wetzel 1992). DOC concentration in surface waters generally depends on watershed attributes, such as the area of adjacent wetlands, watershed vegetation, or water flushing rates (Engstrom 1987; Rasmussen et al. 1989; Hemond 1990). Lakes without surface inflows are linked to their watersheds primarily through groundwater and subsurface flow (interflow, Freeze and Cherry 1979). Therefore, DOC inputs from subsurface waters may depend on groundwater DOC concentration, which in turn depends on hyporheic sediments adjacent to ground water recharge zones (Moore 1989).

Various watershed perturbations alter DOC inputs into surface waters (e.g. fire, Schindler et al. 1992; flooding, Jackson and Hecky 1980), but we have little information on how lakes respond to such perturbations of DOC inputs. When we divided a seepage lake with an impermeable barrier, DOC concentration and water color changed dramatically in the separated lake basins. The pelagic environment was altered significantly, with profound effects on the biotic community. This note evaluates limnological changes that accompanied a substantial, sustained DOC perturbation, considers the causes for the changes, and discusses implications for split-lake ecosystem experiments.

Long Lake and Paul Lake are small, steep-sided seepage lakes at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin (46°13'N, 89°32'W; Carpenter and Kitchell 1993). Both lakes are on glacial outwash and have weakly acidic soils that are relatively nutrient poor; the lakes have no surface inflows and each has one surface outflow. In Long Lake, the outflow is through the central section of the lake (Fig. 1). Both lakes were weakly stained prior to manipulation (Elser 1987) and both stratify almost immediately after ice-out.

In May 1991, Long Lake was divided in two locations

with a plastic barrier. After division, there were discrete west (surface area, 3.6 ha; mean depth, 4.4 m; max depth, 17.7 m), east (surface area, 2.5 ha; mean depth, 4.9 m; max depth, 14.4), and central (surface area, 2.2 ha; mean depth, 1.1 m; max depth, 4.0 m) basins. Because the central basin receives water input from the other basins, it is not considered here. Paul Lake (surface area, 1.5 ha; mean depth, 3.9 m; max depth, 12.0 m) is an unmanipulated reference system ~1.6 km away from Long Lake (Carpenter and Kitchell 1993).

Long Lake was divided to separate fish communities in a whole-lake experiment contrasting food-web structure and nutrient inputs (Carpenter et al. 1995). However, planktivore populations did not persist in the east basin, so both basins had similar planktonic food webs dominated by *Daphnia* during the study. Zooplankton community structure remained similar in both basins throughout the study period. From 1990 to 1993, zooplankton in the east basin were dominated by *Daphnia* spp. (mean 51% by biomass) with a mean length of 0.74–0.88 mm. In the west basin, *Daphnia* comprised 47% of the zooplankton biomass and ranged in mean length from 0.68 to 0.87 mm from 1990 to 1993. Paul Lake, the reference system, has been monitored consistently since 1984 (Carpenter and Kitchell 1993; Carpenter et al. 1995). Beginning in May 1993, nitrogen and phosphorus were added to the east and west basins of Long Lake daily from a floating central station at an rate of $\sim 1.29 \mu\text{g P liter}^{-1} \text{d}^{-1}$ and $\sim 1.43 \mu\text{g P liter}^{-1} \text{d}^{-1}$ with a nitrogen to phosphorus ratio of 25:1 by atoms (Carpenter et al. 1996).

In Long Lake, physical-chemical profiles were collected at deep central stations in the east and west basins during summer stratification (May–September) biweekly in 1990 and weekly from 1991 to 1993; Paul Lake was sampled at a deep central station weekly during summer stratification from 1990 to 1993. Temperature and dissolved oxygen were measured at 0.5-m intervals with a YSI model 58 combination electrode. Underwater irradiance was measured at 0.5-m intervals to the depth of 1% of surface light intensity with a LiCor model 193SA spherical quan-

tum sensor equipped with a cosine collector. The light extinction coefficient was calculated by linear regression of the measured irradiance profiles with depth.

We determined littoral organic sediment depth around the lake at 48 sites spaced ~ 10 m apart. We used a metal rod to measure the depth of sediment above the solid mineral soil. We determined watershed vegetation by point quarter sampling (Curtis 1959) along transects spaced ~ 30 m apart perpendicular to the shoreline. Transects were sampled from the lake to the watershed edge. Trees > 5 cm in diameter were measured at breast height and identified to species. Species dominance was calculated as the sum of basal (cross-sectional) area for each tree species, weighted for the relative abundance of these species.

Groundwater chemistry and flow direction were monitored with piezometers and seepage meters. In June 1994, we installed pairs of minipiezometers (Lee and Cherry 1978) at nine sites in the east and west basins (Fig. 1). Sites were spaced approximately uniformly around each basin and divided between regions of expected groundwater recharge and discharge. Paired piezometers were installed at each site using plastic tubing ~ 0.5 and 1.5 cm in diameter. A fine mesh screen covered 7–10 inflow holes that were drilled within 5 cm of the bottom of each piezometer. At each site, piezometers were submerged 1 and 2 m below the sediment surface in the littoral zone of the lake (water depth, < 0.5 m), as most groundwater enters at the water–land margin (Freeze and Cherry 1979). Piezometers were sampled weekly by vacuum pumping by hand into a collection flask. Because we generally obtained small sample volumes, samples were analyzed in alternate weeks for conductivity and pH or DOC and water color (g_{440} , absorption coefficient g at 440 nm).

Seepage meters, placed in shallow water (< 0.5 m deep) at each piezometer site to determine flow regime, consisted of a 0.45-m-diameter steel cylinder with one end open and one end sealed, except for a sampling port (Lee and Cherry 1978). The open end of the seepage meter was pushed into the lake bottom to a depth at which the sealed end was within 5 cm of the sediment surface. The sampling port of the cylinder was left open for 24–48 h after installation, which allowed inflowing groundwater to displace lake water in the cylinder at sites of groundwater discharge. A collapsed sampling bag was placed over the sampling port. At inflow sites, discharging groundwater caused positive pressure and filled the sample-collecting bag. Sampling bags that did not fill with water were checked for outflow by filling bags and measuring water loss. Seepage meters were sampled once at each site in August 1994 and were analyzed for conductivity, pH, and g_{440} .

We measured g_{440} from epilimnetic, metalimnetic, and hypolimnetic strata by passing lake water through Whatman GF/F glass-fiber filters and measuring absorbance of the filtrate at 440 nm in 10-cm cells (Cuthbert and del Giorgio 1992). Samples for DOC analysis were prepared by passing lake water through precombusted Whatman GF/F glass-fiber filters, collecting the filtrate in a clean flask, and freezing the sample until analysis. DOC concentration was then measured with an Astro 2001 total

carbon analyzer. Conductivity and pH were measured with Beckman and Orion digital meters. We measured chlorophyll from water samples taken with an opaque Van Dorn sampler at discrete depths of 100, 50, 25, 10, 5, and 1% of surface light. Chlorophyll samples were filtered onto Whatman GF/F filters and frozen until extracted. Chlorophyll was extracted for 24 h in methanol at 5°C, measured by fluorometry, and corrected for pheopigments by acidification (Carpenter and Kitchell 1993). Phytoplankton were subsampled from three pooled discrete epilimnetic water samples, preserved in glutaraldehyde, and counted by species (Carpenter and Kitchell 1993). Zooplankton were collected by vertical tow from the deepest portion of the lake, preserved in ethanol, and counted to species (Carpenter and Kitchell 1993).

The separation of Long Lake increased concentrations of light-attenuating DOC in the east basin; concentrations in the west basin decreased slightly. Flushing rates, vegetation, or DOC concentrations in groundwater are thought to determine DOC differences among lakes (Engstrom 1987; Rasmussen et al. 1989; Hemond 1990). The dilution rates in the two basins were very similar: 0.006 d^{-1} in 1992 and 0.0028 d^{-1} in 1993 for the east basin and 0.0061 d^{-1} in 1992 and 0.0025 d^{-1} in 1993 for the west basin (Carpenter et al. 1996; J. J. Cole and M. L. Pace unpubl.). Thus, the differences between basins cannot be explained by differences in flushing rate.

Differences in watershed vegetation cannot explain the changes in the two basins. The vegetation directly surrounding the lake is dominated by *Sphagnum* bog. A second-growth mixed hardwood forest occupies the remainder of the watershed. The watershed was clearcut in about 1890, with continued selective removal of aspen (*Populus* spp.) through 1980 (Leavitt 1988). The catchment of the west basin is dominated by an early-to-mid-successional conifer forest (balsam fir, *Abies balsamea*), and dominance in the catchment is 63.2% coniferous and 36.8% deciduous. The catchment of the east basin has an opposite pattern of dominance and is dominated by mid-to-late successional deciduous species (red and sugar maple, *Acer rubrum* and *Acer saccharum*). Deciduous species account for 74.1% of the forest basal area, and conifers comprise only 25.9%. The west basin has more adjacent wetlands and a higher proportion of coniferous vegetation in its watershed and would therefore be expected to have higher DOC and color than the east basin (Engstrom 1987; Rasmussen et al. 1989; Cronan 1990). The opposite trend was observed.

Groundwater contribution of DOC into Long Lake seemed to be low. Groundwater sampled below the sediment–water interface was chemically similar in both basins (Table 1). In the east basin, g_{440} and DOC concentration were low in groundwater but increased as water flowed into the lake (Fig. 2). Low water color and DOC concentrations are common for groundwater because it contacts relatively mineralic soils, which leach little DOC (Thurman 1985). Although DOC concentration in groundwater tended to be higher in the east basin than in the west basin, the difference was not significant (Table 1). Also, water sampled after it crossed the sediment–

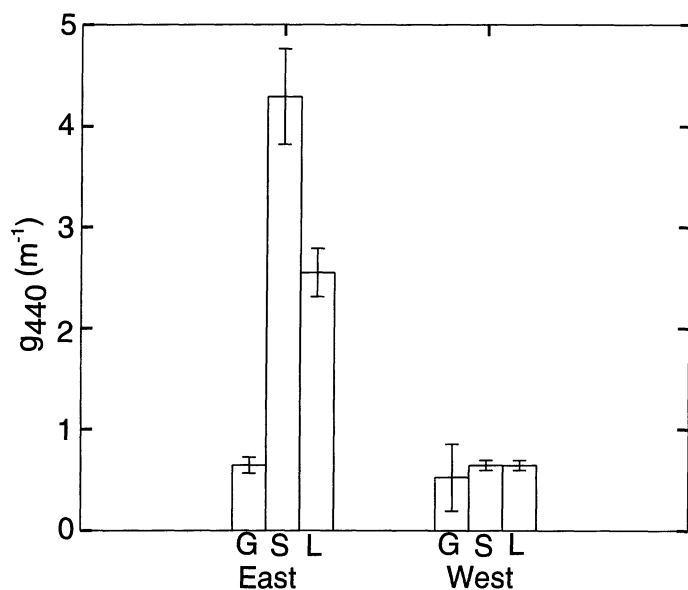


Fig. 2. Water color (g_{440}) for water obtained from different sources in the east and west basins of Long Lake. Values are summer means for 1994; error bars represent 1 SD. Groundwater, sampled at 1 and 2 m below the sediment-water interface—G; discharging groundwater, sampled just above the sediment surface with a seepage meter—S; the lake value, sampled at the deep central sampling station—L. Groundwater samples had multiple samples temporally and spatially; seepage meters had multiple samples spatially; lake samples had multiple samples temporally.

water interface (from inflow sites with seepage meters) was much more colored ($g_{440} > 4.0$) than either the lake water or groundwater (Fig. 2). Conversely, water color was not modified in the west basin at the sediment-water interface (Table 1).

Interbasin differences in water color and DOC concentration correspond well to the depth of the organic sediment layer. A primary route for allochthonous DOC input into surface waters involves leaching of organic material at the land-water interface (Cronan 1990; Wetzel 1992). Hyporheic zones can strongly influence the humic and DOC content of inflow waters by being active sites

Table 1. Conductivity ($\mu\text{mhos cm}^{-1}$), pH, and DOC (mg liter^{-1}) from various water sources to Long Lake. Values represent seasonal means for the three sites in each basin with groundwater recharge. (In parentheses—SD.)

Source	Conductivity	pH	DOC
East basin			
In lake	18.9(3.7)	5.88(0.19)	12.18(2.20)
Seepage meter	52.4(20.0)	7.02(0.20)	17.35(3.70)
Piezometer	63.6(20.8)	6.51(0.19)	11.87(2.41)
West basin			
In lake	16.6(2.1)	6.24(0.18)	7.53(1.25)
Seepage meter	23.8(10.0)	6.66(0.13)	11.78(1.73)
Piezometer	40.0(13.1)	6.33(0.15)	9.13(2.15)

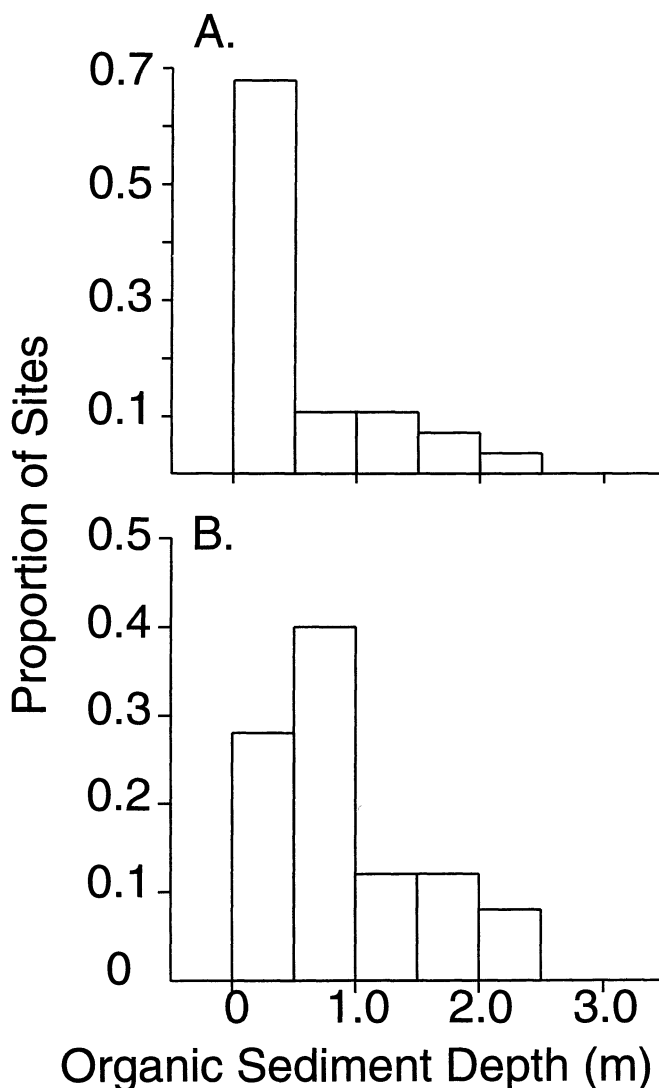


Fig. 3. Depth of organic sediment in Long Lake determined at 28 sites in the west basin (A) and 25 sites in the east basin (B). Depth distributions are significantly different between basins ($P < 0.005$, $\chi^2 = 12.37$, $df = 2$; Zar 1984).

for DOC processing or production (Wetzel 1992). The depth of littoral organic sediment was significantly ($P < 0.005$) deeper in the east basin (mean, 0.90 m) than in the west basin (mean, 0.55 m, Fig. 3). In the east basin, inflowing water contacted deeper organic sediments, potentially increasing water color more than inflowing water did in the west basin.

Changes in the chemical and physical environment in response to lake division began immediately in 1991 in the east basin (Fig. 4). DOC concentration increased steadily, almost doubling between 1990 and 1993 (summer mean, 7.5 mg liter^{-1} in 1990, 14.1 mg liter^{-1} in 1993; Fig. 4). The mean summer light extinction coefficient (k_d) also doubled from 1.19 m^{-1} in 1990 to 2.39 m^{-1} in 1993. Water color in 1993 ($g_{440} = 3.29 \text{ m}^{-1}$) was 3-fold higher than when it was measured in 1985 ($g_{440} = 1.06 \text{ m}^{-1}$),

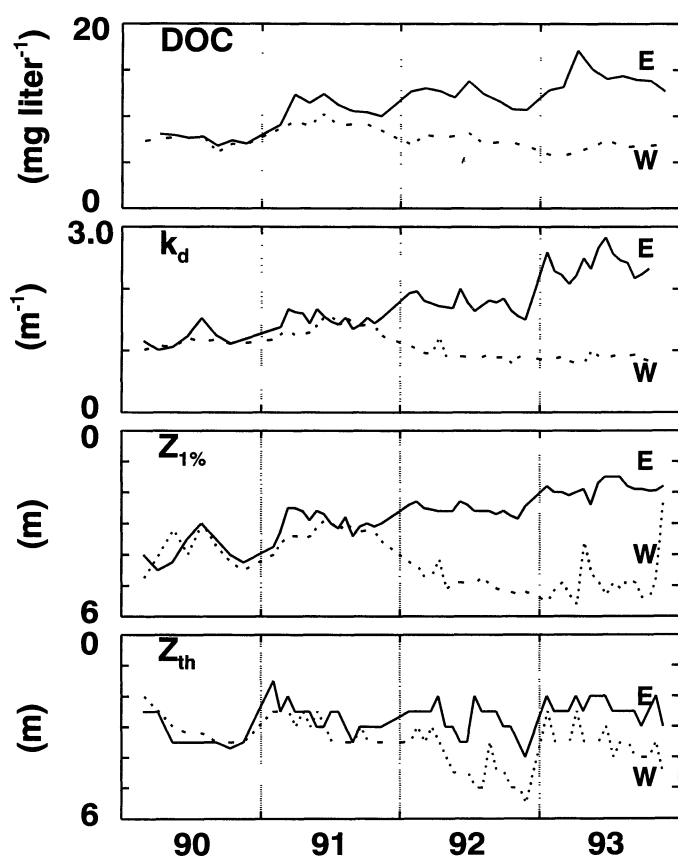


Fig. 4. Time trends for chemical and physical variables for Long Lake from 1990 to 1993. The east basin (E) is shown with solid lines and the west basin (W) with dashed lines. A. Dissolved organic carbon—DOC. B. Extinction coefficient— k_d . C. Photic zone— $Z_{1\%}$. D. Thermocline depth— Z_{th} .

prior to lake division (Elser 1987). Mean thermocline depth during the stratified season decreased by 30% from 1990 to 1993 (Fig. 4). Both light extinction and thermocline depth were altered significantly (Table 2). However, light penetration decreased more than the thermocline depth (Fig. 4); thus the effective light climate (Jones and Arvola 1984) in the epilimnion was reduced. By 1993, only 0.2% of incident solar radiation reached the thermocline, as compared to 2.8% in 1990.

In the west basin, the response to lake separation was generally weaker than in the east basin and lagged 1 yr after lake division. Summer mean DOC concentration increased in the west basin from 1990 ($7.2 \text{ mg liter}^{-1}$) to 1991 ($9.1 \text{ mg liter}^{-1}$) and decreased thereafter (Fig. 4). Light extinction followed a similar pattern to DOC concentration, but the effects of lake division on k_d could be explained by random processes (Table 2). By 1993 g_{440} had decreased to 0.86 m^{-1} —a decrease of $\sim 20\%$ from precursory measurements (Elser 1987). Although the thermocline depth in 1992 and 1993 increased by only 10% relative to thermocline depths measured in 1990 and 1991, the change was nonrandom (Table 2). By 1993 the amount of light penetrating to the thermocline had increased to 5.6% of incident solar radiation.

Table 2. Randomized intervention analysis (RIA, Carpenter and Kitchell 1993) for selected physical, chemical, and biological variables. Units for the effect size (Carpenter and Kitchell 1993) and pooled standard deviation (PSD, Zar 1984) are the same as the dependent variate. For each series, the P -value from RIA and sample sizes before (n -pre) and after (n -post) dividing Long Lake are presented. Sampling before (1989–1991) and after (1991–1993) perturbation followed the identical protocol.

Variate	Effect size	PSD	P -value	n -pre	n -post
East basin					
k_d (m^{-1})	0.76	0.21	<0.001	26	48
Thermocline (m)	0.56	0.53	<0.001	26	48
Oxygenation (m)	1.69	1.99	0.002	26	48
Chl a (mg m^{-3})	0.3	11.3	0.25	25	49
Chl a (mg m^{-2})	2.9	50.9	0.68	25	49
West basin					
k_d (m^{-1})	0.02	0.36	0.78	25	50
Thermocline (m)	0.53	0.54	<0.001	25	50
Oxygenation (m)	1.29	2.17	0.010	25	50
Chl a (mg m^{-3})	6.8	6.2	0.28	25	50
Chl a (mg m^{-2})	0.2	44.0	0.31	25	50

Although generally correlated, changes in DOC and color were not equivalent in Long Lake. In the east basin, DOC concentration increased ~ 2 -fold while g_{440} tripled, suggesting that a greater proportion of DOC was composed of light-attenuating materials after lake separation. Similarly, in the west basin, DOC decreased $\sim 10\%$ after lake separation, while water color decreased by 20%. Apparently, light-attenuating DOC made up less of the total DOC after lake separation in the west basin. This pattern is similar to the finding of Thurman (1985) that humic and fulvic acids (light-attenuating DOC) comprise a low proportion of DOC in clear and eutrophic lakes. Our data suggest that there were qualitative differences of DOC in the two basins, which could have important ecosystem-scale implications (i.e. Jones 1992; Schindler et al. 1992).

Division of Long Lake led to significant changes in the physical and chemical environment. Fluctuations in the reference system, Paul Lake, were much smaller than those in Long Lake (Figs. 4 and 5, note scale changes on axes). The many nonrandom changes that were detected in the east and west basins of Long Lake were not explainable by trends in the reference system (Table 2). DOC concentration correlates highly with light penetration in broad surveys across wide ranges of water colors (Jones and Arvola 1984). Increased DOC and color strongly regulated the light climate in both basins of Long Lake, as evidenced by the high correlation between k_d and DOC concentration ($r = 0.90$).

Changes in physical and chemical environment were accompanied by shifts in the vertical distribution of chlorophyll in Long Lake, but not in the reference system (Paul Lake). Chlorophyll was distributed nearly equally between the epilimnion and metalimnion in both basins of Long Lake in 1990 and (Fig. 6). After 1991, chlorophyll was primarily located in the epilimnion in the east basin

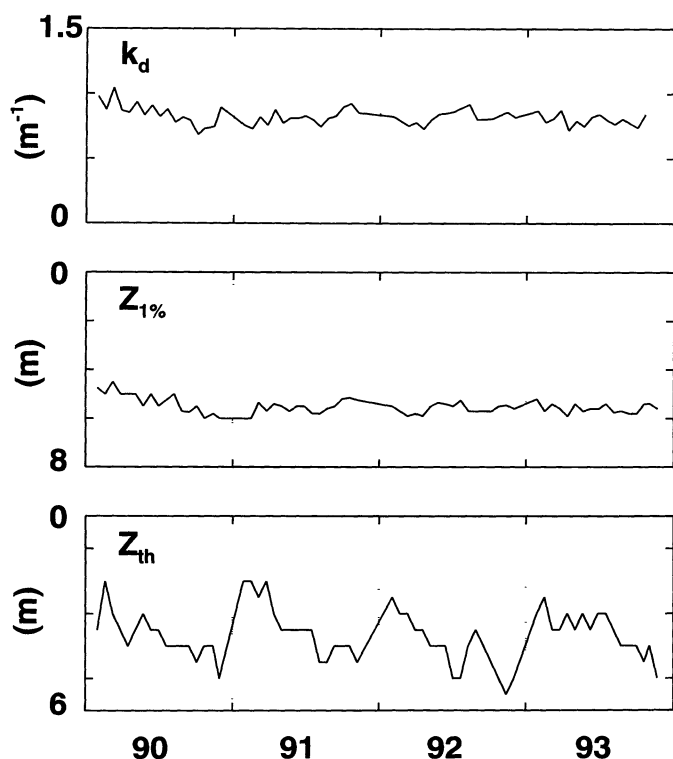


Fig. 5. As Fig. 4, but of physical variables in Paul Lake from 1990 to 1993.

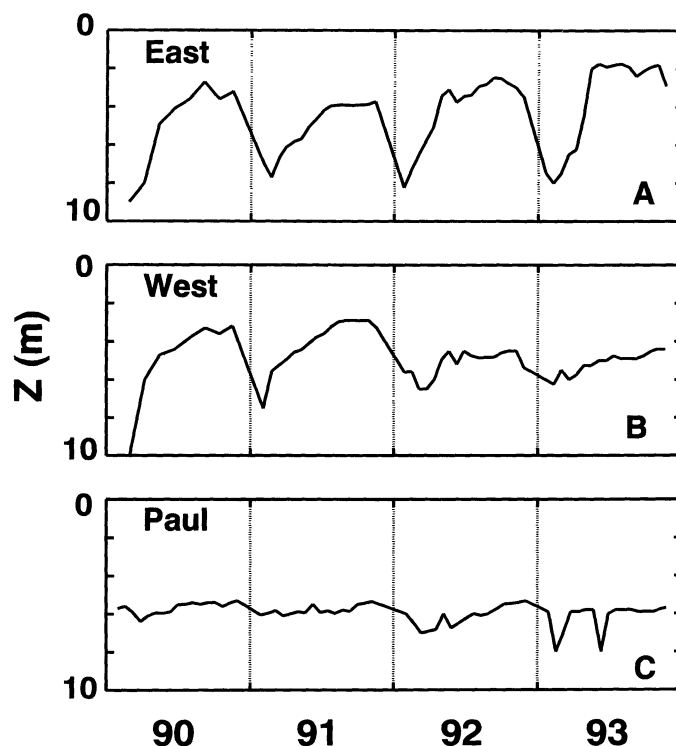


Fig. 7. Maximum depth of oxygenation for the east (A) and west (B) basins of Long Lake and for Paul Lake (C).

and in the metalimnion of the west basin. Despite shifts in phytoplankton distribution, areal chlorophyll and epilimnetic chlorophyll concentration were unchanged in both basins after lake division (Table 2). Chlorophyll concentrations in Paul Lake were stable throughout the study period (Carpenter et al. 1995).

After enrichment, blue-green algae became abundant in the west basin but not in the east basin. Blue-greens were a prominent component of the west basin phyto-

plankton community (Carpenter et al. 1995). Blue-greens (dominated by *Anabaena spiroides* and *Anabaena flos-aquae*) comprised up to 95% of the biovolume of pelagic phytoplankton. The east basin contained few blue-greens in 1993 ($<0.1 \text{ g m}^{-3}$ wet wt), never $>5\%$ of the total algal biovolume, and was dominated by chrysophytes and dinoflagellates (*Synura* and *Gymnodium* spp). The differences in phytoplankton may be due to direct or indirect effects from DOC and physical or chemical interactions with pH, CO_2 , nutrient or trace metal availability, and light quality or intensity (Shapiro 1990). Regardless of the mechanism, it seems that DOC loading may interact with P loading to determine the abundance of blue-greens in lakes.

Changes in chlorophyll distribution, light penetration, and mixing depth led to predictable changes in the depths at which net production of oxygen was occurring. The maximum depth of oxygenation ($1 \text{ mg O}_2 \text{ liter}^{-1}$) decreased in the east basin from 1990 to 1993 (Fig. 7A). By 1993, the west basin had more light penetrating to the thermocline and thus had more metalimnetic photosynthesis, which in turn increased the depth of oxygenation (Fig. 7B). Seasonal trends changed as the depth of oxygenation in the west basin became more constant over the course of the stratified season. This pattern was more consistent with Paul Lake (Fig. 7C), which had a well-developed metalimnetic chlorophyll layer for the duration of the study.

We have summarized an example of the role of surprise in whole-ecosystem experiments. Because pelagic com-

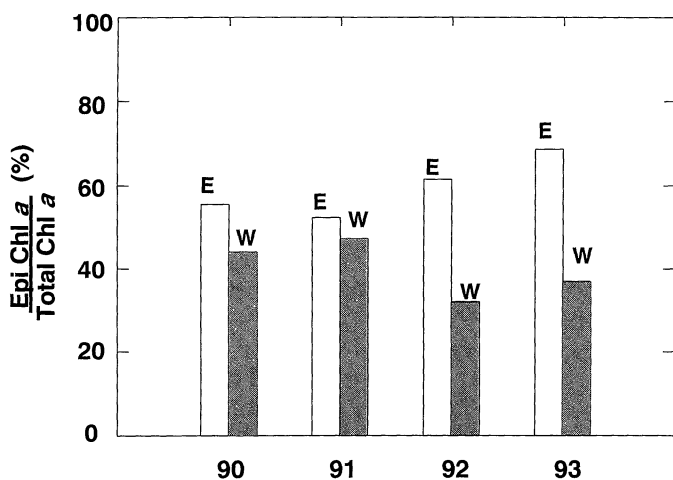


Fig. 6. Proportion of epilimnetic chlorophyll (mg m^{-2}) to total water-column chlorophyll (mg m^{-2}) in Long Lake. Bars represent summer mean values. East basin—E; west basin—W.

munities and lake ecosystems are driven by processes from their watersheds (Wetzel 1992), the phenomena that we documented could not have been studied at spatial scales smaller than the entire watershed and lake. Split-lake designs have been a powerful tool for such whole-lake ecosystem analysis (Likens 1985). Differences that were not apparent before manipulation led to substantial differences in DOC, water color, transparency, mixing depth, and response of phytoplankton to nutrient enrichment. Key elements of our study that enabled us to understand these unexpected changes included multiyear baseline data, a reference ecosystem, and a sampling program that encompassed a comprehensive set of limnological variables. In planning and funding whole-ecosystem experiments, it may be tempting to cut costs by reducing the duration of baseline studies, eliminating reference ecosystems, or limiting the sampling program. The responses that we measured, such as a 1-yr lag for DOC response in the west basin of Long Lake, demonstrate that such economies could compromise the interpretation of the experiment.

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