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Limnology and Oceanography, Vol. 34, No. 4 (Jun., 1989), 700-717.

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Whole-lake experiments: The annual record of fossil pigments and zooplankton

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Abstract

The annual record of fossil pigments and zooplankton was compared with detailed contemporaneous records from two manipulated lakes from 1940 to 1986. Annually resolved sedimentary records accurately monitored known changes in plankton communities, identified periods of trophic change, and proved a powerful tool for examining long-term, complex interactions. Both Paul and Peter Lakes underwent the same three complete changes in their fish assemblages (trout, cyprinid, bass), and Peter Lake received repeated inputs of lime. Alterations in fish community composition produced long-lived changes in zooplankton communities that cascaded to the microbial level of the food web. Liming, in concert with trophic changes, caused distinctive phytoplankton dynamics in Peter Lake.

Paleolimnological data recorded all major plankton dynamics known from coeval limnological data. Specifically, the sediment record showed transitions in cladoceran size structure and species composition, changes in water clarity resulting from both food web and chemical manipulations that affected vertical zonation of primary producers, and changes in absolute abundance of all algal divisions except dinoflagellates. Undegraded Chl *a* indicated deep blooms and, in conjunction with Chl *c*, fucoxanthin and β -carotene, indicated metalimnetic chrysophytes. Transient (2-3 yr) non-selective increases in sedimentation corresponded with increases in grazing rates. Isorenieratene indicated overlap of photic and anoxic zones, revealing changes in transparency and conditions for pigment preservation.

A historical perspective of the intrinsic variability of lakes is necessary to evaluate the effects of manipulative or natural disturbances (Likens 1983; Schindler 1987). Whole-lake experiments demonstrate that nutrient loading ultimately delimits potential productivity and much of the unexplained variation may be due to dynamic food web effects (Schindler 1987; Carpenter and Kitchell 1988). Cascading trophic interactions are strongest in lakes in which size-selective planktivory by fish influences the abundance of large-bodied zooplankton (Carpenter et al. 1985, 1987). Both chemical and trophic perturbations may induce fluctuations in ecosystem structure that develop

over years to decades (Schindler 1987; Carpenter 1988). These temporal dynamics are difficult to quantify in studies lasting only a few years.

Paleolimnology rapidly yields long-term data that are often otherwise unattainable. The sedimentary record integrates over both time and space, synthesizing ecosystem responses to manipulation. Zooplankton fossils monitor populations, size structure, and the effects of planktivory (Kerfoot 1974, 1981; Kitchell and Kitchell 1980). Carotenoids can record the dynamics of algal communities (Züllig 1981; Sanger 1988). Unfortunately, unambiguous interpretation of sedimentary signals is difficult (Binford et al. 1983; Swain 1985). These difficulties can be resolved through paleolimnological studies of manipulated lakes where results have been documented for many years. However, direct comparisons of coeval limnological and paleolimnological records are rare (Haworth 1980).

This paper compares the annual record of fossil pigments and pelagic zooplankton remains with contemporaneous limnologi-

Acknowledgments

This work was supported by NSF grants BSR 86-04996, BSR 86-06271, and BSR 85-21832 and the Sigma Xi Grants-in-Aid-of-Research program. We thank Arthur Hasler and coworkers for conducting the original whole-lake manipulations, Sharon Barta for zooplankton microfossil analyses, Martin Berg and Marianne Douglas for assistance with coring, and John P. Smol for preliminary algal microfossil analysis and helpful comments.

cal records from two lakes in northern Michigan. Peter and Paul Lakes have undergone three major changes in fish community structure since 1951 (Elser et al. 1986). Because both lakes have annually laminated sediments, they provide an excellent opportunity to compare high resolution sedimentary signals with known trophic manipulations. Additionally, Peter Lake has received periodic inputs of hydrated lime, thereby allowing quantification of the joint effects of predator and chemical perturbations.

To date, no study has examined the sedimentary pigment record for evidence of predator-mediated changes in algal community composition. Few paleolimnological studies attribute changes in fossil zooplankton assemblages to alterations in fish community structure (e.g. Kerfoot 1974; Kitchell and Kitchell 1980) despite early appreciation of this approach (Hrbáček 1969). Fish-induced changes in zooplankton communities should produce recognizable sedimentary pigment signals. Photooxidation is a major loss process for photosynthetic pigments (Carpenter et al. 1986; Welschmeyer and Lorenzen 1985*a,b*). Pigments in the feces of large-bodied zooplankton bypass bleaching due to rapid sedimentation from the photic zone whereas egesta of microzooplankton sink slowly and are oxidized high in the water column (Welschmeyer and Lorenzen 1985*a,b*; Carpenter et al. 1988). Thus replacement of small grazers by large herbivores, or replacement of epilimnetic grazers by metalimnetic herbivores, increases pigment deposition (Kitchell and Carpenter 1987; Carpenter et al. 1988).

Replacement of a small-bodied, inefficient herbivore assemblage by large, efficient grazers also reduces algal standing crop and leads to increased water transparency (Shapiro and Wright 1984; Carpenter et al. 1987; Mazumder et al. 1988). Changes in water clarity regulate the presence of deep bloom-forming algae (Pick et al. 1984) and bacteria (Brown et al. 1984). These blooms are well preserved in lacustrine deposits (McIntosh 1983; Brown et al. 1984). This paper examines the sedimentary record of fossil pigments and zooplankton for evi-

dence of long-term responses of lakes to biotic and abiotic manipulation.

Site history

Peter and Paul Lakes are small, humic-stained, seepage kettle lakes located on the University of Notre Dame Environmental Research Center (Section 36, T45N, R42W, Gogebic County, Michigan). Site description, regional physiography, and geology are presented elsewhere (Potzger 1942; Kitchell and Kitchell 1980). Recent limnological characteristics are described by Elser et al. (1986) and below. These lakes have a well-documented history, much of which is unpublished but available to scholars in the University of Notre Dame Archives, File Series UVBG (referred to herein as UNDA 1988). Originally contiguous, the lakes were separated in 1951 as part of an experimental program to improve fisheries yield (Johnson and Hasler 1954). Disturbance and manipulation have been extensive and can be divided into three categories: watershed disturbances (deforestation, fire, flooding, basin division), trophic manipulations (natural and experimental species replacements), and manipulation of water chemistry (liming, dike washout).

Watershed disturbance—Watershed disturbances began before the turn of the century. Survey maps from 1852 show the original forest to consist of hemlock, birch, sugar maple, balsam, and cedar. These lands were cut-over during 1870–1890 (UNDA 1988). Ownership of land surrounding the lakes was retained by logging companies until 1936, when it was conveyed to the Department of Agriculture. No further logging occurred until 1954 when selective removal of aspen, poplar, and white pine was allowed for a 10-yr period.

Although wildfires were common in northern Wisconsin (Vogl 1970), there are few records of burns in the vicinity. In 1910 and again in 1913, fires devastated forests 1.6 km south of the lakes (UNDA 1988). It is unknown if any part of the lake basin was affected. The last fire in the region occurred ~1924 (P. Allard, Jr. pers. comm.).

Comparison of aerial photographs taken in 1937 and 1947 reveals increased water levels in this decade. Currently, cut tree

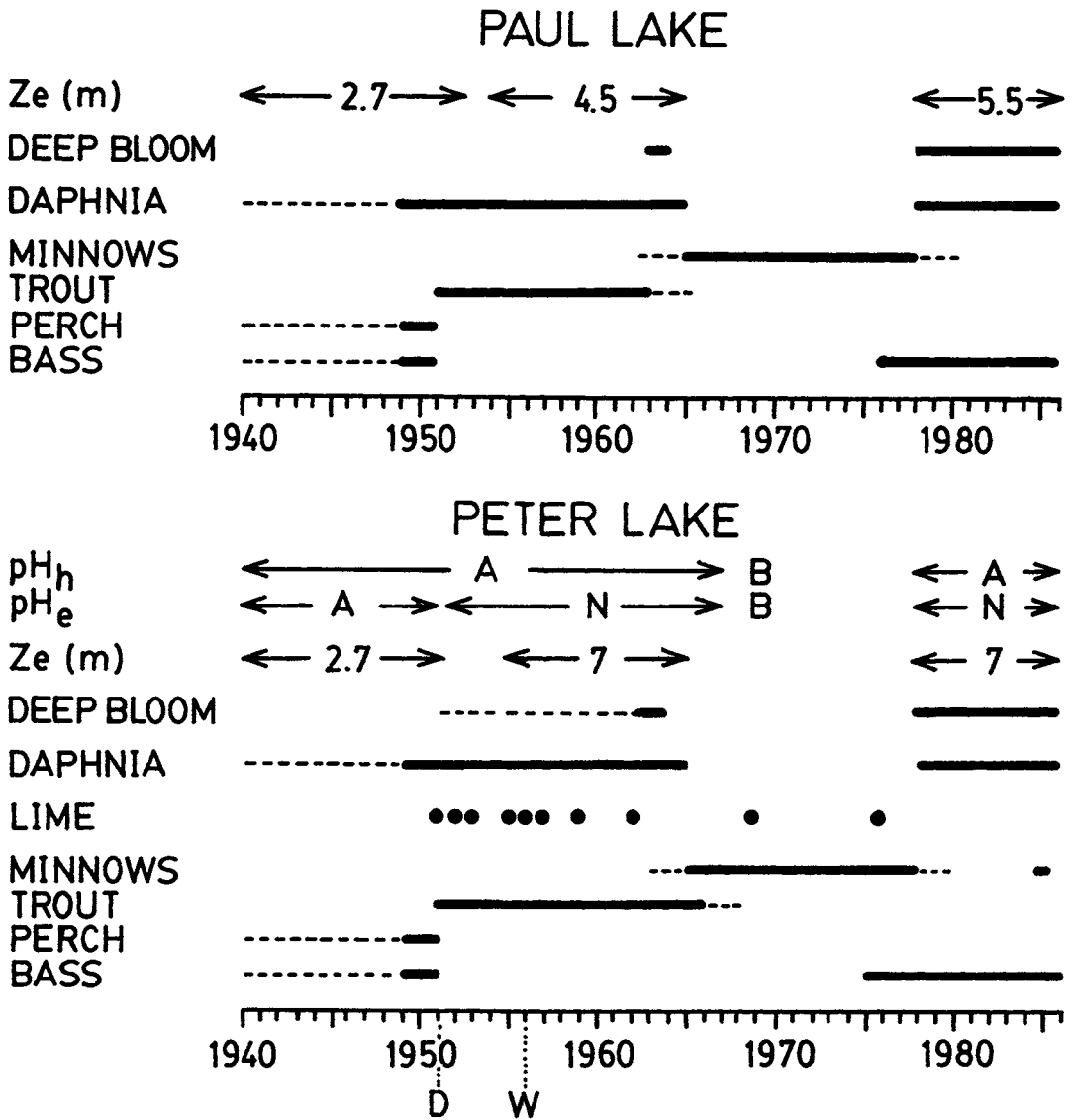


Fig. 1. Summary of historical data presented in text. Solid lines—documented presence or dominance; dashed lines—inferred; Ze—photic zone depth; pH_h—hypolimnetic pH; pH_e—epilimnetic pH; A—acidic (pH 5–6); B—basic (>8); N—circumneutral pH; D—dike construction; W—dike and road washout.

stumps are present under 1 m of water in both lakes. These rises may be due to increased runoff from a gravel-bed road (constructed 1938; UNDA 1988) and damming of the outlet of Peter Lake by beavers. Aging of a black spruce (*Picea mariana*) growing on the dam suggested beaver abandonment in 1941 (P. R. Leavitt pers. obs.).

The final change in the lakes' watershed occurred in May 1951 when the shallow

channel between basins was closed with an earthen dike (Johnson and Hasler 1954) (Fig. 1). During periods of high water, Paul Lake drains into Peter Lake through a culvert that traverses the dike.

Trophic manipulations—Trophic manipulations began after basin division in 1951 (Fig. 1) when rotenone was used to remove the native fish assemblage of yellow perch (*Perca flavescens*) and largemouth bass (*Mi-*

Table 1. History of rainbow trout addition to Paul Lake. (Not recorded—nr.)

		Density (ind. ha ⁻¹)	Size* (cm)	Mass† (kg ha ⁻¹)	Reference
1951	Spring	500	15–18	20	Johnson and Hasler 1954
1952	Spring	1,000	15–18	40	Johnson and Hasler 1954
		325	25–28	51	
1953	Spring	nr	15–18	nr	Stross 1958
	Fall	312	7–10	2	
1954	Fall	nr	7–10	nr	UNDA 1988
1956	Spring	500	20–25	56	UNDA 1988
1957	Spring	nr	nr	nr	UNDA 1988
1959	Fall	93	20–25	9	UNDA 1988
1961	Spring	610	15–18	29	UNDA 1988

* Standard length.

† If unknown, estimated from length–weight regressions of Carlander 1969.

cropterus salmoides) (Johnson and Hasler 1954). Rainbow trout (*Oncorhynchus mykiss*) were regularly stocked to Paul Lake between 1951 and 1961 (Table 1), but did not reproduce and declined due to periodic winterkill. By 1970, the failing trout population was replaced by a cyprinid assemblage (Elser et al. 1986). Although not well documented, the fish community composition consisted of northern redbelly dace (*Phoxinus eos*), finescale dace (*Phoxinus neogaeus*) and mudminnows (*Umbra limi*) (W. Tonn and C. Paszkowski unpubl. obs.;

O. J. Stewart pers. comm.). Minnows dominated the fish community until 1976, when largemouth bass invaded from Peter Lake (R. Gordon pers. comm.). Minnows were still present in 1978 but rare by 1980. Currently, Paul Lake is a virtual monoculture of bass and has a zooplankton community dominated in biomass by large-bodied *Daphnia pulex*, *Daphnia rosea*, and *Diaptomus oregonensis* (Carpenter et al. 1987).

The trophic manipulation history of Peter Lake is more complex than that of Paul Lake (Table 2, Fig. 1). In 1985, 90% of the adult

Table 2. Manipulation history of Peter Lake. All lime additions as hydrated lime, except 1976, as CaCO₃. All fish additions are rainbow trout, except 1975 and 1985. (Not recorded—nr.)

		Fish stocking			Lime addition (kg ha ⁻¹)	Reference‡
		Density (ind. ha ⁻¹)	Size* (cm)	Mass† (kg ha ⁻¹)		
1951	Spring	365	15–18	19	1,040	Johnson and Hasler 1954
1952	Spring	750	15–18	40	1,115	Johnson and Hasler 1954
1953	Spring	nr	15–18	nr	303	Stross 1958
	Fall	313	7–10	2		
1954	Fall	nr	7–10	nr		UNDA 1988
1955	Spring				10	
1956	Spring	375	20–25	55	43	UNDA 1988
1957	Spring	nr	nr	nr		UNDA 1988
	Fall				530	
1959	Spring				492	
	Fall	42	20–25	6		UNDA 1988
1961	Spring	458	15–18	29		UNDA 1988
1962	Spring				115	
1965	Spring	nr	nr	93		UNDA 1988
1969	Fall				1,890	
1975	Spring	10§	nr	nr		Kitchell and Kitchell 1980
1976	Fall				378	
1985	Spring	–194	nr	–56		Carpenter et al. 1987
		18,709	nr	56		

* Standard length.

† If unknown, estimated from length–weight regressions of Carlander 1969.

‡ All references for liming from Elser et al. 1986, except 1957 from UNDA 1988.

§ Largemouth bass stocked.

|| Largemouth bass removed, cyprinids stocked.

bass were removed and an equivalent mass of cyprinids stocked. The minnow population was eaten by remnant bass within 6 weeks and the zooplankton remained similar to that of Paul Lake (Carpenter et al. 1987).

Chemical manipulation—Addition of hydrated lime to Peter Lake began in 1951 and continued sporadically until 1976 (Table 2, Fig. 1). Effects of liming are described in detail by Elser et al. (1986) and consisted of increased transparency, pH, and alkalinity, relative to the unlimed reference basin (Paul Lake). The largest lime addition occurred in 1969 and was followed in 1976 by the sole addition of CaCO_3 (UNDA 1988).

Some change in the chemical environment of the lakes may have occurred as a result of a partial washout and repair of the road and dike in 1956.

Effects of manipulation and disturbance—Manipulations of the lakes had significant effects on both their biotic and abiotic properties (Fig. 1). Unpublished records of Birge and Juday show that Peter and Paul Lake was colored (platinum cobalt scale, 60; Secchi depth, 1.5 m) and acidic (epilimnetic pH, 5.4–5.9) in 1939 (UNDA 1988). These conditions were believed to be due to logging activities and fire (Juday in UNDA 1988), rather than the influence of a bog mat, which, although present, was less extensive than in later years (aerial photographs in UNDA 1988). Similar transparency and pH existed before construction of the dike separating the two basins of the lake in 1951 (Johnson and Hasler 1954). With the addition of hydrated lime to Peter Lake, humic acids were precipitated and photic zone depth (Z_e , depth of 1% incident light measured by submersible photometer) increased from 2.7 to 4.3 m, while Paul Lake maintained premanipulation conditions (Johnson and Hasler 1954; Elser et al. 1986) (Fig. 1). By 1955, the Z_e of Paul Lake was 4.2 m and this clarity was maintained until at least 1965 (Malueg 1963; Stross and Hill 1968). The cause of increased water clarity is unknown. During this period, the Z_e of Peter Lake increased to 7 m (Stross 1958; Malueg 1963).

Between 1951 and 1965 the zooplankton

of Paul Lake was dominated by the pre-manipulation assemblage of *D. pulex* and secondarily *D. rosea*. In Peter Lake, *D. rosea* had replaced *D. pulex* by 1964 (Johnson and Hasler 1954; Stross and Hill 1968). Phytoplankton communities in Peter Lake became more diverse concurrent with liming. Large chlorophytes, cyanophytes, and chrysophytes dominated the net phytoplankton in the early 1950s (Johnson 1954). Quantitative algal enumerations show that by 1962, metalimnetic populations of both chrysophytes and cyanophytes were present in Peter Lake (Malueg 1963). These changes led to an increase in areal, but not volumetric, primary productivity (Stross and Hasler 1960). In Paul Lake, the net phytoplankton of the 1950s was dominated by dinoflagellates (Johnson 1954). Metalimnetic populations of chrysophytes were also present by 1962 (Malueg 1963).

By the early 1970s *Bosmina longirostris* was the dominant zooplankton in both lakes. *Bosmina* was replaced by *D. pulex* and *D. rosea* after bass introduction (Kitchell and Kitchell 1980; Hodgson and Kitchell 1987). Limnological records are scarce for the period 1967–1975. In 1970 the epilimnetic thickness in Peter Lake was only half that either before or after the 1969 liming (UNDA 1988), while by 1975 the relative color (absorbance at 445 nm) had doubled compared to Paul Lake (UNDA 1988). Parkin and Brock (1980; UNDA 1988) noted that the photic zones of Peter Lake and Paul Lake had increased to 7.5 and 5.5 m, respectively, by 1978–1979 and that deep blooms of green photosynthetic sulfur bacteria were present in both lakes. Chlorophytes were dominant in epi- and metalimnetic waters. Limnological conditions and plankton communities remained relatively stable through 1986 (Elser et al. 1986; Carpenter et al. 1987), although metalimnetic populations of chrysophytes have been a consistent feature of recent years (St. Amand and Carpenter unpubl. data).

Materials and methods

Sediment sampling in June 1987 used the freeze-coring technique of Swain (1973). Cores were taken from the deepest portion of each lake (Peter, 19.6 m; Paul, 15 m).

Frozen cores were quartered vertically on a bandsaw, cleaned with a woodplane, and the uppermost 15 cm lyophilized for 4 h in the dark. The inner surface of the core was lined with aluminum foil to promote lyophilization from the outer surface. Surface contaminants were removed with adhesive tape before an additional 20 h of freeze-drying, after which a 1-cm-thick region of lyophilized sediment lay over a frozen base. All sediment sections were laminated throughout their length.

Individual annual laminations were separated manually at 3°C; two distinct clay layers served as markers for 1951 (dike construction) and 1956 (dike washout). To prevent thawing, we sectioned sediment cores on an ice-filled bottle of circumference equal to that of the inner surface of the core. Each varve was transferred to a 25-ml gastight glass vial, homogenized, and stored in the dark at -20°C.

Before analysis, samples were re-lyophilized to remove residual ice. Aliquots were analyzed for organic matter by weight loss on ignition (Dean 1974) and for photosynthetic pigment content. Carotenoids, chlorophylls, and their derivatives were extracted by soaking 20–75 mg of sediment (dry wt) in 6 ml of acetone:methanol:water (80:15:5 by vol.) for 24 h at 10°C (Leavitt and Brown 1988). This procedure completely extracted all pigments in comparison to replicated exhaustive extractions by ultrasonic homogenization of both lyophilized and freshly thawed sediments. This test also verified that no significant degradation occurred in sectioning or extracting procedures. Extracts were filtered (0.2- μ m Acropore membrane filter), dried under a stream of nitrogen gas, sealed, and stored at -20°C until analysis. No pigment degradation resulted from this procedure (Carpenter et al. 1986). Extractions were conducted under low, indirect lighting with degassed HPLC-grade solvents.

Pigment concentrations were quantified by reversed-phase HPLC (modified from Mantoura and Llewellyn 1983) with a Beckman model 421 controller, model 110A pumps, and model 165 detector, a Rainin Microsorb C₁₈ column (5- μ m particle size), and a Shimadzu electronic integrator. Pig-

ment samples were dissolved in a mixture of acetone, ion-pairing reagent (IPR), and methanol (70:25:5 by vol.) before injection. IPR consisted of 0.75 g of tetrabutyl ammonium acetate and 7.7 g of ammonium acetate in 100 ml of water. Analytical separation was achieved by isocratic delivery (1.5 ml min⁻¹, 21,000 kPa) of mobile phase A (10% IPR in methanol) for 1.5 min, followed by a linear ramp to 100% B (27% acetic methanol) over 7 min, and isocratic hold for an additional 12.5 min. The column was re-equilibrated between samples by linear ramping to 100% A over 7 min and maintenance for 4.5 min before sample injection. Samples were scanned at both 660 and 430 nm. Analysis of replicate samples yielded a C.V. of <10%.

The HPLC system was calibrated with a dilution series of each chromatographically pure pigment, where the amount of pigment in each standard was determined spectrophotometrically (Davies 1976). Specific extinction coefficients were obtained from Davies (1976), Foppen (1971), and Brown (1968). Pigment identifications were based on comparisons of the spectral characteristics and chromatographic mobility of pigments isolated from sediments with those from unialgal cultures (*see below*), water samples of known phytoplankton composition, and published values. Pigments from all sources were isolated from HPLC elutant, diluted 50% with water and collected on Waters C₁₈ SEP-PAK cartridges. Spectra were obtained and compared in acetone, methanol, ethanol, hexane, and diethyl ether with matched quartz cuvettes and a Beckman recording spectrophotometer (model DU-7). The chromatographic mobility and light extinction characteristics of the pigments were compared to those listed by Mantoura and Llewellyn (1983), Davies (1976), Foppen (1971), and Wright and Shearer (1984). Isorenieratene was further identified by NMR and mass spectroscopic analysis by S. Liaen-Jensen and was donated by H. J. McIntosh.

Chl *a* and *b* derivatives were created by extracting *Poa pratensis* with either 50% aqueous acetone or methanol to produce acid or methyl chlorophyllides and acidifying (1 h, 5% solution of 1 N HCl) to con-

Table 3. Pigments quantified and their taxonomic affinities (after Bold and Wynne 1985).

Pigment	Taxa
Alloxanthin	Cryptophyta
Lutein-zeaxanthin*	Tracheophyta, Chlorophyta, Euglenophyta, Cyanophyta
Fucoxanthin	Chrysophyta†
β -carotene	Plantae, some photosynthetic bacteria
Chlorophyll <i>a</i>	Plantae
Chlorophyll <i>b</i>	Tracheophyta, Chlorophyta, Euglenophyta
Chlorophyll <i>c</i>	Chrysophyta, Pyrrophyta
Isorenieratene	Chlorobiaceae (brown varieties)

* Not separated.

† Also one species of dinoflagellate.

vert these to their respective pheophorbides (N. Welschmeyer pers. comm.). Pheophytin derivatives were produced by acidification in acetone (as above) of pure chlorophyll samples obtained from either Sigma Chemical Co. or extracts of *P. pratensis* or *Fucus* sp. Pigments quantified and their taxonomic affinities are presented in Table 3.

Unialgal cultures were obtained from Carolina Biological Supply or the University of Texas Culture Collection (UTEX) and included the cyanophytes *Synechococcus* spp. (UTEX 1191, 563, 625) and *Coccolchlois peniocystis* (UTEX 1548) (β -carotene, zeaxanthin sources); the dinoflagellate *Peridinium cinctum* (peridinin); the chlorophytes *Chlamydomonas reinhardtii*, *Ulothrix* sp., *Micrasterias* sp., and *Trachelomonas* sp. (β -carotene, lutein, α -carotene); the chrysophytes *Synedra* sp. and *Ochromonas danica* (fucoxanthin, Chl *c*; also from *Fucus* sp.); and *Cryptomonas ovata* (UTEX 358) (alloxanthin).

Zooplankton microfossils were analyzed on a deep-water core collected in 1984 with our technique. Laminae were isolated from a partially thawed core with sectioning procedures similar to those used here. Samples were subject to KOH digestion and dispersion (Kitchell and Kitchell 1980) before microscopic quantification of the abundance of daphnid remains relative to those of *Bosmina* [% *Daphnia* = $Daphnia / (Daphnia + Bosmina)$]. Presence of two clay layers (1951, 1956) and annual laminae in all cores allowed direct comparison of fossil pigment and zooplankton profiles.

Results and discussion

We organize data in blocks of time (zones) that correspond to the major biotic dynamics. The most dynamic fossil signals occurred at transitions between communities. Therefore, our presentation of each lake is organized around transitions between zones. For each lake, an overview of major inferences from paleolimnology is followed by detailed mechanisms and interpretations. Organic matter content was relatively constant throughout the cores in both lakes except during periods of high clay influx (Leavitt and Carpenter 1989).

Overview of Paul Lake—Two of the three changes in the fish assemblage altered the plankton of the lake (Fig. 2). Removal of native fishes and addition of trout (zones I–II) had no effect. Decline of trout populations and expansion of cyprinid populations (zones II–III) caused replacement of large-bodied *Daphnia* by small-bodied *Bosmina*. Algal standing crops increased in the presence of these inefficient grazers, leading to reduced light penetration and loss of metalimnetic chrysophyte blooms. Elimination of cyprinids by piscivorous largemouth bass (zones III–IV) allowed large *Daphnia* to return and reduce algal standing crops. Water transparency increased and deep populations of both chrysophytes and photosynthetic bacteria developed.

Premanipulation—The bass-perch assemblage extends from 1940 to 1951 and is characterized by slowly decreasing concentrations of all algal carotenoids (zone I, Fig. 3). Historical data show that this zone represents a period of recovery from watershed disturbance (UNDA 1988). Deforestation of the watershed was complete by 1937 and, in concert with road-building (1938), would be expected to increase runoff and nutrient loading to the lake (Likens et al. 1970). Increased water levels due to damming of the outlet by beavers (~1937–1941) would inundate surrounding soils and further increase leaching of nutrients. Thus, the most plausible explanation for the carotenoid declines is that they represent reductions in algal productivity due to decreased erosion, leaching, and nutrient input during recovery from disturbance. Unfortunately, due to multiple causal mechanisms, it is difficult

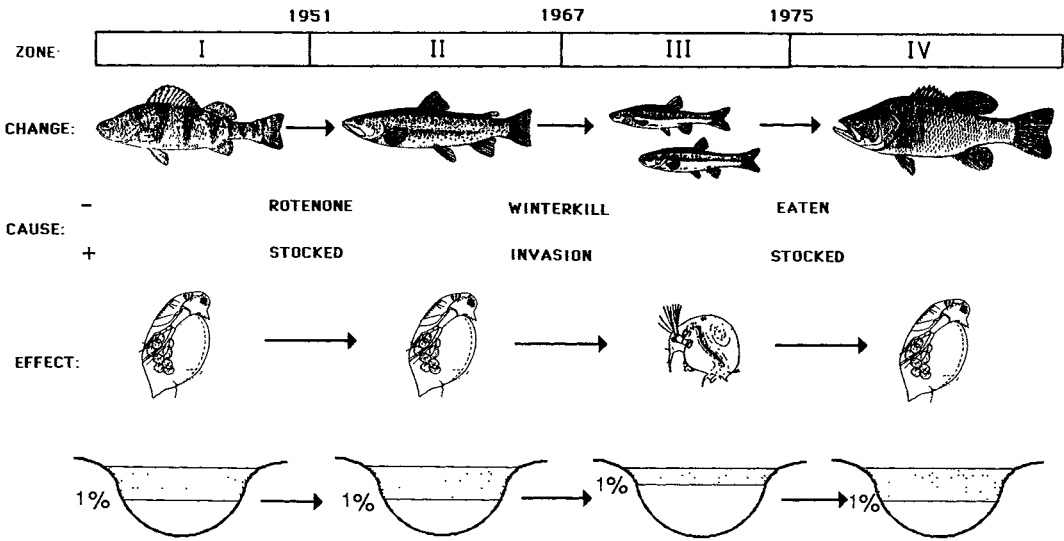


Fig. 2. Summary of the effects of trophic manipulation in Paul Lake. Lower limit of light penetration—1%; reason for species loss—(-); reason for species gain—(+). See text.

to ascribe the pigment declines to recovery from a given disturbance.

Unlike other pigments, Chl *a* concentrations decline only slightly in zone I, presumably because Chl *a* is extremely labile (Carpenter et al. 1986, 1988; Leavitt and Carpenter in press). Accumulation rates of undegraded chlorophyll are governed by the position of the algae in the water column and the hypolimnetic environment rather than algal productivity (Swain 1985; Engstrom et al. 1985).

By 1951, the net phytoplankton of Paul

Lake was dominated by *Peridinium* sp. (Johnson 1954). Although this alga remained dominant in net tow collections through 1954, its characteristic carotenoid (peridinin) was absent throughout the core. Similar underrepresentation of dinoflagellates has been recorded for other lakes (Zülbig 1982; Hurley 1988). Because peridinin is very labile, losses during sedimentation exceed those of most other carotenoids (Hurley 1988; Leavitt and Carpenter in press).

Transition zone I-II—The first change in

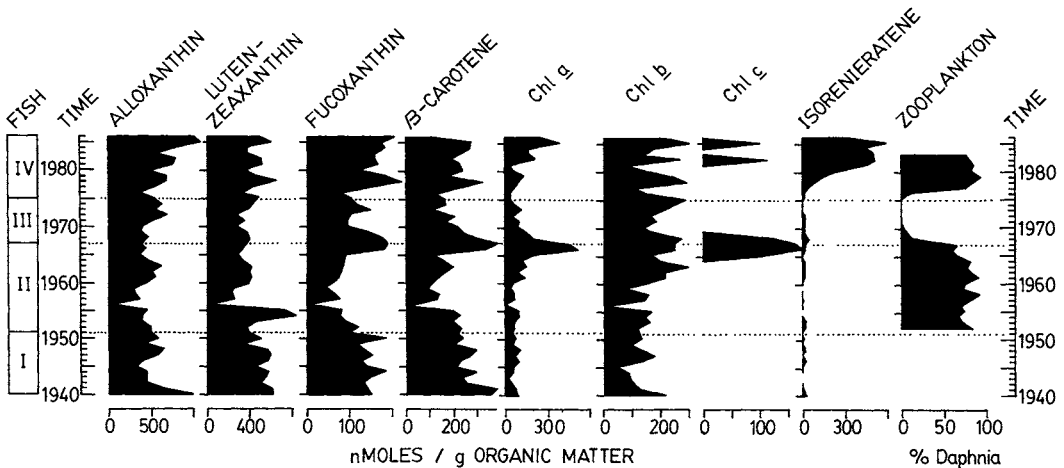


Fig. 3. The sedimentary record of fossil pigments and zooplankton in Paul Lake, 1940-1986. Fish zones as follows: largemouth bass and yellow perch—I; rainbow trout—II; cyprinids—III; largemouth bass—IV. % *Daphnia* = *Daphnia*/(*Daphnia* + *Bosmina*). Zooplankton were quantified from 1952 to 1983.

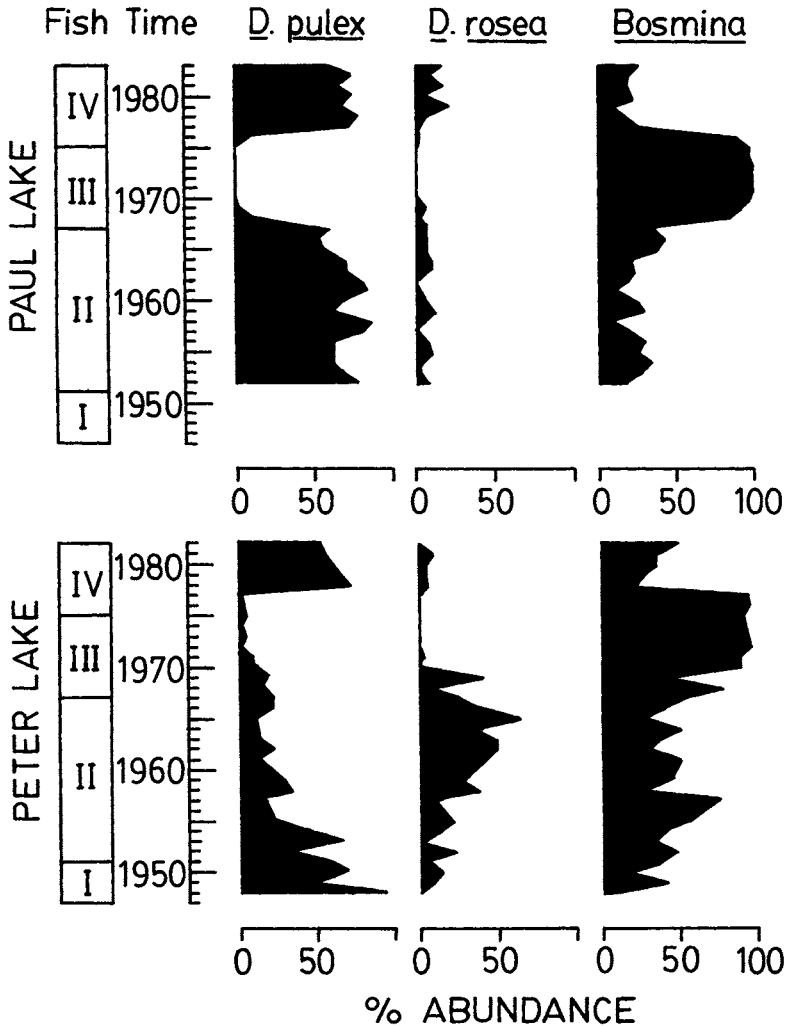


Fig. 4. Relative abundance of pelagic zooplankton microfossils. Fish zones as in Fig. 3.

fish community structure occurred in 1951 when the original bass-perch assemblage was removed, the lake divided, and rainbow trout stocked (Figs. 2, 3) (Johnson and Hasler 1954). This transition had little effect on the biological structure of Paul Lake and the plankton community remained dominated by large *D. pulex* and *Peridinium* sp. (Johnson and Hasler 1954; Johnson 1954). Kitchell and Kitchell (1980) argued that large Cladocera were unaffected because of the presence of an oxygenated, aphotic, deep-water refuge from predation. This interpretation is supported by our study, which shows that *D. pulex* and *D. rosea* account

for 70 and 5% of the fossil cladoceran assemblage, respectively, throughout fish zone II (Fig. 4) despite an intensive stocking program (Table 1).

Dike construction and fish community change had little effect on the annual concentrations of photosynthetic pigments. Trends of decreasing carotenoid levels generally continue until 1959 (Fig. 3). An exceptional increase in lutein-zeaxanthin (1953–1954), coupled with parallel increases in pheophytin *b* (not shown), suggests rises in deposition of either chlorophytes or terrestrial plant fossils. Selective harvest of aspen, poplar, and white pine oc-

curred in the watershed during 1954–1955 (UNDA 1988). However, the terrestrial contribution of pigments to sediments is thought to be slight due to substantial degradation on land (Daley and Brown 1973; Gorham and Sanger 1975). The lack of macroscopic leaf remains in the deep-water sediments of Peter Lake and Paul Lake, despite their small surface areas (2.4 and 1.2 ha), supports this view. Alternatively, the increased lutein-zeaxanthin and pheophytin *b* levels may reflect small chlorophytes that escaped detection by the large mesh net (76- μ m mesh) (Johnson 1954).

The bloom of green algae was truncated in 1956 by a partial washout of the road and dike separating the lakes (UNDA 1988). This event resulted in deposition of 0.5 cm of clay across the entire basin of Paul Lake and caused strikingly low pigment concentrations (Fig. 3). Cladocera were apparently unaffected, perhaps because the washout occurred in early May (UNDA 1988), a time when *Daphnia* is often scarce. Because pigment concentrations are expressed per unit organic matter, their reduced levels signify either reduced algal productivity or decreased pigment preservation. Regardless of the mechanism, the effects of dike washout were short-lived.

Transition zone II–III—Pigment concentrations increased slightly between 1959 and 1963. During the period 1964–1970, sedimentary concentrations of fucoxanthin, β -carotene, and Chl *a* all rose dramatically, while Chl *c* was present at detectable levels for the first time since 1940. This pigment assemblage is characteristic of the Chrysophyta (Withers et al. 1981) and represents the formation of metalimnetic chrysophyte blooms for the following reasons. First, metalimnetic blooms of *Dinobryon sertularia*, *Mallomonas* sp., and *Chrysosphaerella* sp. first became abundant in 1962 (Malueg 1963). These blooms were believed to result from increased water transparency (Malueg 1963). By 1962, the *Ze* of Paul Lake had reached 4.4 m and remained there through 1965 (Stross and Hill 1968). Second, the siliceous algal microfossil community associated with the peaks of fucoxanthin, β -carotene, Chl *a*, and Chl *c* is composed of chrysophyte scales and cysts,

with lesser quantities of littoral diatoms (J. P. Smol pers. comm.). The absence of pelagic diatoms is consistent with coeval limnological records (Malueg 1963). It is unknown whether chrysophyte remains dominate other sections of the core.

Third, although photooxidation is the major loss process for all pigments (Carpenter et al. 1988), Chl *a* and Chl *c* are also rapidly degraded aphotically in the presence of oxygen (Daley 1973; Leavitt and Carpenter in press). Thus high sedimentary concentrations of the two chlorophylls could not result from an abnormal bloom of diatoms during turnover because the requisite high turbulence would suspend moribund cells in the photic zone, where elevated oxygen levels would rapidly degrade pigments in sinking cells. In contrast, metalimnetic blooms are suspended at low light intensities and are deposited relatively quickly in the anoxic waters overlying the sediments. Pigment degradation under anoxia is extremely slow (Hurley 1988; Leavitt 1988; Leavitt and Carpenter in press).

Enhanced water clarity, signaled by deep blooms, had other effects on trophic interactions. By the mid-1960s, declining rainbow trout populations had been supplanted by a minnow community (Elser et al. 1986). Cyprinid invasion, coupled with greater water clarity, resulted in a complete replacement of large daphnids by small bosminids (Figs. 3, 4). The dominant cyprinid in this assemblage is usually redbelly dace (*P. eos*) which exhibits rapid population growth and diel migration behavior that maximize its effects as a size-selective zooplanktivore (Naud and Magnan 1988). Size-selective planktivory removes both large *Daphnia* and invertebrate predators (e.g. *Chaoborus*), thereby allowing smaller *Bosmina* to flourish (Hall et al. 1976; Kitchell and Kitchell 1980).

Whole-lake experiments and allometric considerations suggest that replacement of large, efficient grazers by small, inefficient herbivores should result in reduced herbivory, increased algal standing crops, and decreased water clarity (Carpenter et al. 1985, 1987, 1988; Peters 1986). Consistent with these expectations, chrysophyte bloom indicators all declined coincident with reduc-

tion in *Daphnia* (Fig. 3). Metalimnetic chrysophyte populations are sensitive to alterations in light penetration (Pick et al. 1984).

Transition zone III–IV—Lake conditions remained stable until the end of fish zone III (1975), when largemouth bass invaded through the culvert from Peter Lake. By 1980 these predators had removed the cyprinid community (Kitchell and Kitchell 1980; Hodgson and Kitchell 1987). Several whole-lake manipulations have shown that removal of planktivorous fishes reduces the intensity of size-selective planktivory and allows large-bodied zooplankton to increase water clarity by reducing algal standing crops (Carpenter and Kitchell 1988). These events are clearly recorded in the sedimentary record of Paul Lake.

Within 2 yr of bass invasion, *D. pulex* and *D. rosea* once again dominated the fossil zooplankton community, consistent with contemporary records (Kitchell and Kitchell 1980; Hodgson and Kitchell 1987). These efficient herbivores reduced algal standing crops, leading to transient increases in the sedimentary concentrations of most pigments (1978–1980). Replacement of small *Bosmina* by large *Daphnia* produces such signals by both increasing the pigment concentration relative to fecal organic matter (Daley 1973; Leavitt and Brown 1988) and increasing the rates of pigment sedimentation (Carpenter et al. 1988).

Resultant increases in water clarity are shown by the establishment of deep populations of green photosynthetic sulfur bacteria (*Prosthecochloris* sp.) by 1979 (Parkin and Brock 1980) and by a striking increase in the carotenoid isorenieratene (1978–1986). This pigment is characteristic of brown varieties of the green sulfur bacteria in the group Chlorobiaceae (Schmidt 1978). Because these bacteria require H₂S for photosynthesis, high sedimentary levels of isorenieratene signal that light penetrates to anoxic waters. The photic zone of Paul Lake has been maintained at its deepest extent (> 5.5 m) for the last 10 yr (Parkin and Brock 1980; Elser et al. 1986; Carpenter et al. 1987).

Presently, the lake supports metalimnetic populations of chrysophytes (St. Amand and

Carpenter unpubl. data). These blooms are recorded both by the return of Chl *c* to the sedimentary record and by increased levels of fucoxanthin in surficial deposits (Fig. 3). Interestingly, these changes are less dramatic than those which occurred 1964–1970 and suggest that the weak response of isorenieratene during that period was the result of shading of the bacteria by the intense chrysophyte bloom, combined with the observed difference in transparency (1965, 4.4 m; 1985, 5.5 m). Chlorobiaceae characteristically form the deepest photosynthetic layer in lakes and can be excluded by shading from overlying populations (McIntosh 1983; Brown et al. 1984; Züllig 1985).

Concentrations of Chl *b* generally parallel those of lutein-zeaxanthin throughout the core (*but see above*). Changes in Chl *b* are more dramatic, perhaps because it is relatively refractory to degradation in the presence of oxygen (Daley 1973; Leavitt and Carpenter in press) and is degraded less during sedimentation. Consequently, it is difficult to assign significance to annual fluctuations in Chl *b* concentrations relative to those of lutein-zeaxanthin.

Overview of Peter Lake—Trophic manipulations were augmented by repeated additions of hydrated lime (Fig. 5). Removal of native fishes and stocking of trout (zones I–II), in concert with lime additions that increased water transparency, initiated a decade-long replacement of large, apparent *D. pulex* by the more cryptic *D. rosea*. Biomasses of chlorophytes, chrysophytes, and cyanophytes increased. When cyprinids assumed dominance (zones II–III), small *Bosmina* replaced large *Daphnia*. A massive liming occurred at the same time (1969). Primary production, pigment preservation, and biomasses of photosynthetic bacteria increased. Addition of largemouth bass eliminated cyprinid populations (zones III–IV), large-bodied *Daphnia* regained dominance of the herbivore assemblage, algal standing crops decreased, transparency increased, and deep populations of chrysophytes have been sustained to the present.

Premanipulation—As in Paul Lake, sedimentary concentrations of algal carotenoids declined during recovery from disturbance (1940–1951, fish zone I, Fig. 6).

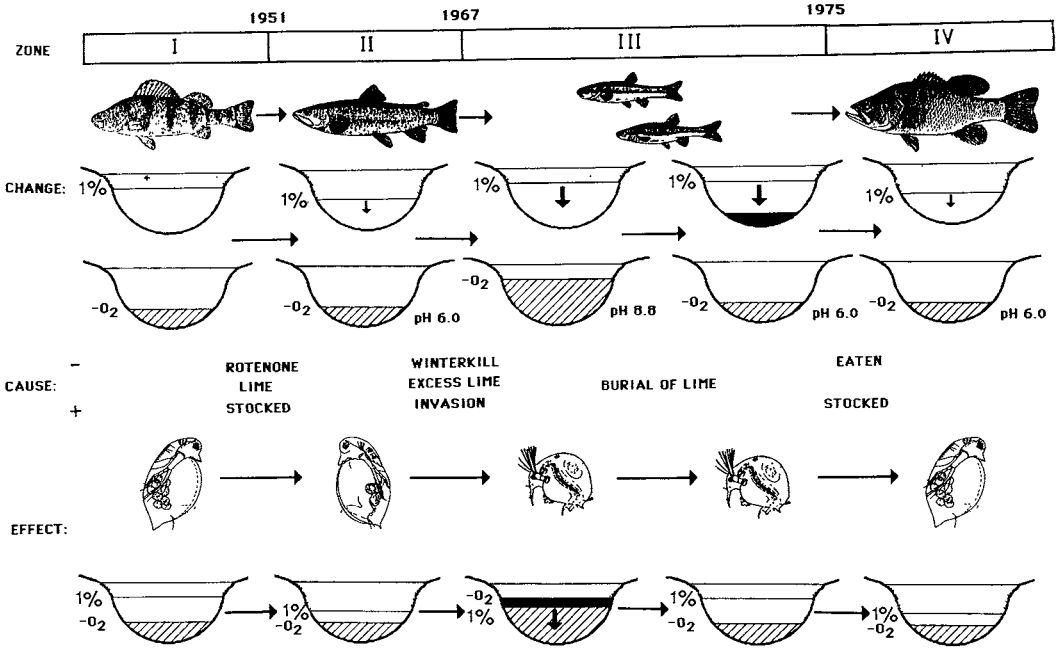


Fig. 5. Summary of the effects of trophic manipulation and liming in Peter Lake. Upper limit of anoxic waters (-O₂). Cause of trophic changes as in Fig. 2. See text.

Pigment concentrations were substantially lower than those in Paul Lake during the same period, despite the fact the lakes were contiguous. Undegraded Chl *c* (1938-1939) suggests metalimnetic chrysophyte populations and hence good light penetration, but historical records state that water clarity was similar in both basins (Johnson and Hasler 1954; UNDA 1988). Therefore, dif-

ferences in photooxidative pigment loss are unlikely to account for the lower pigment concentrations in Peter Lake sediments. More likely, these differences reflect differences in oxygen penetration in the two basins. Before basin separation, detectable oxygen (>1 mg liter⁻¹) was recorded at 8 m in Peter Lake, while Paul Lake was anoxic at 4 m (UNDA 1988). Because both carot-

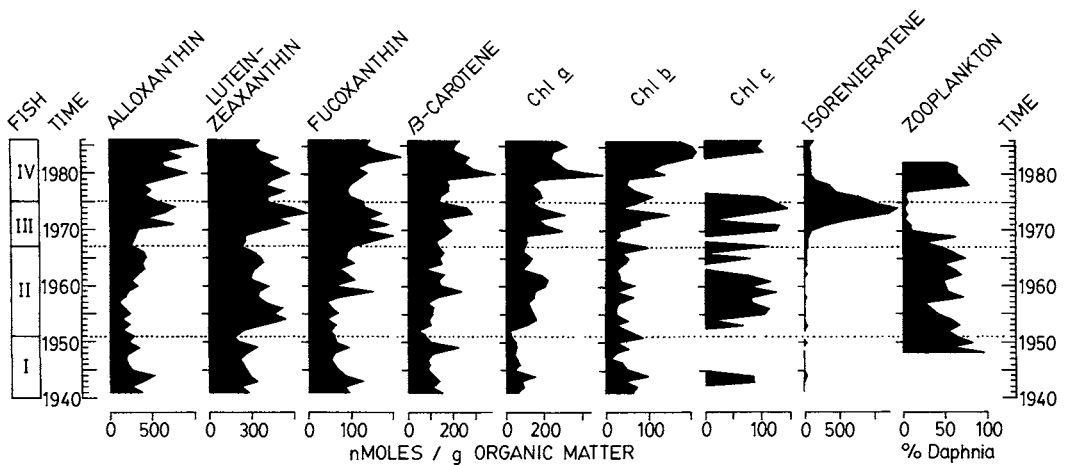


Fig. 6. As Fig. 3, but in Peter Lake. Zooplankton were quantified from 1948 to 1982.

enoids and chlorophylls are rapidly degraded in the presence of oxygen (Daley 1973; Hurley 1988; Leavitt and Carpenter in press), the greater oxic zone in Peter Lake results in increased pigment decomposition before deposition.

Premanipulation fossil zooplankton communities were dominated by large *D. pulex* and *D. rosea* (Fig. 4), consistent with contemporaneous records (Kitchell and Kitchell 1980). As with Paul Lake, labile peridinin is absent from the sedimentary record, despite the importance of dinoflagellates in the premanipulation algal community (Johnson and Hasler 1954).

Transition zone I-II—Unlike Paul Lake, transition between fish zones I and II (1951) was marked by distinct changes in plankton communities, presumably due to liming (Table 2). Because hydrated lime precipitates humic acids (Hasler et al. 1951; Johnson and Hasler 1954), the photic zone depth (*Ze*) in Peter Lake increased from 2.7 to 4.5 m in 1951. Repeated liming further increased the *Ze* to 7.0 m by 1955 (Stross 1958).

With increased water clarity came a steady decline in *Daphnia* abundance between 1951 and 1956 (Fig. 6). This reduction reflects the selective loss of *D. pulex* from the pelagic zooplankton community (Fig. 4). The gradual change contradicts the suggestions of Johnson and Hasler (1954) and Kitchell and Kitchell (1980) that manipulation resulted in immediate reciprocal changes in the relative abundance of the two daphnids. However, the former study misidentified *D. rosea* as *Daphnia longispina* (Kitchell and Kitchell 1980) indicating taxonomic difficulties, whereas the latter was analyzed at coarse intervals, so precise determination of the rate of species replacement is impossible. Our study shows that *D. rosea* dominance was not clearly established until the 1960s (Fig. 4).

Kitchell and Kitchell (1980) detailed the mechanism for these zooplankton community dynamics. Liming increased light penetration to 4.5 m (1951) and removed the daphnids' aphotic, deep-water predation refuge (Johnson and Hasler 1954). Because *D. pulex* is more apparent than *D. rosea* to visual-feeding planktivorous trout,

it was selectively eaten. By 1955 the photic zone had increased to 7.0 m (Stross 1958)—a level that was maintained throughout the early 1960s (Malueg 1963). With release from competition with *D. pulex* and predation by *Chaoborus*, the abundance of cryptic *D. rosea* increased (1957–1965) and the relative importance of *Daphnia* returned to approximately predisturbance levels (Figs. 4, 6).

The algal community of Peter Lake was substantially altered by lake manipulation. Net-tow collections indicate that *Peridinium* sp. was rapidly replaced by a complex assemblage of large chlorophytes, cyanophytes, and chrysophyte algae (Johnson 1954). Areal primary production doubled relative to Paul Lake (Stross and Hasler 1960), and an *Aphanizomenon* sp. bloom was recorded in 1954 (Stross 1958). By 1962, *D. sertularia*, *Mallomonas* sp., *Chryso-sphaerella* sp., and *Anabaena planctonica* had established metalimnetic populations, although their presence had been qualitatively noted during the 1950s (Johnson 1954). Such multiyear, postliming blooms of *D. sertularia* and cyanophytes have been recorded from other lakes in this region (Waters 1957; Waters and Ball 1957).

Algal community dynamics are remarkably well preserved in the sedimentary record (Fig. 6). Establishment of metalimnetic chrysophyte populations appears to be signaled by both increases in Chl *a* and the return of Chl *c* after an 8-yr absence. These pigment levels remain high throughout the 1950s but lapse slightly with the end of intensive liming during the 1960s. Interestingly, fucoxanthin and β -carotene do not show such strong dynamics, perhaps because both are less labile than Chl *c* (Leavitt and Carpenter in press) and hence are less affected by the position of the bloom in the water column (*see above*).

Increased production by chlorophytes and cyanophytes is recorded by elevated concentrations of lutein-zeaxanthin, Chl *a*, and both pheophytin *a* and *b* (not shown) from 1952 to 1963. Unfortunately, because lutein (Chlorophyta) and zeaxanthin (Cyanophyta) were not resolved by HPLC, it is difficult to disentangle the relative abundance of the two algal groups. However, sedimentary

patterns of pheophytin *b* abundance exactly parallel those of lutein-zeaxanthin, indicating that green algae were important after liming began in Peter Lake.

Although the stimulation of cyanophyte populations probably resulted from increased alkalinity (Waters 1957; Shapiro 1984), mechanisms that enhance the growth of green algae are more difficult to identify. Chlorophytes may compete better at high light intensities (Wall and Briand 1979), but others suggest that liming stimulates algal growth nonselectively through enhanced release of hypolimnetic phosphorus (Waters and Ball 1957; Stross and Hasler 1960). Predator-mediated changes in zooplankton community composition may have affected algal dynamics. Replacement of *D. pulex* by *D. rosea* resulted in a modest change in mean herbivore size and total density (figure 4 in Kitchell and Kitchell 1980). Similar reduction in mean *Daphnia* size in the lake in 1985 corresponded with a transient bloom of the green alga *Sphaerocystis Schroeterii* (Carpenter et al. 1987).

Photosynthetic bacteria, as measured by isorenieratene, did not respond to increased light penetration. This observation is consistent with coeval limnological records that document that light did not penetrate to anoxic waters, despite repeated application of lime (Johnson and Hasler 1954).

Dike washout (1956) had little effect on plankton communities in Peter Lake. The sedimentary clay layer that marks this event is only 2–3 mm thick, suggesting that either most particulate matter flowed into Paul Lake or the larger surface area of Peter Lake diluted the clay effects.

Transition zone II–III—Planktivory by rainbow trout and the growing population of cyprinids (~1967) had dramatic effects on zooplankton. Large-bodied *Daphnia* gave way to an assemblage of small *Bosmina* (Fig. 6). This transition is less sharply demarcated than that in Paul Lake (Figs. 3, 4) and reflects the continuing influence of planktivory by rainbow trout. In 1965, stocking introduced almost twice the mass of trout as previous additions (Table 2). By 1968, these fish drove daphnid abundance to its lowest level since 1956.

Fish zone III, the cyprinid assemblage, is

characterized by sharply increased concentrations of all fossil pigments (Fig. 6). These dynamics result from the complex interaction between concurrent alterations in food web structure and manipulation of the abiotic environment. In concert with predator-driven changes in the zooplankton community, Peter Lake received its single largest addition of hydrated lime (Table 2). This event is clearly marked in the sediments by a gray band in the laminae corresponding to 1969. Unfortunately, historical documentation of this event is poor.

After liming, the pH of hypolimnetic waters increased from <6 to ~8.8 (UNDA 1988). By 1970, epilimnetic thickness was only half that of either 1965 or 1978 (UNDA 1988), while by 1975 water color had doubled relative to Paul Lake (UNDA 1988). Because adding hydrated lime removes humic acids (Hasler et al. 1951; Johnson and Hasler 1954), these changes probably document an increase in algal production and consequent reduction in light penetration. Enhanced primary production is consistent with the sedimentary record of fossil pigments and is a common result of adding excess lime (Waters 1957; Waters and Ball 1957; Stross and Hasler 1960). Increased hypolimnetic pH stimulates bacterial decomposition of organic matter and facilitates the release of inorganic phosphorus (Waters 1957; MacPherson et al. 1958). In the case of Peter Lake, high primary production was maintained through the presence of small-bodied, inefficient herbivores which were unable to effectively control algal standing crop (Carpenter et al. 1985, 1987).

A massive bloom of green photosynthetic sulfur bacteria began immediately after liming and rose to a peak in 1974 (Fig. 6). As with Paul Lake, these high levels of isorenieratene indicate that light penetrates to anoxic waters. However, rather than signaling an increase in transparency, the bacterial bloom follows a reduction in hypolimnetic oxygen concentrations. Stimulation of organic matter decomposition by sedimentary lime has the additional effect of reducing hypolimnetic oxygen levels (Waters 1957; Waters and Ball 1957). As the volume of anoxic water increases, the hydrogen sulfide

layer is moved into the photic zone. Once again, juxtaposition of light and anoxic waters allows the photosynthetic bacteria to bloom. Similar bacterial blooms occur high in the water column of other productive lakes (Parkin and Brock 1981*a,b*). A further consequence of increased hypolimnetic volume is that pigment decomposition during sedimentation is reduced. Thus, high sedimentary concentrations of all pigments during the period of fish zone III result from both increased algal production and reduced pigment degradation, consistent with the predictions of Swain (1985).

Isorenieratene concentrations decline slowly after 1974 and are paralleled by both the loss of Chl *c* from the sedimentary record and the return of other pigments to pre-liming levels (Fig. 6). Although 25 adult largemouth bass were stocked to Peter Lake in 1975 (Kitchell and Kitchell 1980), effects were not apparent in zooplankton community composition until the first progeny of the stocked adults became piscivorous (~1978). Thus, the declines in pigment concentrations were not a result of trophic manipulation. The simplest explanation is that the declines represent amelioration of the effects of adding lime.

High algal productivity induced by liming was likely maintained through the presence of a small-bodied, inefficient zooplankton community (cf. Węgleńska et al. 1979; Carpenter et al. 1985, 1987). Therefore, as the lime is buried, its buffering capability is lost, hypolimnetic pH declines, and decomposition processes slow. With reduced oxygen demand, the volume of anoxic water decreases, hydrogen sulfide withdraws from the photic zone, and the bacterial bloom is lost. Furthermore, with the return of oxygen to deep waters, pigment preservation is reduced (Hurley 1988; Leavitt 1988; Leavitt and Carpenter in press) and sedimentary pigment concentrations decline, despite high levels of algal production.

The attempted alkalization of Peter Lake in 1976 (Elser et al. 1986) did not affect plankton dynamics and may actually have contributed to the burial of hydrated lime. Unlike prior additions, calcium carbonate was introduced instead of hydrated lime and hypolimnetic pH remained acidic (UNDA 1988). As documented by Waters and Ball

(1957), CaCO_3 is rapidly adsorbed onto sedimentary organic matter and consequently has a greatly reduced buffering capacity.

Transition zone III-IV—Sedimentary pigment concentrations remained low until the predator-mediated transition in zooplankton community structure (1978). As occurred in Paul Lake, introduction of largemouth bass reduced the intensity of size-selective planktivory by cyprinids and allowed large *D. pulex* and *D. rosea* to regain their former abundance (Fig. 4).

Introduction of an efficient herbivore community resulted in decreased algal standing crops and sharply increased rates of pigment sedimentation in 1980. Mechanisms producing these transient increases in sedimentary pigment concentration are discussed above. Interestingly, zooplankton-mediated increases in sedimentary pigment concentrations are greater than those in Paul Lake. This difference probably occurs both because Peter Lake had substantially larger *Daphnia* and because partial winterkill in 1980 reduced bass populations ~50% (Hodgson and Kitchell 1987).

Reduced algal standing crop once again resulted in increased light penetration. Photic zone depth in Peter Lake increased to 7.5 m in 1978 (Parkin and Brock 1980) and was maintained through 1984 (Elser et al. 1986). Unlike Paul Lake, isorenieratene does not respond to increased transparency, although the return of Chl *c* to the sediments (1985–1986) suggests the re-establishment of deep chrysophyte blooms. This interpretation is supported by current phytoplankton surveys showing that Peter Lake now supports metalimnetic populations of chrysophytes, while photosynthetic bacteria populations are at low levels due to the presence of oxygen in deep waters (Elser et al. 1986; St. Amand and Carpenter unpubl. data). Dense populations of chlorococcoid and euglenoid algae have been common elements of the plankton since 1978 (UNDA 1988). The presence of these chlorophytes appears to be signaled by greatly increased concentrations of Chl *b* in surficial sediments, although this trend is not repeated in the lutein-zeaxanthin profile. As discussed above, deep algal blooms may reduce bacterial populations through shading.

Removal of 90% of the largemouth bass

population in 1985 had little effect on fossil pigment deposition. Sediment trap studies in 1984 and 1985 are consistent with the core data (Carpenter et al. unpubl. data). Although an equivalent mass of cyprinids was added to Peter Lake (Table 2), these fish rapidly disappeared and had only a transient effect on zooplankton community composition (Carpenter et al. 1987). Although enhanced planktivory by juvenile bass reduced mean *Daphnia* size by ~1 August, the sole algal response to the manipulation was a dense bloom of colonial *S. Schroeterii* lasting about 6 weeks (Carpenter et al. 1987). This green alga presumably contributes to the elevated Chl *b* levels in surficial sediments.

Synthesis and conclusions

Changes in fish community structure have substantial, long-lasting effects that cascade to the microbial level of the food web. The physical and chemical consequences of liming interact with fish manipulations in complex ways that affect herbivores, primary producers, and decomposers. Thirty-four years of trophic change, documented in contemporaneous limnological records, are preserved in detail in the sediments of Paul and Peter Lakes.

The trophic dynamics demonstrated in these whole-lake experiments also occur naturally, at rates set by fish lifespans and community dynamics (Carpenter et al. 1987; Kitchell and Carpenter 1987; Carpenter 1988; Carpenter and Kitchell 1988). This paper establishes that paleolimnology can deduce these fluctuations. However, paleolimnological studies are conducted for many other purposes, such as reconstruction of edaphic and climatic change, watershed disturbances, and successional trends (Binford et al. 1983). Signals of these dynamics will be mixed with those of food web processes in the sediments of most lakes. Methods used here permit the separation of food web signals from those of other processes. Cladoceran size appears to be a specific marker of food web change (Kerfoot 1974; Kitchell and Kitchell 1980). Although terrestrial pigments have been thought to be important in small lakes, our data show that luteinzeaxanthin concentrations in sediments in-

dicate known changes in green and blue-green algal populations.

High resolution sedimentary records of fossil pigments provide information on community dynamics that would be impossible to obtain otherwise except through multidecade studies. Changes in the absolute concentrations of individual pigments faithfully record the dynamics of their representative taxa, while pigment assemblages are useful for resolving the vertical zonation of phytoplankton communities. For example, the presence of undegraded Chl *c*, often in combination with Chl *a*, fucoxanthin, and β -carotene, is a sensitive indicator of metalimnetic chrysophyte blooms. Similarly, isorenieratene is a specific monitor of conditions in which photic and anoxic waters overlap. Transient (2–3 yr), nonselective increases in pigment sedimentation that accompany introductions of large-bodied zooplankton may be a widespread phenomenon of considerable paleolimnological value.

Although absolute concentrations of individual pigments are informative, it is unclear if relative concentrations are a useful measure of algal community composition. Different taxa have unique specific pigment contents (Goodwin 1980) and may make assignment of relative importance difficult. Difference in the susceptibility of taxa to the various degradative processes provides further complications. For example, alloxanthin is usually the most abundant sedimentary pigment, yet cryptophytes are not the primary element of the algal communities (Carpenter et al. 1987). Similarly, peridinin is never preserved, thereby making quantification of dinoflagellate dynamics impossible, except through the use of cysts. Further experimentation will refine the taxonomic information available from pigment records in sediments.

References

- BINFORD, M. W., E. S. DEEVEY, AND T. L. CRISMAN. 1983. Paleolimnology: An historical perspective on lacustrine ecosystems. *Annu. Rev. Ecol. Syst.* 14: 255–286.
- BOLD, H. C., AND M. W. WYNNE. 1985. Introduction to the algae, 2nd ed. Prentice-Hall.
- BROWN, S. R. 1968. Absorption coefficients of chlorophyll derivatives. *J. Fish. Res. Bd. Can.* 25: 523–540.

- , H. J. McINTOSH, AND J. P. SMOL. 1984. Recent paleolimnology of a meromictic lake: Fossil pigments of photosynthetic bacteria. *Int. Ver. Theor. Angew. Limnol. Verh.* **22**: 1357–1360.
- CARLANDER, K. D. 1969. Handbook of freshwater fishery biology. V. 1. Iowa State.
- CARPENTER, S. R. 1988. Transmission of variance through lake food webs, p. 119–135. *In* S. R. Carpenter [ed.], Complex interactions in lake communities. Springer.
- , M. M. ELSER, AND J. J. ELSER. 1986. Chlorophyll production, degradation, and sedimentation: Implications for paleolimnology. *Limnol. Oceanogr.* **31**: 112–124.
- , AND J. F. KITCHELL. 1988. Consumer control of lake productivity. *BioScience* **38**: 764–769.
- , AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**: 634–639.
- , AND OTHERS. 1987. Regulation of lake primary productivity by food web structure. *Ecology* **68**: 1863–1876.
- , P. R. LEAVITT, J. J. ELSER, AND M. M. ELSER. 1988. Chlorophyll budgets: Response to food web manipulations. *Biogeochemistry* **6**: 79–90.
- DALEY, R. J. 1973. Experimental characterization of lacustrine chlorophyll diagenesis. 2. Bacterial, viral and herbivore grazing effects. *Arch. Hydrobiol.* **72**: 409–439.
- , AND S. R. BROWN. 1973. Experimental characterization of lacustrine chlorophyll diagenesis. 1. Physiological and environmental effects. *Arch. Hydrobiol.* **72**: 277–304.
- DAVIES, B. H. 1976. Carotenoids, p. 38–165. *In* T. W. Goodwin [ed.], Chemistry and biochemistry of plant pigments. V. 2. Academic.
- DEAN, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: Comparison with other methods. *J. Sediment. Petrol.* **44**: 242–248.
- ELSER, M. M., J. J. ELSER, AND S. R. CARPENTER. 1986. Paul and Peter Lakes: A liming experiment revisited. *Am. Midl. Nat.* **116**: 282–295.
- ENGSTROM, D. R., E. B. SWAIN, AND J. C. KINGSTON. 1985. A palaeolimnological record of human disturbance from Harvey's Lake, Vermont: Geochemistry, pigments and diatoms. *Freshwater Biol.* **15**: 261–288.
- FOPPEN, F. H. 1971. Tables for identification of carotenoid pigments. *Chromatogr. Rev.* **14**: 133–198.
- GOODWIN, T. W. 1980. The biochemistry of the carotenoids. V. 1. Plants. Chapman and Hall.
- GORHAM, E., AND J. SANGER. 1975. Fossil pigments in Minnesota lake sediments and their bearing upon the balance between terrestrial and aquatic inputs to sedimentary organic matter. *Int. Ver. Theor. Angew. Limnol. Verh.* **19**: 2267–2273.
- HALL, D. J., S. T. THRELKELD, C. W. BURNS, AND P. H. CROWLEY. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annu. Rev. Ecol. Syst.* **7**: 177–208.
- HASLER, A. D., O. M. BRYNILDSON, AND W. T. HELM. 1951. Improving conditions for fish in brown-water lakes by alkalization. *J. Wildl. Manage.* **15**: 347–352.
- HAWORTH, E. Y. 1980. Comparison of continuous phytoplankton records with the diatom stratigraphy in recent sediments of Blelham Tarn. *Limnol. Oceanogr.* **25**: 1093–1103.
- HODGSON, J. R., AND J. F. KITCHELL. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). *Am. Midl. Nat.* **118**: 323–336.
- HRBÁČEK, J. 1969. On the possibility of estimating predation pressure and nutrition level of populations of *Daphnia* from their remains in sediments. *Mitt. Int. Ver. Theor. Angew. Limnol.* **17**, p. 262–274.
- HURLEY, J. P. 1988. Diagenesis of algal pigments in lake sediments. Ph.D. thesis, Univ. Wisconsin, Madison. 160 p.
- JOHNSON, W. E. 1954. Dynamics of fish production and carrying capacity of some northern soft water lakes. Ph.D. thesis, Univ. Wisconsin, Madison. 51 p.
- , AND A. D. HASLER. 1954. Rainbow trout production in dystrophic lakes. *J. Wildl. Manage.* **18**: 113–134.
- KERFOOT, W. C. 1974. Net accumulation rates and history of cladoceran communities. *Ecology* **55**: 51–61.
- . 1981. Long-term replacement cycles in cladoceran communities: A history of predation. *Ecology* **62**: 216–233.
- KITCHELL, J. A., AND J. F. KITCHELL. 1980. Size-selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnol. Oceanogr.* **25**: 389–402.
- KITCHELL, J. F., AND S. R. CARPENTER. 1987. Piscivores, planktivores, fossils, and phorbins, p. 136–146. *In* W. C. Kerfoot and A. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. New England.
- LEAVITT, P. R. 1988. Experimental determination of carotenoid degradation. *J. Paleolimnol.* **1**: 215–228.
- , AND S. R. BROWN. 1988. Effects of grazing by *Daphnia* on algal carotenoids: Implications for paleolimnology. *J. Paleolimnol.* **1**: 201–214.
- , AND S. R. CARPENTER. 1989. Effects of sediment mixing and benthic algal production on fossil pigment stratigraphies. *J. Paleolimnol.* **2**: in press.
- , AND ———. In press. Pigment degradation in lakes: Implications for sedimentation studies and paleolimnology. *Limnol. Oceanogr.*
- LIKENS, G. E. 1983. A priority for ecological research. *Bull. Ecol. Soc. Am.* **64**: 234–243.
- , F. H. BORMANN, N. M. JOHNSON, D. W. FISHER, AND R. S. PIERCE. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in Hubbard Brook watershed-ecosystem. *Ecol. Monogr.* **40**: 23–47.
- McINTOSH, H. J. 1983. A paleolimnological investigation of the bacterial carotenoids of Sunfish Lake. M.S. thesis, Queen's University, Kingston. 129 p.
- MACPHERSON, L. B., N. R. SINCLAIR, AND F. R. HAYES. 1958. Lake water and sediment. 3. The effects of

- pH on the partition of inorganic phosphate between water and oxidized mud or its ash. *Limnol. Oceanogr.* **3**: 318-326.
- MALUEG, K. W. 1963. A study of the vertical distribution of phytoplankton with respect to the effects of lime-treatment. M.S. thesis, Univ. Wisconsin, Madison. 102 p.
- MANTOURA, R. F. C., AND C. A. LLEWELLYN. 1983. The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reversed-phase high-performance liquid chromatography. *Anal. Chim. Acta* **151**: 297-314.
- MAZUMDER, A., D. J. MCQUEEN, W. D. TAYLOR, AND D. R. S. LEAN. 1988. Effects of fertilization and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: Large enclosure experiments. *Limnol. Oceanogr.* **33**: 421-430.
- NAUD, M., AND P. MAGNAN. 1988. Diel onshore-offshore migrations in northern redbelly dace, *Phoxinus eos* (Cope), in relation to prey distribution in a small oligotrophic lake. *Can. J. Zool.* **66**: 1249-1253.
- PARKIN, T. B., AND T. D. BROCK. 1980. Photosynthetic bacterial production in lakes: The effects of light intensity. *Limnol. Oceanogr.* **25**: 711-718.
- , AND ———. 1981a. The role of phototrophic bacteria in the sulfur cycle of a meromictic lake. *Limnol. Oceanogr.* **26**: 880-890.
- , AND ———. 1981b. The effects of light quality on the growth of phototrophic bacteria in lakes. *Arch. Microbiol.* **125**: 19-27.
- PETERS, R. H. 1986. The ecological implications of body size. Cambridge.
- PICK, F. R., C. NALEWAJKO, AND D. R. S. LEAN. 1984. The origin of a metalimnetic chrysophyte bloom. *Limnol. Oceanogr.* **29**: 125-134.
- POTZGER, J. E. 1942. Pollen spectra from four bogs on the Gillen Nature Reserve, along the Michigan-Wisconsin state line. *Am. Midl. Nat.* **28**: 501-511.
- SANGER, J. E. 1988. Fossil pigments in paleoecology and paleolimnology. *Palaeogeogr. Palaeoclim. Palaeoecol.* **62**: 343-359.
- SCHINDLER, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. *Can. J. Fish. Aquat. Sci.* **44**(suppl. 1): 6-25.
- SCHMIDT, K. 1978. Biosynthesis of carotenoids, p. 729-750. *In* R. K. Clayton, and W. R. Sistrom [eds.], *The photosynthetic bacteria*. Plenum.
- SHAPIRO, J. 1984. Blue-green dominance in lakes: The role and management significance of pH and CO₂. *Int. Rev. Gesamten Hydrobiol.* **69**: 765-780.
- , AND D. I. WRIGHT. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biol.* **14**: 371-383.
- STROSS, R. G. 1958. Experimentally induced changes in lakes. 1. Environmental changes following lime application to stained lakes. 2. Changes in the planktonic crustacea following the introduction of trout to a fish free lake. Ph.D. thesis, Univ. Wisconsin, Madison. 125 p.
- , AND A. D. HASLER. 1960. Some lime-induced changes in lake metabolism. *Limnol. Oceanogr.* **5**: 265-272.
- , AND J. C. HILL. 1968. Photoperiodic control of winter diapause in the fresh-water crustacean, *Daphnia*. *Biol. Bull.* **134**: 176-198.
- SWAIN, A. M. 1973. A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. *Quat. Res.* **3**: 383-396.
- SWAIN, E. B. 1985. Measurement and interpretation of sedimentary pigments. *Freshwater Biol.* **15**: 53-75.
- UNDA. 1988. Gillen-Land O'Lakes file UBVG. Univ. Notre Dame Arch.
- VOGL, R. J. 1970. Fire and the northern Wisconsin pine barrens. *Proc. Tall Timbers Annu. Fire Ecol. Conf.* **9**: 175-209.
- WALL, D., AND F. BRIAND. 1979. Response of lake phytoplankton communities to in situ manipulations of light intensity and colour. *J. Plankton Res.* **1**: 103-112.
- WATERS, T. F. 1957. The effects of lime application to acid bog lakes in northern Michigan. *Trans. Am. Fish. Soc.* **86**: 329-344.
- , AND R. C. BALL. 1957. Lime application to a soft-water, unproductive lake in northern Michigan. *J. Wildl. Manage.* **21**: 385-391.
- WĘGLEŃSKA, T., K. DUSOGE, J. EJSMONT-KARABIN, I. SPODNIEWSKA, AND J. ZACHWIEJA. 1979. Effect of winter-kill and changing fish stock on the biocenose of the pond-type Lake Warniak. *Ekol. Pol.* **27**: 39-70.
- WELSCHMEYER, N. A., AND C. J. LORENZEN. 1985a. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific Gyres. *Limnol. Oceanogr.* **30**: 1-21.
- , AND ———. 1985b. Role of herbivory in controlling phytoplankton abundance: Annual pigment budget for a temperate marine fjord. *Mar. Biol.* **90**: 75-86.
- WITHERS, N. W., A. FIKSDAHL, R. C. TUTTLE, AND S. LIAAEN-JENSEN. 1981. Carotenoids of the Chrysophyceae. *Comp. Biochem. Physiol.* **68B**: 345-349.
- WRIGHT, S. W., AND J. D. SHEARER. 1984. Rapid extraction and high-performance liquid chromatography of chlorophylls and carotenoids from marine phytoplankton. *J. Chromatogr.* **294**: 281-295.
- ZÜLLIG, H. 1981. On the use of carotenoid stratigraphy in lake sediments for detecting past developments of phytoplankton. *Limnol. Oceanogr.* **26**: 970-976.
- . 1982. Untersuchungen über die Stratigraphie von Carotinoiden im geschichteten Sediment von 10 Schweizer Seen zur Erkundung früherer Phytoplankton-Entfaltungen. *Schweiz. Z. Hydrol.* **44**: 1-98.
- . 1985. Pigmente phototropher Bakterien in Seesedimenten und ihre Bedeutung für die Seenforschung. *Schweiz. Z. Hydrobiol.* **47**: 87-126.

Submitted: 26 October 1988

Accepted: 7 February 1989

Revised: 17 March 1989