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## TEMPORAL VARIATION IN A PALEOLIMNOLOGICAL RECORD ARISING FROM A TROPHIC CASCADE<sup>1</sup>

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**Abstract.** A food-chain model based on trophic cascade theory predicts substantial variance in ecosystem function at time scales near the lifespan of the dominant predator. We tested this prediction using time series (1889–1982) of algal pigment concentrations in annually laminated sediments from a lake dominated by planktivorous fishes with lifespans of 3–5 yr. For pigments that are deposited in sediments mainly by herbivory and are known to be direct indicators of the trophic cascade (alloxanthin, pheophorbide *a*), variance was pronounced at scales similar to the fish lifespan, consistent with predictions of the model. Several other sedimentary pigments that have mainly pelagic sources (native chlorophylls,  $\alpha$ -carotene) also had variance peaks consistent with predictions of the model. Pigments with multiple sources (fucoxanthin, lutein-zeaxanthin,  $\beta$ -carotene, pheophytin *c*) had only weakly significant or nonsignificant variance peaks. Pigments with mainly terrestrial sources (pheophytins *a* and *b*) had no variance peaks. These results indicate that some of the variance in this paleolimnological record is due to the trophic cascade. Since the scale of this variance component is  $\approx 3$ –5 yr, a 5-yr moving average filters out variance due to the trophic cascade. Residuals from the 5-yr moving average accentuate variance due to the trophic cascade. Filtering of the pheophytin time series revealed longer-term cycles ( $\approx 15$  yr), which may arise from terrestrial or climatic processes.

**Key words:** food web processes; fossil pigments; lake; lake sediment; paleolimnology; pigment; predation; sedimentation; time series; trophic cascade; variability.

### INTRODUCTION

The variability of ecosystem function must be known in order to evaluate large-scale experiments, effects of perturbations, and management actions. The variances and covariances of dynamic ecosystem variables (e.g., biomasses, productivities, and cycling rates) depend upon the time period over which data are integrated or averaged (Allen and Starr 1982, O'Neill et al. 1986). This scale dependency can complicate statistical analyses of ecosystem data, but also provides the opportunity for new insights (Shugart 1978, Carpenter and Kitchell 1987, 1988, Carpenter 1988). For example, sources of variance can sometimes be identified by their scales, and one can filter out unwanted variance from a particular source if its scale is known.

Paleoecology is among the major sources of information about temporal variance. At time scales of decades or longer, direct ecological observations are rare, and paleoecology is often the only source of data (Strayer et al. 1986, Kitchell et al. 1988, Likens 1989).

Lake sediments are rich sources of paleoecological information derived from the functioning of the lake ecosystems themselves as well as their surrounding watersheds and airsheds (Binford et al. 1983, Davis 1989).

Data from lake sediments apply to a diversity of questions, including large-scale forest dynamics (Davis 1989), biogeochemical development of watershed ecosystems (Davis et al. 1985), lake ontogeny (Wetzel 1970, Whitehead 1973), effects of settlement and urbanization on watersheds and lakes (Edmondson 1974, Devey et al. 1979), acidification (Charles and Smol 1988), and food web dynamics (Kerfoot 1974, Kitchell and Kitchell 1980, Kitchell and Carpenter 1987, Leavitt et al. 1989). In all applications the challenge arises of discriminating variance due to a particular process from interferences due to other processes. Information on time scales may be useful in amplifying signals of interest while filtering out interferences. Such amplifiers or filters could significantly advance the calibration of paleolimnological indicators.

The general hypothesis of this paper is that variance due to food web processes in lakes is maximal at scales near the lifespan of the dominant predator (Carpenter 1988). This hypothesis follows from analyses of a stochastic model of lake food chains which show, for a wide range of life-history scenarios, that spectrograms of primary production have variance peaks near the lifespans of the fishes at the top of the food chain (Carpenter 1988). We expect similar spectrograms for fossil pigment concentrations because deposition of plant pigments is regulated either by grazing of zooplankton or by direct sedimentation of primary producers (Carpenter et al. 1986, 1988, Leavitt et al. 1989, Leavitt and Carpenter 1990a).

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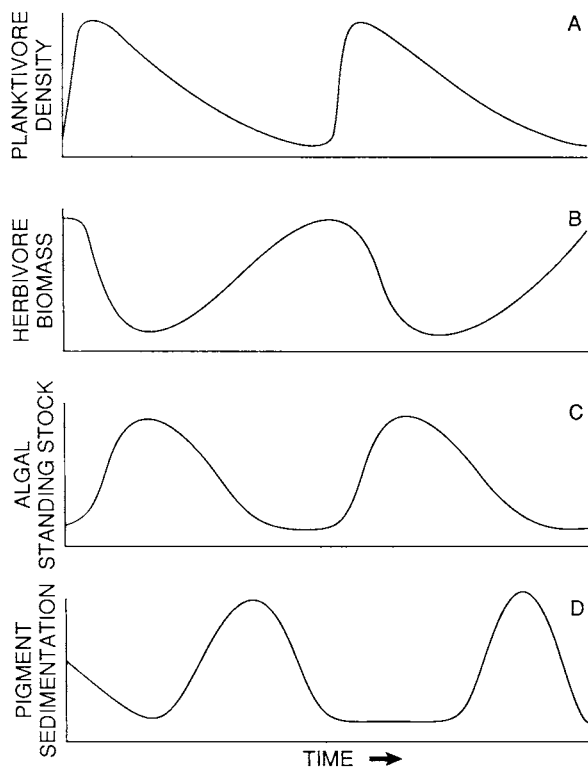


FIG. 1. Generalized sequence of variance transmission from planktivorous fish populations (A), through large-bodied zooplankton (B), to phytoplankton (C) and pigment sedimentation (D). Herbivore response is delayed from peak planktivore density because maximal planktivory occurs after some growth of young fish. Pigment sedimentation is maximal when grazing pressure by zooplankton is rising and algal production is high but declining (Leavitt et al. 1989).

The spectral regularities derive from variable recruitment of fishes, coupled with the trophic cascade (Carpenter and Kitchell 1987). In this paper, trophic cascade refers to sequences of perturbations transmitted from top predators to lower trophic levels (Paine 1980), a concept distinct from the cascade model of food webs used by Cohen (1988) and colleagues. Life histories that enable the fishes to persist in our lake food-chain model lead to large year classes about once per lifespan (Carpenter 1988). More frequent reproductive outbursts are suppressed by negative density dependencies, including cannibalism in certain species. On the other hand, if large year classes are too infrequent, the fish population eventually dies out. These results are consistent with the episodic nature of fish recruitment (Pitcher and Hart 1982, Strong 1986). Once established, a large year class alters herbivory and primary production through the trophic cascade (Carpenter et al. 1985, Carpenter and Kitchell 1987, 1988) (Fig. 1). When the next large year class is established, the sequence repeats. Thus, an oscillation in algal biomass

and primary production arises, with periods near the lifespan of the fish population.

Sedimentation of algal pigment should have the same periodicity as the fish fluctuations, with peaks and troughs offset in time (Fig. 1). Grazing by large-bodied zooplankton increases deposition rates of pigments derived from edible algae (Carpenter et al. 1988, Leavitt and Carpenter 1990a). Further, herbivory creates novel derivatives such as pheophorbide *a* (Daley 1973), and can increase the concentration of pigments in the remaining undigested material (Leavitt and Brown 1988). Thus, both accumulation rates and concentrations of sedimenting pigments are maximal when algal biomass is high but declining and when zooplankton are becoming more abundant (Fig. 1). These patterns are strongest for pigments derived from edible plankton, which would normally be degraded prior to deposition (Leavitt and Carpenter 1990a).

All trophic cascades in lakes transmit fluctuations in fish populations to phytoplankton, but the lags, sequences, and magnitudes of effects may be quite different from community to community (Carpenter et al. 1985, McQueen et al. 1986, Carpenter and Kitchell 1988, Crowder et al. 1988). Our general hypothesis is independent of most of the lake-specific details of the trophic cascade. It merely requires that, in a given lake, each large year class have a similar sequence of effects on lower trophic levels, and that variable recruitment and density dependence lead to large year classes about once per generation. Variability in the magnitude of cascading effects and in the interval between large year classes can be accounted for by analyzing data that span many fish generations (Carpenter 1988).

We tested this hypothesis in a small lake that is well described ecologically. Fish-induced fluctuations in herbivory and primary production cause parallel fluctuations in sedimentation of certain algal pigments (Carpenter et al. 1988, Leavitt and Carpenter 1990a). We recovered an annually laminated sediment core and determined pigment concentrations each year from 1889–1982. Time series analysis was then used to test for periodicities in fossil pigment concentration consistent with life histories of the dominant fish species in the lake.

#### STUDY SITE AND SPECIFIC HYPOTHESES

Tuesday Lake, near Land O'Lakes Wisconsin, has been studied occasionally since 1956 (Schmitz 1958), and continuously and intensively since 1983 (Carpenter and Kitchell 1988). To our knowledge the lake has never mixed naturally. It was artificially destratified by aeration in 1956, but effects were short-lived. The continually cold and anoxic deep waters offer an excellent environment for preservation of pigments. The presence of annual laminae (varves) in the sediments allows reliable chronology to be established.

The native fish fauna is typical of winterkill lakes in this region (Tonn and Magnuson 1982) and includes

northern redbelly dace (*Phoxinus eos*), finescale dace (*P. neogaeus*), and mudminnow (*Umbra limi*). These fishes have indeterminate lifespans of 3–5 yr in the lake (Stasiak 1978, He 1986). Tuesday Lake was stocked with rainbow trout (*Oncorhynchus mykiss*) in 1961; however, cyprinids had re-established dominance by 1970 (UNDA 1988).

The model of Carpenter (1988, 1989) was used to calculate the specific scales of variance hypothesized for algal biomass and pigment sedimentation in Tuesday Lake. Two scenarios bracketed the range of conditions possible in the lake during our study. In one scenario, the top carnivore was a planktivorous fish with a three-year semelparous life history (Carpenter 1988). In the other scenario, the top carnivore was a planktivorous fish with a five-year iteroparous life history, reproducing in years 3–5. Variance peaks occurred at periods of 2.9 to 4.6 yr in these simulations.

The pigments we studied originate in different habitats (Table 1). Since our hypothesis applies only to sedimentary pigments derived from the plankton and whose deposition is regulated by herbivory, we carefully considered the origins of each pigment using published literature and sediment-trap studies in the lake (Carpenter et al. 1986, 1988, Leavitt and Carpenter 1990a). Associations of pigments with particular taxonomic groups of plants follow Goodwin (1980), Goodwin and Britton (1988), and Rudiger and Schoch (1988).

Sediment-trap studies in Tuesday Lake and nearby lakes indicate that deposition of alloxanthin and pheophorbide *a* closely tracks responses of phytoplankton to herbivores (Carpenter et al. 1986, 1988, Leavitt and Carpenter 1990a). Alloxanthin is a carotenoid of the Cryptophyta, and its only source in Tuesday Lake is the phytoplankton (Table 1). Sedimentation of alloxanthin is regulated by herbivory, not production, because all cryptophytes are small in Tuesday Lake (Leavitt and Carpenter 1990a). Small cells sink slowly, and photo-oxidation completely destroys alloxanthin prior to deposition (Leavitt and Carpenter 1990a). Incorporation of alloxanthin into rapidly sinking fecal material bypasses this loss (Leavitt and Carpenter 1990a). Pheophorbide is a degradation product of chlorophylls produced mainly in herbivore guts, and its main source in Tuesday Lake is the zooplankton (Carpenter et al. 1986, 1988), though grazing in the littoral zone may produce some of the pigment in the lake. We expect variance in deposition of alloxanthin and pheophorbide to be scaled by fish effects.

Several other pigments are mainly planktonic in origin (Table 1). While their couplings to food web dynamics are less clear than those of alloxanthin and pheophorbide *a* (Leavitt and Carpenter 1990a), we would expect their variance to be influenced by fishes.  $\alpha$ -carotene is widespread (Cryptophyta, Chlorophyta, Tracheophyta); however, the plankton are probably the major source because  $\alpha$ -carotene is the primary caro-

TABLE 1. Pigments reported in this study. \*\* denotes major sources, \* denotes minor sources. Pigments are listed in order of increasing influence by pelagic sources.

Pigment†	Terrestrial	Littoral	Limnetic
Pheophytin <i>a</i>	**	**	**
Pheophytin <i>b</i>	**	**	**
Beta carotene	*	**	**
Lutein-zeaxanthin	*	**	**
Pheophytin <i>c</i>		**	**
Fucoanthin		**	**
Alpha carotene	*	*	**
Chlorophyll <i>a</i>	*	*	**
Chlorophyll <i>b</i>	*	*	**
Chlorophyll <i>c</i>		*	**
Pheophorbide <i>a</i>		*	**
Alloxanthin			**

† For taxonomic specificity of pigments, see Goodwin (1980, 1981), Goodwin and Britton (1988), and Rudiger and Schoch (1988). For limnological sources in Tuesday Lake, see Carpenter et al. (1986, 1988) and Leavitt and Carpenter (1990).

tene of the Cryptophyta, while only a minor or infrequent component of the pigment assemblage of other plants (Goodwin 1980, Goodwin and Britton 1988). Chlorophyll *c*, pheophytin *c*, and fucoxanthin have no terrestrial sources, but can be contributed from pelagic chrysophytes as well as abundant littoral diatoms (He 1986). Planktonic diatoms are rare in Tuesday Lake (Elser and Carpenter 1988). Chlorophylls *a* and *b* are present in terrestrial and littoral vegetation as well as phytoplankton. However these pigments degrade very rapidly, and therefore the plankton is their dominant source (Leavitt and Carpenter 1990b).  $\beta$ -carotene (all algae and higher plants) and lutein-zeaxanthin (Chlorophyta, cyanophytes and higher plants) also have terrestrial, littoral, and aquatic sources. However, these carotenoids degrade much more slowly than the chlorophylls, and may also reflect terrestrial or littoral processes (Leavitt and Carpenter 1990b).

All locations are potential sources of pheophytins *a* and *b*, the dominant degradation products of chlorophylls (Table 1). Therefore, these pigments are the least likely to respond to fish population dynamics.

## METHODS

### *Coring and pigment analysis*

Sediments were recovered from the deepest portion of the lake (19 m) using the freeze-coring technique of Swain (1973). Sediments in Tuesday Lake are visibly laminated throughout the core. These laminae are assumed to be varves (i.e., annual deposits) because production, sedimentation, and lamination thickness in Tuesday Lake are similar to those in adjoining lakes where laminae are known to be annual (Leavitt and Carpenter 1989, Leavitt et al. 1989). Varves (1889–1985) were isolated from lyophilized core material following Leavitt et al. (1989) and Leavitt and Carpenter (1989). Varves were analyzed for pigment content by

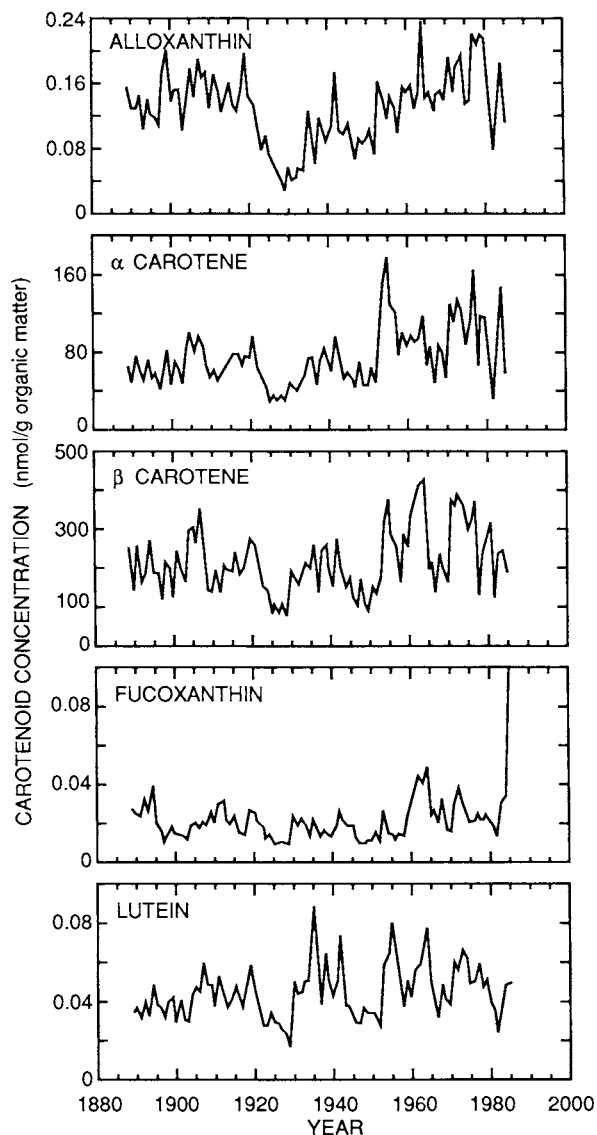


FIG. 2. Concentrations of carotenoids in sediments, 1889–1985.

reverse-phase high-pressure liquid chromatography (RP-HPLC) (Leavitt et al. 1989, Leavitt and Carpenter 1990b) and total organic matter by loss of mass on ignition at 550°C. Lutein (chlorophytes) and zeaxanthin (cyanophytes) were not resolved using this RP-HPLC technique. Pheophorbide *a* and its major derivatives (methyl pheophorbide *a*, and its acid and methyl isomers) were summed to calculate total pheophorbide *a* concentrations. Carotenoid and chlorophyll and derivatives concentrations were expressed as nanomoles of pigment per gram of organic matter.

#### Statistical analyses

We discarded data from 1983–1985 because of obvious pigment degradation in situ in most recent sed-

iments. The time series from 1889–1982 were detrended using first differences (Chatfield 1980). Periodograms were calculated using SAS (Helwig and Council 1979). To judge statistical significance we compared each normalized cumulative periodogram with the 95% confidence interval of a white-noise process (Fuller 1976: 285–287). Periodogram ordinates that fell above the upper 95% confidence limit were assumed to represent significant deviations from white noise. For each pigment we defined the range of periods for which variance deviated from white noise as the dominant scale of variance in the time series.

Detrending the data prior to analysis was necessary to produce interpretable periodograms, but the process has unavoidable effects on the statistical tests. Detrending decreases variance at long periods, and increases variance at short periods. For the first-difference detrending used in this study, variance is multiplied by the gain factor  $2[1 - \cos(2\pi p/N)]$  where  $N$ , the length of the time series, is 94 yr and  $N/p$  is period in years (Chatfield 1980). The gain factor declines as period increases, and equals 1 (i.e., the detrending has no effect) at a period of 6 yr. Because of the unavoidable effects of detrending, we regard the white-noise tests as an index of periodicity rather than a rigorous test, and emphasize the differences among pigments.

#### RESULTS

Stratigraphies of the major carotenoids (Fig. 2) and chlorophylls (Fig. 3) exhibited considerable variability. The trends evident in the concentrations of fucoxanthin and some chlorophylls probably result from in situ pigment degradation (Hurley and Armstrong 1990), and were removed by the first-difference transformation.

Spectra were of three general types (Fig. 4). Variance was high in a broad band between 2 and 5 yr for alloxanthin. Chlorophylls *a*, *b*, and *c*, and  $\alpha$ - and  $\beta$ -carotene had spectra similar to that of alloxanthin. Variance peaks occurred between 2.5 and 6.5 yr for total pheophorbide *a*. Relatively flat spectra with peaks near 2 yr were obtained for pheophytins *a*, *b*, and *c*, lutein, and fucoxanthin.

The periodograms of all three pheophytins were indistinguishable from white noise (Fig. 5). All other periodograms departed significantly from white noise, but most had rather broad peaks that suggested a mixture of sinusoidal components rather than a single pure sine wave. The broadest and widest peaks, relative to white noise, were found for alloxanthin, total pheophorbide *a*,  $\alpha$ -carotene, and chlorophyll *a*. Only marginally significant periodogram ordinates were found for lutein,  $\beta$ -carotene, and fucoxanthin.

Pheophorbide *a* has significant ordinates at periods  $>6$  yr, and alloxanthin's spectrogram increases steeply over a range (2–4 yr) where the gain factor declines from 4 to 2. Statistical evidence for periodicity is therefore convincing for these pigments. Several other pig-

ments ( $\alpha$ -carotene, chlorophylls *a*, *b*, and *c*, lutein,  $\beta$ -carotene) have distinct variance peaks, although significance tests may be affected by detrending. Four of these pigments ( $\alpha$ -carotene, the chlorophylls) are principally pelagic in origin. In contrast, there is no evidence of periodicity for pheophytins *a* and *b*, which are mainly influenced by terrestrial sources (Carpenter et al. 1986, 1988, Leavitt and Carpenter 1990a).

DISCUSSION

The data are consistent with expectations from the food-chain model, and support our specific hypotheses. Pigments dominated by terrestrial inputs, which should not be strongly influenced by the trophic cascade, do not exhibit periodicities. Pigments dominated by pelagic sources and herbivory have the most pronounced

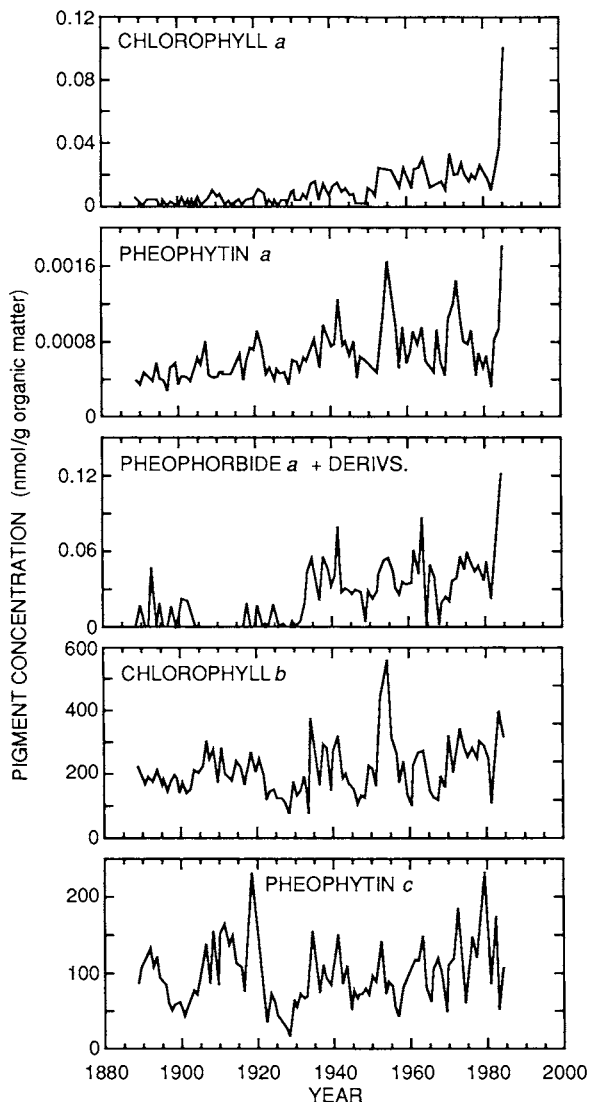


FIG. 3. Concentrations of the major chlorophyllous pigments in sediments, 1889–1985.

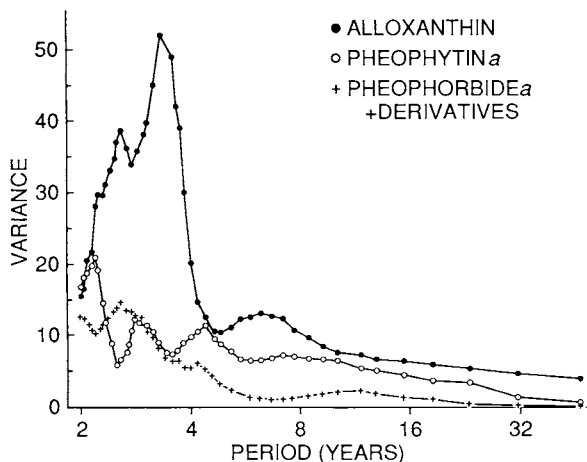


FIG. 4. Variance (spectral density) vs. period (years) for alloxanthin, pheophytin *a*, and pheophorbide *a* plus its derivatives. Smoothed periodograms were calculated using the weighting vector [1 2 3 4 5 4 3 2 1]. We found that these weightings produced acceptably small confidence intervals for each spectral ordinate, yet did not smooth out the major peaks.

cyclic behavior. The durations of the cyclic components are  $\approx 2.5$ – $6.5$  yr, consistent with expectations from the model. Statistical evidence for periodicity is especially strong for alloxanthin and pheophorbide *a*. Because experimental studies have shown that sedimentation of these pigments is linked directly with the trophic cascade, their periodicity provides strong evidence that fishes set the tempo of algal deposition (Carpenter et al. 1986, 1988, Leavitt and Carpenter 1990a).

Cyclic behavior in the plankton may also arise from periodicities in climate unrelated to food-web effects. For example, El Nino-Southern Oscillation events (ENSO) can cause extreme variance in physical properties of lakes (Strub et al. 1985, Goldman et al. 1989, Robertson 1989). These events are of similar duration to those predicted by our model (2–7 yr cycles) (Quinn et al. 1978). ENSO events may contribute to the periodicities of sedimentary pigment concentrations observed in our study through direct effects on phytoplankton, and indirectly, through influences on fish recruitment and the trophic cascade. Jassby et al. (1990) have shown how climatic forcing and fish dynamics interact to determine time series of primary production in Castle Lake, California.

Several lines of evidence show that the trophic cascade influenced the periodic variation of pigment sedimentation in Tuesday Lake. First, if weather alone regulated primary production, we would expect all pigments to show similar periodicities in deposition. Deposition of chlorophyll derivatives should be directly related to production (Leavitt 1988). Instead, pigments known to be regulated by herbivory show the strongest signals (i.e., alloxanthin and pheophorbide *a*), while

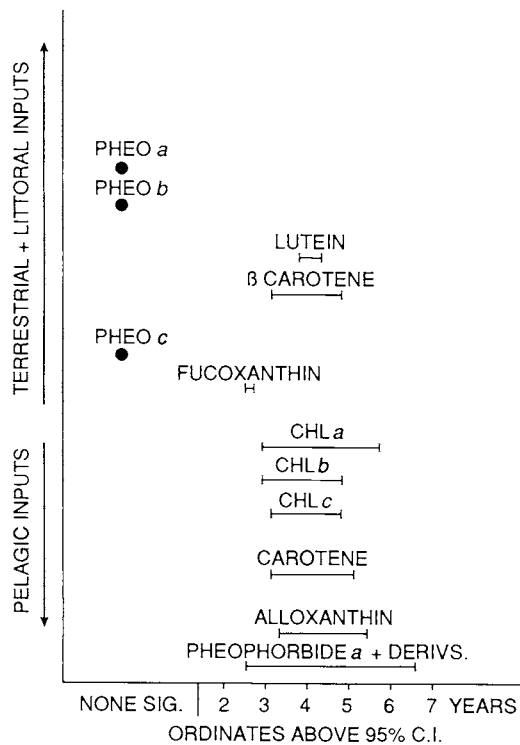


FIG. 5. Results of white-noise tests for periodograms of pigments. The vertical sequence represents a gradient from exclusively pelagic sources (alloxanthin, pheophorbide *a*) to dominance by littoral and terrestrial sources (pheophytins *a* and *b*). The horizontal axis indicates the periods (years) of the periodogram ordinates that lie above the 95% confidence interval for a white-noise process (Fuller 1976). For the pheophytins, no ordinates were significantly different from those expected in a white-noise sequence.

other pigment signals are less pronounced (e.g., lutein-zeaxanthin, fucoxanthin,  $\beta$ -carotene) or show no significant variance peaks (pheophytins).

Second, ENSO events do not produce a consistent effect on lakes (Goldman et al. 1989). Although ENSO events are related to extremes in the physical behavior of lakes (e.g., duration of ice cover, heat budgets), the directions of the effects are not predictable (Goldman et al. 1989). This variability in direction of effects would make ENSO signals less apparent in periodograms for pigment deposition.

Finally, Robertson (1989) has analyzed records of physical data for Lake Mendota, Wisconsin, from 1856 to 1988 and found clear correspondence with ENSO events only for 1940–1988. Prior to 1940 there was little correspondence between ENSO events and anomalies in the Lake Mendota data set. Robertson points out that changes in atmospheric pressure distributions and circulation patterns around 1940 (Rogers 1984) may lead to weaker ENSO signals in Wisconsin during the first half of the century (Rasmusson and Wallace

1983, Salstein and Rosen 1986). Our record includes significant periodicities prior to 1940, which may not be explainable by ENSO events.

We emphasize that weather and the trophic cascade are not mutually exclusive alternatives, because weather can influence the fish recruitment processes that drive the trophic cascade. Trophic cascade theory does provide us with a filter that can be used to separate food-chain effects from other sources of variance in lakes. In Tuesday Lake, variance at scales  $> \approx 5$  yr is largely free of food-chain effects, while variance at scales  $< \approx 5$  yr is influenced by food-chain dynamics (Carpenter 1988, Jassby et al. 1990). We applied a 5-yr running average to diminish variance at short scales and emphasize longer scale processes (Chatfield 1980). The residuals from the 5-yr running average have low variance at long scales, and emphasize shorter term processes dependent on the food chain. These filters amplified different features of the data set, and suggested new prospects for further work.

The 5-yr running averages stripped away variability attributable to the food chain in Tuesday Lake, and revealed several longer term patterns (Fig. 6). Deposition of all pigments was reduced in 1920–1930, and recovered during the next decade. Clear cutting during the turn of the century was followed by a series of fires, the last of which burned in 1924 (UNDA 1988). High pigment concentrations prior to 1921 are thought to result from increased nutrient loading to lakes in this region (UNDA 1988, Leavitt et al. 1989). Green algal blooms, indicated by simultaneous high inputs of chlorophyll *b*,  $\beta$ -carotene, and lutein, apparently occurred in the 1950s following road building. The running average of pheophytin *a* deposition reveals 15–20 yr cycles that are masked by short-term variability in the original stratigraphy. Since the pheophytins are more heavily influenced by terrestrial processes than are other pigments, and the running average filters out variance due to food-chain effects, we suggest that terrestrial processes underlie the cycles of pheophytin deposition. However, our record contains only four repetitions of this cycle, and a longer time series would be helpful.

Residuals from the running average emphasize the rapid resonance of food-chain effects derived from the relatively short-lived fishes of Tuesday Lake (Fig. 7). Especially extreme fluctuations of alloxanthin and pheophorbide deposition in the early 1960s followed liming and trout stocking in the lake (UNDA 1988). These events are the subject of ongoing analyses.

Analyses of annually resolved pigment data are uncommon, and further studies at this level of resolution will be valuable. In lakes dominated by longer lived fishes, variance components attributable to food-chain effects should occur at longer scales than in Tuesday Lake (Carpenter 1988). In fishless lakes we would expect any periodicities derived from food-chain dynamics to match the life cycle of the dominant invertebrate

predator. The resulting 1- or 2-yr signals could not be detected in annually resolved sediment records.

More complex possibilities will arise in fish communities with multiple piscivores. When nonlinear predator-prey models are forced by "red noise," population booms and crashes can occur at surprisingly long intervals (Steele 1985). Red noise is provided by a random variable that has a periodicity longer than the turnover times of the populations in the model (Steele 1985). Steele (1985) concludes that long-term environmental trends can interact with stochastic, nonlinear population processes to generate cyclicities with periods longer than the life-spans of the fishes. We propose that recruitment variance in long-lived fishes

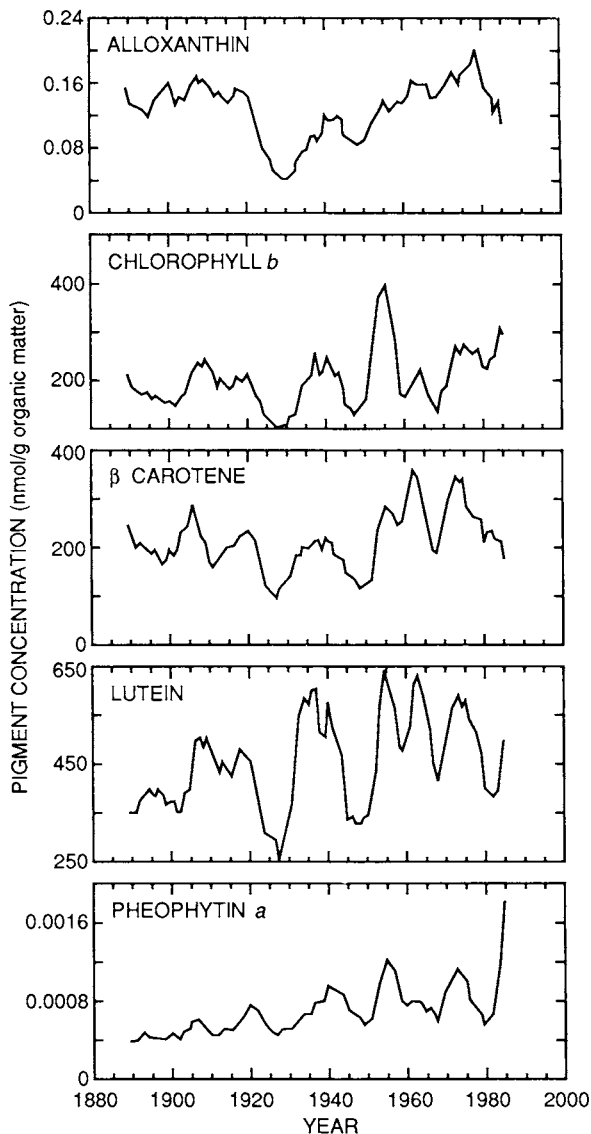


FIG. 6. Concentrations of selected pigments vs. time, 1889–1985. Time series have been filtered by presentation of a 5-yr running mean, to minimize variance at periods <5 yr and accentuate variance at periods >5 yr.

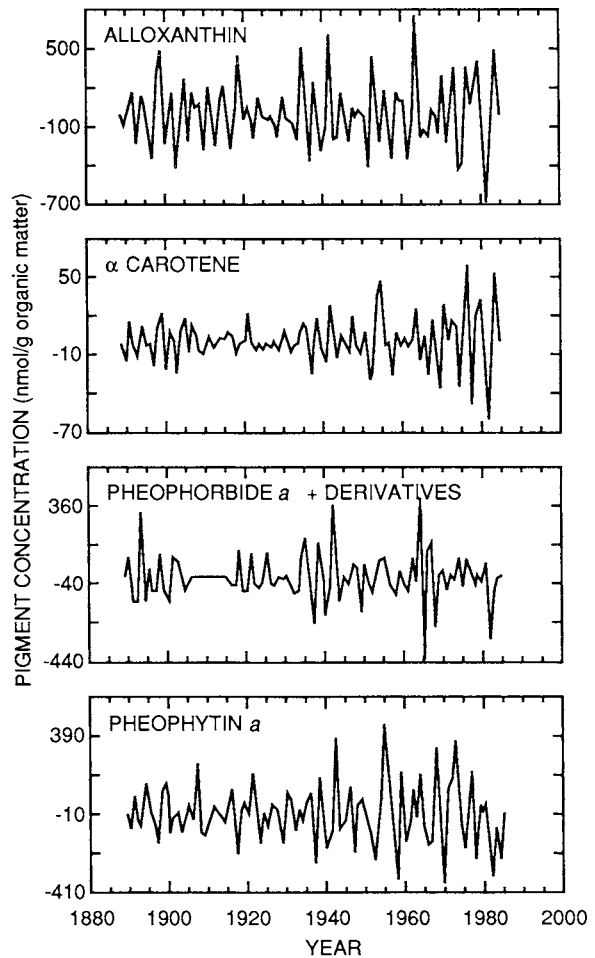


FIG. 7. Concentrations of selected pigments vs. time, 1889–1985. Graph shows residuals from the 5-yr running average, which minimize variance with periods >5 yr and accentuate variance at periods <5 yr.

can impose red noise on shorter lived prey, possibly leading to community cycles with very long periods. Further modeling and paleolimnological research is needed to explore these possibilities.

Some important food-chain dynamics in lakes are abrupt step changes that are distinctly different from the periodic phenomena discussed in this paper. These aperiodic events include invasions, extinctions, community changes implemented by fish managers, and major perturbations in the watershed. Such major community transitions can leave distinctive signatures in the sedimentary record (Soutar and Isaacs 1974, Kitchell and Kitchell 1980, Kitchell and Carpenter 1987, Leavitt et al. 1989). The relatively frequent and roughly periodic processes that we have analyzed are the background variance upon which more sweeping community changes are imposed. Improved analyses of the background variance will allow these less predictable, but often extraordinary, changes to be more sharply resolved.

Given a community structure, extant models of lakes can yield quite good data fits and predictions, in spite of stochastic forcing functions and recruitment. This encouraging evidence of regularities has not produced effective generalizations about perturbations that reconfigure communities and ecosystems. Contingent events, the intrusions of history that shape and constrain communities and ecosystems over the long term, have shown few regularities, and have eluded modeling attempts. Paleolimnological analyses, coupled with effective models of baseline variability, may be our best window on the historical contingencies that have structured ecosystems, and the key to forecasting ecosystems' responses to future perturbations.

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