Trend, seasonality, cycle, and irregular fluctuations in primary productivity at Lake Tahoe, California-Nevada, USA

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Abstract

Primary productivity has been measured routinely at Lake Tahoe since 1967, and a number of mechanisms underlying variability in the productivity record have now been identified. A long-term trend due to nutrient loading dominates the series. Seasonality also is prominent, apparently controlled by direct physical factors unrelated to the trophic cascade. A 3-yr cycle has been detected and several possible mechanisms are considered. Irregular fluctuations also are present, caused in part by isolated events (a forest fire) and recurring but variable phenomena (spring mixing). Except possibly for the 3-yr cycle, the known sources of variability appear to operate 'bottom-up' through direct physical and chemical effects on the phytoplankton.

Introduction

Because of the many processes affecting ecological variables such as primary productivity, the trend or long-term change in the mean may often be obscure (Schindler, 1987). As a result, many techniques have been developed to assess whether or not a significant change is underway and what its magnitude might be (Hipel, 1988). It is not possible, however, to identify change as a trend based solely on the statistical significance of an increase or decrease. Isolated events, for example, may result in perturbations with a recovery time of many years. Unless we know the frequency of isolated events and the time course for responding to them, even 'smooth' variation cannot necessarily be ascribed to a trend. A similar problem occurs with cyclical variation of sufficiently long period. Even if our interest is only the long-term change, it is difficult to escape the need for understanding all significant processes at work.

Describing the sources of variability in a series of monthly primary productivity, as in any series, involves decomposing the variation according to some model, explicit or implicit. When the data analysis is exploratory, as it is here, the ultimate justification is whether the analysis succeeds in identifying the separate mechanisms underlying variability. An inductive and flexible approach is therefore warranted. Here, we are guided by the traditional classification of a series into trend, seasonal variation, other cyclic changes, and irregular fluctuations (e.g., Chatfield, 1990).

Although this classification of variability is traditional, we use a relatively novel method for achieving it. The main emphasis will be on an analysis of year-to-year variability in the seasonal

pattern. Principal component analysis (PCA) techniques can be used to uncover the major modes of variability in the seasonal pattern and the intensity of these modes from one year to the next. This particular application of PCA was introduced over 25 years ago (Craddock, 1965), but appears to have received little attention in ecological studies until recently (Smith & Hayden, 1984; Jassby & Powell, 1990; Jassby *et al.*, 1990 have extended the method to the space-time domain). The approach permits the data to indicate both the number of significant mechanisms at work and other, temporal characteristics of the mechanisms that can lead to their identification.

Several sources of variability in primary productivity have already been uncovered for Lake Tahoe. Trend has been a subject of intensive study for over 20 years (Goldman, 1988) and two sources of irregular fluctuations, spring mixing depth (Goldman *et al.*, 1989; Goldman & Jassby, 1990) and forest fires (Goldman *et al.*, 1990), have also been detected. Here we present some new work that has uncovered a multi-year, cyclical patten in the productivity series. The reasons for the cycle are uncertain, but a biological mechanisms is suspected. We also offer some additional clarification of the irregular fluctuations dealt with in previous work. Finally, our aim includes presentation of a more unified and complete picture of the variability in Tahoe's primary productivity.

Lake Tahoe is situated at the crest of the Sierra Nevada (39°N, 120°W), lying in a graben at an altitude of 1898 m. The lake is 500 km^2 in area, with a maximum depth of 505 m and a mean depth of 313 m. Tahoe is ultra-oligotrophic, warm monomictic, and free of ice the entire year.

Methods

Primary productivity has been measured since 1967 with the ^{14}C method of Steeman Nielsen (1952). Samples were taken every 10 days, on average, from an index station off Homewood, California. Water was collected from depths of 0, 1, 2, 5, 10, 15, 20, 30, 40, 50, 60, 75, and 105 m (the approximate mean depth of the photic zone),

and incubated *in situ*. Details of the gas phase calibration and incubation methods have been described by Goldman (1968, 1988).

NO_3^- (as well as other chemical species) has been measured routinely both at the index station and at a midlake station by the cadmium reduction or hydrazine methods (American Public Health Association, 1985; Kamphake *et al.*, 1967). Samples were collected at the mid-lake station at 50-m intervals down to a depth of 450 m, enabling us to follow the seasonal evolution of the nitracline and deduce the approximate depth of spring mixing (Paerl *et al.*, 1975; Goldman *et al.*, 1989).

Several methods were used to collect zooplankton. Routine vertical tows from 150 m to the surface have employed a 0.75-m-diameter mouth, 80 μm mesh Nitex net. Additionally, since 1975, a 1-m^2-mouth Tucker trawl has been used for vertical distribution studies; paired 0.75-m-diameter mouth, 202 μm mesh Bongo nets for areal estimates of mysid densities; and a bottom sled for estimation of epibenthic populations. Richards *et al.* (1991) give a recent overview of the mysid studies at Lake Tahoe and further references to the zooplankton sampling techniques.

Mechanisms underlying interannual variability in productivity were investigated by means of principal component analysis. The utilization of PCA for studying interannual variability has been described in general by Jassby & Powell (1990), and a practical application to Castle Lake, California, was reported by Jassby *et al.* (1990). These publications can be consulted for details regarding rationale, calculations, and significance tests. In the case of Lake Tahoe, productivity values were first integrated over the water column and month, resulting in a series of 240 monthly means for water years 1968 through 1987 (a California 'water year' extends from 1 October of the previous year through 30 September). Next, the long-term trend was defined to be the linear regression of monthly mean productivity on month. Each monthly mean was then divided by the corresponding monthly value for the long-term trend to remove nonstationarity both in the mean and the variance. Finally, the adjusted data set consisting

of 20 observations (years) of 12 variables (monthly means) was subjected to a PCA, using the covariance matrix. Significant components were identified on the basis of the scree test (Cattell, 1966) and 'Rule N' (Preisendorfer, 1988) and subjected to a varimax and a promax (power = 2) rotation (Richman, 1986).

Results

The basic series of monthly primary productivity exhibits strong seasonality and an upward trend (Fig. 1a). The line running through the center of the series was determined by a locally-weighted straight-line smoother that uses the nearest 5 years of data (a 'loess' smooth with span =
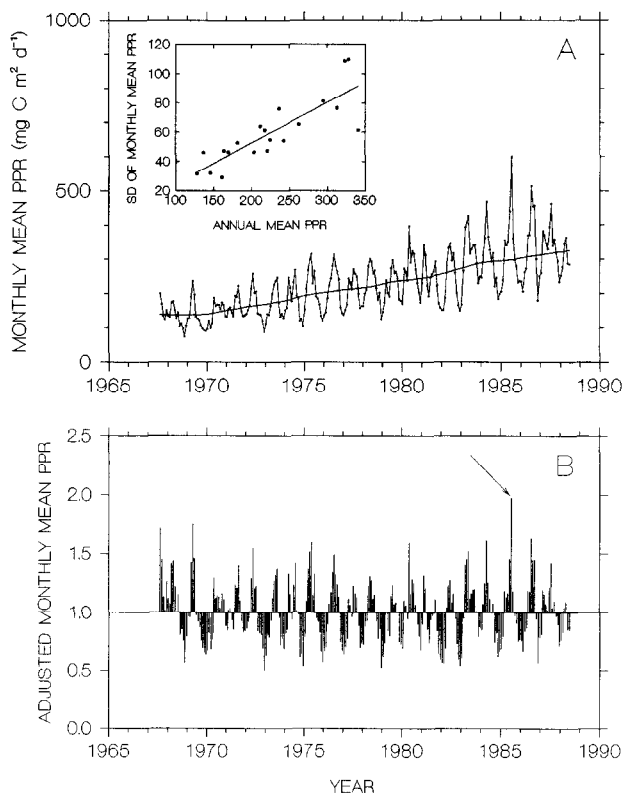
0.25: Cleveland, 1979). The smoothed line shows no remarkable features and the long-term change in the mean can be appropriately described as a linear upward trend. Productivity increased at an average rate of 11 g m^{-2} yr^{-1}, equivalent to an average increment of 3.8% yr^{-1}, over water years 1968–1987. The standard deviation of the monthly values is proportional to the annual mean (Fig. 1a, inset). Thus, the variance of the series also increases with time.

In order not to have this increase in the mean and variance dominate the PCA and overwhelm more subtle processes, the series must be transformed. The approximate linearity of the trend and the proportionality between standard deviation and mean suggest a multiplicative model. Several methods can be used to remove nonstationarity in trend and variance in such models; here, we simply divide the monthly means in the original series by the corresponding monthly values in the linear trend. The resulting adjusted series is free from these forms of nonstationarity and more suitable for subsequent analysis (Fig. 1b).

A typical seasonal cycle can be extracted from the adjusted series of monthly mean primary productivity (Fig. 2). The pattern formed by the monthly medians peaks in July and has a mini-

Fig. 1. (A) Monthly mean primary productivity (PPR) for Lake Tahoe; smooth line, loess smooth, span = 0.25; inset, standard deviation (SD) of monthly values for a given year vs. the mean of all monthly values for that year. (B) Monthly departures from the long-term mean after division by the linear trend; arrow, July 1985.
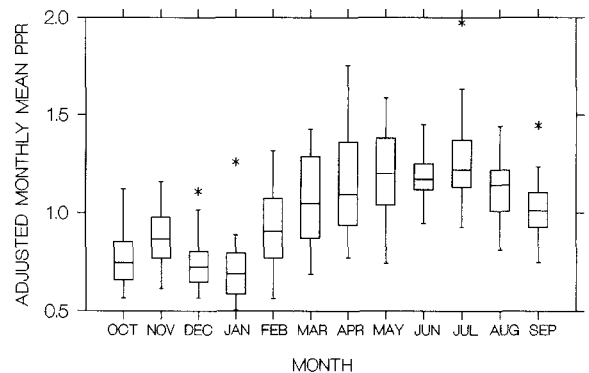

Fig. 2. Box-and-whiskers plot (Tukey, 1977) of monthly mean primary productivity from 1968–1987, adjusted as in Fig. 1b. The center horizontal line in each box is the median. The lower and upper edges of each box, called hinges, mark the quartiles. The whiskers (vertical lines emanating from each box) show the range of values falling within 1.5 times the interquartile distance from the nearest hinge. Asterisks mark outside values that fall beyond the whiskers.

mum in January, following the annual solar cycle with a lag of 1 month. A local maximum occurs in November and a weak minimum tends to occur in June. The seasonality as a whole is subdued, with less than a factor of 2 between the lowest and highest median monthly values.

PCA can be strongly influenced by extreme values. If outliers are observed in the seasonal pattern, and if they can be explained, then removing their influence is advantageous. Otherwise, as in the case of nonstationary mean and variance, additional unknown sources of variability become harder to ferret out. The seasonal pattern shows four 'outside' values (Tukey, 1977), one each for December, January, July, and September. The reasons for three of these values are unknown. The outside value for July, however, is due to the 1985 'Wheeler' fire occurring in California's Los Padres National Forest, unusual in its massive size and for its effect on Lake Tahoe through atmospheric deposition (Goldman et al., 1990). Other fires are not known to have had such a marked effect on the lake. The unusual nature of the July 1985 productivity can also be picked out easily from the adjusted monthly series of data (Fig. 1b, arrow). This series was further adjusted by replacing the July 1985 value with the long-term mean for July. In view of the lack of understanding regarding the remaining three outliers, these were not altered in any way.

Two criteria were used to determine the number of components to retain for rotation. The scree test (Cattell, 1966) suggested the retention of only the first two principal components (PC-1 and PC-2). Utilizing 'Rule N' (Preisendorfer, 1988), 95% significance levels for the first three eigenvalues were determined to be 0.121, 0.088, and 0.071, compared to sample eigenvalues of 0.190, 0.089, and 0.043, respectively. 'Rule N' therefore also supported the significance of only PC-1 and PC-2, which accounted for a majority (63.4%) of the variability in the seasonal pattern. The first two components were then subjected to a varimax rotation (Richman, 1986). A further, oblique rotation (promax, power = 2) resulted in little change: the angle between the two components was 91.2°. As a result, the varimax solution was used for further analysis, retaining complete orthogonality (and lack of correlation) for the two components.

PC-1 accounts for 42.4% of the variability in the seasonal patten and is therefore the single largest mode of variability. The main feature of PC-1 is a peak in late winter and early spring, just before the onset of stratification in May (Fig. 3a). The amplitude time series for PC-1 has a remarkably regular structure: five successive cycles occur from 1970 through 1985, each consisting of two annual increases followed by one annual decrease (Fig. 3b). Note that the signs of loadings and amplitudes are arbitrary: they are determined using the convention that a majority of the loadings should have a positive sign.

To verify the presence of a cycle using another approach, we also computed the power spectrum of the original monthly series, first transforming with logarithms and then subtracting the linear trend (Fig. 4a). A peak was observed at 0.0278 cycles month^{-1}, corresponding to a 3-yr period. This peak appears to be well above the baseline spectral levels, using the 0.95 confidence interval based on the chi-squared distribution (Shumway, 1988). The largest peak occurs, of course, at
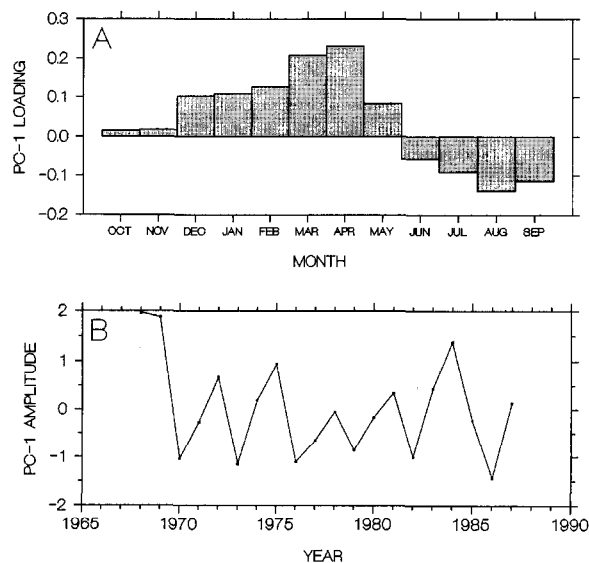

Fig. 3. (A) Component loadings for the first principal component (PC-1) of the adjusted PPR series. (B) Amplitude time series for PC-1.
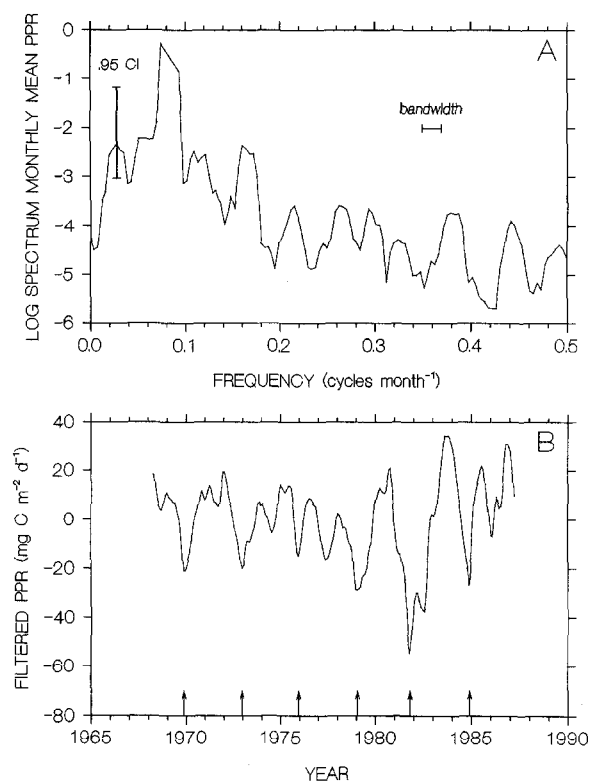
Fig. 4. (*A*) Natural log of the power spectrum of logged, detrended monthly mean primary productivity. The series was tapered with a full cosine bell. Note also the bandwidth and 0.95 confidence interval (CI). As this is a log spectrum, the CI is independent of the frequency, but it has been positioned at 0.0278 cycles month^{-1} (a period of 3 yr). (*B*) Original primary productivity series (Fig. 1a) filtered with a centered, 12-term moving average. The filtered series was detrended for clarity. Arrows on the abscissa mark the positions of local minima occurring at intervals of approximately 3 yr.

0.0833 cycles month^{-1}, representing the seasonal cycle with a 1-yr period.

A 3-yr cycle can also be discerned directly in the series if higher-frequency variation is suppressed with a low-pass filter. Here, we applied a centered, 12-term moving average to the unadjusted series (Fig. 1a), suppressing those cycles with a period of less than approximately 1 yr (Shumway, 1988). Local minima can be observed in the filtered series at intervals of approximately 3 yr (Fig. 4b).

PC-2 accounts for an additional 21.0% of the variability. The main feature of PC-2 is a peak in midspring (Fig. 5a). A contrasting peak may be
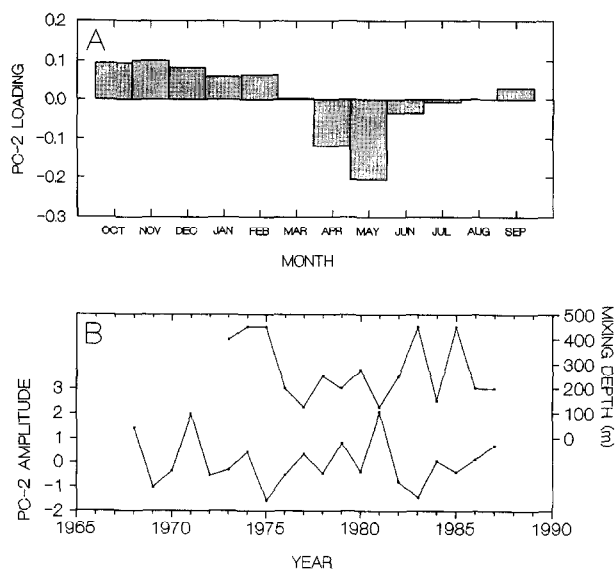

Fig. 5. (*A*) Component loadings for the second principal component (PC-2) of the adjusted primary productivity series. (*B*) Amplitude time series for PC-2. Also shown is the spring mixing depth since 1973; mixing depth was not estimated in earlier years.

present earlier in the water year, but it is definitely of secondary size and will not be considered further. The amplitude time series by itself exhibits no remarkable features, but it clearly has an association with the spring mixing depth (Fig. 5b; Spearman $r = -0.579$, $p < 0.05$).

Discussion

Trend and seasonality

The fundamental reason for the long-term trend is accumulation of nutrients, primarily N and P, from both atmospheric deposition and watershed runoff. As the trend has been discussed in some detail elsewhere (e.g., Goldman, 1988), we will not deal with further particulars here. Note that the long-term trend defined by the loess smooth (Fig. 1a) does not appear to be changing significantly, at least on the decadal scale. One cannot conclude, however, that the underlying dynamics has not changed. From the data of Marjanovic (1989), it can be deduced that the time constants for change in the pools of 'available' N and P are

at least 10 yr. The time series studied here, although relatively long for a limnological series, may therefore be too short to assess changes due to control of watershed development and emissions from combustion and other processes.

Seasonality at Tahoe has also been treated in detail in several other publications (Goldman & de Amezaga, 1975; Tilzer *et al.*, 1977; Abbott *et al.*, 1984). Suffice it to say here that the mechanisms driving seasonality differ from those of many higher-productivity lakes, at least as summarized in the Plankton Ecology Group model of seasonal succession (Sommer *et al.*, 1986). Little feedback occurs from the sparse mesozooplankton populations (Elser *et al.*, 1990), so that seasonal dynamics are driven primarily by the interaction of the solar cycle with stratification. Note, however, that the microbial loop, including bacteria and microbial grazers, is virtually unstudied at Tahoe. Furthermore, the method of counting ^{14}C uptake, namely, after filtration onto 0.45 μm membrane filters, may miss part of the picoplankton, which typically constitute a significant fraction of the productivity in oligotrophic lakes (Stockner & Antia, 1986). A different picture of the role of grazing at Lake Tahoe may very well emerge as more information about its microbial community becomes available.

Cycle

Although the existence of a 3-yr cycle in productivity appears to be well-supported by the data and can be extracted by both a PCA and spectral analysis, the reason for this cycle has not been established. Several mechanisms can be considered *a priori* for oligotrophic lakes, some more likely than others:

1. No cycles of similar period are apparent in meteorological conditions at Tahoe. Solar radiation and water temperature exhibit no detectable cycles greater than 1 yr in period. Also, principal component analysis of the monthly series for both insolation and temperature revealed no cycles in any of the individual modes contributing to the seasonal pattern of these variables. Furthermore, the regularity of the cycle, as evidenced by the PC-1 amplitude (Fig. 3b), would be unexpected if meteorological forces were the underlying cause.

2. In principle, as well as in practice, oscillations in primary production can be generated by oscillations at higher trophic levels through cascading trophic interactions (Carpenter & Leavitt, 1991). It has also been demonstrated in simulation models that animal populations tend to oscillate with a period equal to their generation time (Carpenter, 1988a). Conceivably, then, the 3-yr cycle in primary productivity could arise from grazer or predator populations with a 3-yr generation time. An apparent problem with this hypothesis for oligotrophic lakes like Tahoe is the lack of significant grazing control, at least from metazoan grazers. Variability at higher trophic levels, however, can be transmitted in ways other than through the trophic cascade. In particular, large zooplankters can transport significant quantities of nutrients from the epilimnion to below the thermocline during their diel migrations (Kitchell *et al.*, 1979; Wright & Shapiro, 1984; Longhurst & Harrison, 1988).

The opossum shrimp, *Mysis relicta* Lovén, has been hypothesized to play a significant role in the downward transport of nutrients in Lake Tahoe (Rybock, 1978). Marjanovic (1989) further argued on the basis of anomalous N profiles that active, biologically-mediated transport must be taking place. *Mysis*, which is primarily carnivorous in Tahoe, migrates between the upper hypolimnion where the productivity maximum is located (30–50 m) and deep waters at 300–400 m. A crude estimate of potential daily N ingestion can be obtained from typical peak abundances of 200 m^{-2}, a dry weight (DW) of 6 mg, a daily ration equal to 25% of body weight, and an N:DW ratio of 0.093 for mesozooplankton (Rybock, *op. cit.*; Longhurst & Harrison, 1988), yielding 28 mg N m^{-2} d^{-1}. In 1990, the lake content of biologically available N was between 2900 t (the dissolved inorganic nitrogen pool) and 14000 t (the total nitrogen pool), equivalent to 2.0–9.4 g N m^{-2} in the photic zone when the lake mixes

completely during vernal isothermy. According to these estimates, only ca. 2–11 months would be required for *Mysis* to ingest all of the 'available' N in the photic zone. As a significant portion of ingested material is excreted at depth, *Mysis* clearly has the potential to influence nutrient availability and therefore primary productivity.

The generation time for *Mysis* in Lake Tahoe was originally estimated to be 4 yr (Morgan , 1980), but the longer data set now available suggests a generation time of 2–3 yr (C. Levitan, pers. comm.). This is longer than the 1–2 yr characteristic of most lakes, due to the ultra-oligotrophic conditions and the energetic demands of migration over large distances (Morgan, *op. cit.*). Regardless of the generation time, however, no statistically significant cycle of any length can be discerned in the *Mysis* density series obtained from vertical tows. A subpopulation of *Mysis* may be responsible for the nutrient transport, as the vertical tows did not distinguish between migrating and nonmigrating animals. The resolution of this matter awaits further sampling of the *Mysis* population.

3. Regular oscillations also can arise solely from the interactions of phytoplankton populations and their limiting nutrients. The effects of organisms at higher trophic levels are not necessary. Powell & Richerson (1985) explored the nonsteady-state consequences of a model of two phytoplankton species competing for two nutrients over a range of biologically realistic growth and uptake parameters. The model extends the Tilman (1982) resource competition approach to allow explicit spatial and temporal variability. Multi-year limit cycle oscillations result; both the phytoplankton populations and the limiting nutrients cycle in the model with a several-year period. The amplitude and period of the oscillation depend upon the selection of model parameters, and no attempt was made to match these constants to the specific conditions found a Lake Tahoe. Despite the theoretical potential for these oscillations, the whole-lake contents of NO_3^- and total acid-hydrolyzable PO_4^{3-}, the only nutrient fractions for which a long-term record exists, ex-

hibit no multi-year cycles. Data on individual phytoplankton species are not sufficiently detailed at this time to look for multi-year cycles in the numbers or biomass of individual taxa.

Irregular fluctuations

The category of 'irregular fluctuations' is nothing more than a catch-all for variability that does not fit neatly into the other categories. Furthermore, the amount and nature of variability in this category is to some extent arbitrary, as there are no truly universal ways to define trend and seasonality. That said, it is useful to subdivide this category further into several distinct mechanisms made obvious by the analysis of Tahoe data.

The first subcategory can be referred to as 'isolated events', or short-term but substantial discontinuities in the underlying behavior of a time series. They are difficult to discern mathematically, but often extremely informative once identified. The forest fire of July 1985 is clearly a case in point (Fig. 1b): it provided a dramatic demonstration of the vulnerability of Lake Tahoe primary productivity to atmospheric deposition. The actual contribution of these discontinuities to long-term variability may be small. The 1985 fire, for example, although it had an obvious effect on the seasonal pattern of productivity for that year, plays a trivial role in the variability of the long-term record. The importance of these discontinuities is largely one of elucidating mechanisms, reflected more generally by the intense interest in experimental perturbations of lakes (Carpenter, 1988b, 1990).

A second subcategory consists of annually-recurring phenomena with a known mechanism but with irregular magnitudes from one year to the next. The effects of spring mixing depth clearly belong to this group. Although the significance of spring mixing was discovered initially through consideration of the annualized data (Goldman *et al.*, 1989), the PCA results delineate the importance of spring mixing for individual months. Maximum mixing depth is achieved typically in March (Goldman *et al.*, *op. cit.*). According to the

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PC-2 loadings (Fig. 5a), the resulting effects on productivity peak 2 months later in May. In a typical year, stratification begins developing in May and strengthens through July until the formation of a well-defined mixed layer in August. The sharp drop in PC-2 loading values between May and June suggests that contributions of up-welled nutrients from spring mixing are apparently exhausted once stronger stratification begins to develop.

A final subcategory can be designated as 'noise', consisting of all mechanisms that have not yet been recognized. This category is also affected by departures from statistical assumptions regarding the known mechanisms. The nutrient loading underlying the trend, for example, cannot possibly be truly linear with time. We know that watershed loading of both N and P is highly precipitation-dependent and that precipitations is extremely variable from one year to the next. So the effects of deviations from the mean external loading will contribute to the 'noise'. In principle, we should be able to identify this mechanism explicitly by examining how precipitation contributes to variability. In practice, however interannual variability in internal loading dominates variability in external loading, and precipitation does not add significantly to forecasting ability (Goldman et al., 1989). A linear trend due to external loading is therefore appropriate and the relatively small deviations from this assumption are lumped into the 'noise'" category.

Concluding remarks

We emphasize both the number and diversity of variability processes. First and foremost, a trend exists due to nutrient loading. Seasonality is produced by the interaction of insolation with thermal stratification. A 3-yr cycle, possibly related to the generation time of *Mysis*, is present. Isolated events such as forest fires also leave their mark. Finally, the spring mixing depth has a profound effect from one year to the next. Although some 'noise' still exists in our understanding, these processes account for an overwhelming amount of the variability.

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