

Origins and scale dependence of temporal variability in the transparency of Lake Tahoe, California–Nevada

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Abstract

Secchi depth has been measured in Lake Tahoe an average of every 12 d since July 1967. Because of the unusual clarity of the lake, Secchi depth measurement is responsive to small changes in light-attenuating particles, and the record exhibits strong variability at the seasonal, interannual, and decadal scales. Using recently developed methods of applied time-series analysis, the mechanisms of change were delineated at each scale. The seasonal pattern is a bimodal one, with two minima at approximately June and December. The June minimum is due mostly to cumulative discharge of suspended sediments following melting of the snowpack. The December minimum is probably a result of mixed-layer deepening as the thermocline passes through layers of phytoplankton and other light-attenuating particles that reach a maximum below the summer mixed layer. The interannual scale exhibits two modes of variability, one during the weakly stratified autumn–winter period and the other during the more stratified spring–summer period. The first mode is a result of variable depth of mixing in this unusually deep lake, while the second results from year-to-year changes in spring runoff. A decadal trend also exists (-0.25 m yr^{-1}), resulting from accumulation of materials in the water column. It is not yet understood, however, how much of this change is due to phytoplankton or recent phytoplankton-derived materials and how much is due to other materials such as mineral suspensoids. Based on the available measurements and physical considerations, both categories may play a significant role.

Optical clarity is important in making judgments about water quality. Clarity is the first and perhaps the only water quality parameter that many casual observers encounter. Moreover, clarity is often used by the layperson as a basis for judging potability as well as the safety of water contact (Smith et al. 1995). In both freshwater and marine oligotrophic water bodies, optical clarity can also be an important aesthetic characteristic.

Certain lakes have an exceptionally high optical clarity. Several different reasons can account for low concentrations of dissolved and particulate materials (Hakansson 1995). The same characteristics that lend uniqueness to these lakes in the form of transparency and color, however, also render them unusually susceptible to small changes in dissolved and suspended matter. The Secchi disc is commonly used to measure these changes in visual clarity. The Secchi depth, Z_s , or the depth at which the disc disappears from the view of a surface observer, is inversely proportional to the beam attenuation coefficient for luminance, c , plus the attenuation coefficient for illuminance, K :

$$Z_s = \frac{\Gamma}{c + K}, \quad (1)$$

where Γ is approximately constant (Preisendorfer 1986). The sum in the denominator is sometimes referred to as the contrast attenuation coefficient (Kirk 1994). In practice, K covaries with c , and the Secchi depth is highly correlated inversely with c (Davies-Colley et al. 1993; Larson et al. 1996a). The coefficient c is dominated, in turn, by total scattering (Davies-Colley et al. 1993). Regardless of what materials actually control c , the relative decrease in transparency due to a fixed increase in these materials is clearly larger at lower c values. Therefore, in water with a low contrast attenuation coefficient, a small amount of algal growth or a small load of suspensoids can have remarkably large effects on perceived visual clarity.

Large declines in clarity have in fact occurred over the last few decades in some of our most highly transparent water bodies, including Lake Tahoe in the Sierra Nevada mountain range of California–Nevada. Lake Tahoe exhibits many of the characteristics that result in unusual clarity. The ratio of watershed to lake area is only 1.6; the lake has a maximum depth of 505 m, rendering it the eighth deepest freshwater body in the world; the major rock type in the basin is granite (Hyne et al. 1972); and over 85% of the watershed has been forested for the last few decades. Secchi depths of over 40 m occurred in the early years of the measurement program at Lake Tahoe and still occasionally exceed 30 m. The long-term decline, though, is a matter of great concern to the residents of the Tahoe Basin, as well as to the millions of visitors annually who are attracted to the area precisely because of its physical beauty.

Using a long time series of primary productivity, previous studies have shown that algal growth rates have increased over the past few decades (Goldman 1988). The primary

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productivity increases were fueled initially by atmospheric deposition of nitrogen (Jassby et al. 1994). As lake chemistry shifted under the pressures of continuous atmospheric loads, phosphorus originating in the watershed became the dominant controlling nutrient (Goldman et al. 1993; Jassby et al. 1995). In the littoral zone, this increase has been seen in the proliferation of epilithic periphyton around the shores of the lake (Loeb 1986). In the pelagic zone, however, the role of phytoplankton in the transparency decline has not been delineated. The lake has a deep chlorophyll maximum at 60–120 m, well below the Secchi depth, and therefore phytoplankton increases do not necessarily affect visual clarity for a surface observer. In order for phytoplankton to play a role in the transparency decline, biomass increases must take place above the Secchi depth and they must be optically significant compared to increases in material not derived from phytoplankton. Algal cells may be the most important contributors to total scattering in the oligotrophic ocean, at least at chlorophyll concentrations similar to those found in Lake Tahoe (Morel and Ahn 1990; Stramski and Kiefer 1991). Even large lakes, however, are subject to a significant terrestrial influence. Certainly in other lakes, terrigenous particle input and phytoplankton contribute to variability in optical water quality (e.g., Onondoga Lake [Perkins and Effler 1996]). Establishing the cause of changes in the clarity of Lake Tahoe has important implications for management of the Tahoe watershed: it determines whether the focus should be on controlling phytoplankton growth or on controlling allochthonous materials such as mineral suspensoids. The long time series of Secchi depth measurements for Lake Tahoe (one of the longest continuous records [Sanden and Hakansson 1996]) not only records variability in optical clarity but also offers the potential to uncover underlying causes.

Our primary objective was to establish the dominant modes and causes of seasonal, year-to-year, and decadal variability according to the Secchi depth series. The unusual length (29 yr) and resolution (~12 d) of this series offers a unique opportunity to add to our understanding of the natural history of ecosystem variability (Jassby 1998). In earlier studies, we used the series of primary productivity (Goldman et al. 1989, 1990; Jassby et al. 1992), enrichment bioassays (Goldman et al. 1993), nutrient loading (Jassby et al. 1994), and lake chemistry (Jassby et al. 1995) to investigate the nature of and reasons for variability at the seasonal to decadal scales. We found that spring mixing depth played a dominant role at the interannual scale and atmospheric deposition of nitrogen at the decadal scale. At scales intermediate to these two, population cycles of macrozooplankton (*Mysis relicta*) may have played an important role through the biological pumping of nitrogen. In this study, we revisited the issue with a different and considerably longer series in order to build on the earlier conclusions.

Many substances can contribute to light absorption and scattering. For our purposes, we have distinguished four categories on the basis of origin: (1) water molecules, (2) phytoplankton plus detritus recently derived from phytoplankton, (3) autochthonous material not containing photosynthetic pigment, including viruses, bacteria, dissolved and particulate organic matter, and biogenic minerals, and (4) allochthonous material, especially mineral suspensoids but also

dissolved substances and particulate organic materials. A single Secchi depth measurement, of course, cannot allow the analyst to discern from among these various categories. A time series of sufficient resolution does, however, exhibit certain characteristics that enable us to differentiate to some extent among the light-attenuating factors, as these factors respond at different times and with different lags to meteorological and other forces. The attempt to differentiate these factors is further aided by a shorter series for chlorophyll *a* (Chl *a*) and by recent measurements of suspended particulate matter.

A further objective of this study was to demonstrate the utility of several relatively recent developments in applied time series analysis (Cleveland et al. 1990; Jassby in press). These methods provided us with a methodical approach to the analysis of ecological time series that has helped reveal causes of temporal variability in a number of different systems. Note that Secchi depth spatial structure can also be analyzed to reveal underlying mechanisms (Conversi and McGowan 1994), but our data have confined us largely to the time domain.

Methods

Site description—Lake Tahoe occupies a subalpine graben at an altitude of 1,898 m. The surface area of the lake is 501 km² and that of the watershed is 812 km². Maximum depth is 505 m at the highest surface elevation, and mean depth is 313 m. Hydraulic residence time is approximately 650 yr. The lake is warm monomictic and free of ice the entire year. Thermal stratification typically begins to intensify during February–April and reaches a maximum in August when the thermocline is located ~20 m below the surface. Stratification then begins to weaken slowly, usually reaching approximate isothermy by midwinter. Complete mixing, however, does not necessarily take place unless cooling and wind conditions are strong enough at that time (Goldman and Jassby 1990). The maximum mixing depth has been determined from NO₃⁻ profiles since 1973 (Paerl et al. 1975).

Secchi depth—Secchi depth was measured with a 25-cm disc painted matte white. The disc was lowered on the shaded side of the boat to minimize surface reflectance. Because the Secchi depth is so great, however, at Lake Tahoe, the disc itself was illuminated by direct sunlight passing underneath the boat. After adapting to the ambient light conditions, the observer read both the depth at which the disc just disappeared on the way down and the depth of reappearance on the way up. The Secchi depth is the average of the two. Measurements were made near midday, and the time, weather, and water conditions were recorded. Since 1969, measurements have been taken by the same observer (R.C.R.) with 20/20-corrected vision. It is now believed that a larger disc is preferable in the most transparent water bodies and that a black disc is preferable in all water bodies (Davies-Colley et al. 1993). The original methods used at Lake Tahoe, however, were retained to maintain continuity with the historical series, but these data are now supplemented by measurements with a 60-cm disc painted matte black.

Regular measurements at the Index Station (110-m depth)

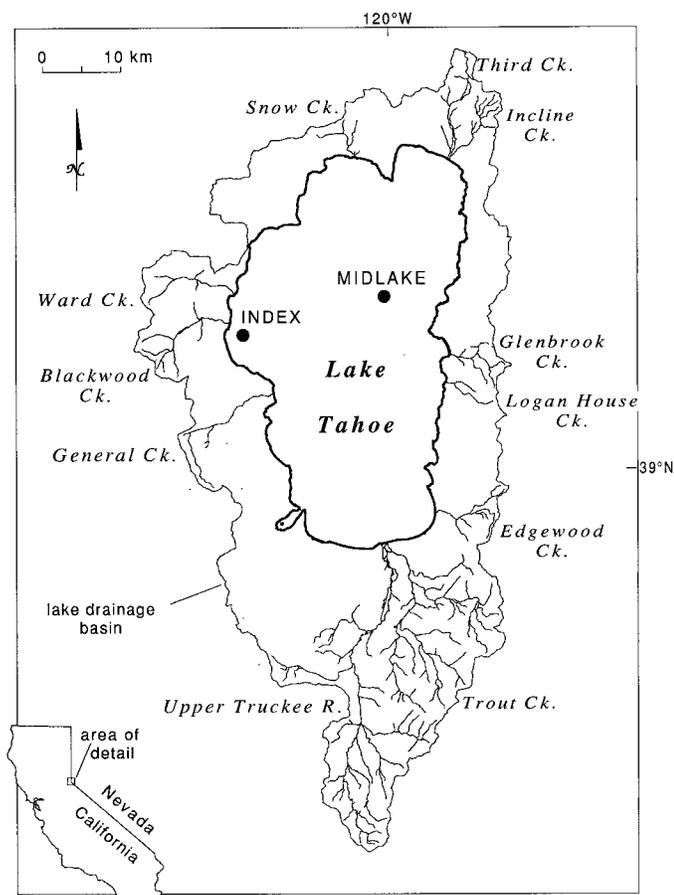


Fig. 1. Lake Tahoe and its watershed, showing some of the most important tributaries and the Index and Midlake Stations.

began in July 1967 and have been made on average every 12.2 d since that time (Fig. 1). Measurements at the Midlake Station (505 m depth) began in December 1969 and have been made on average every 29.9 d since that time. In 1974 and again in 1980–1997, a second observer on a separate vessel also read Secchi depths on 217 occasions. These duplicate measurements were used to assess precision, particularly because of concern that short-term and spatially localized variability in water surface characteristics can significantly affect Secchi depth readings.

Chlorophyll—Measurements of Chl *a* corrected for phaeophytin began in November 1987. Samples were collected at the Index Station at depths of 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 75, 90, and 105 m. On every third sampling day, pigment measurements were made at each of these depths. On other sampling days, a measurement was made on a composite sample from all depths combined. One hundred milliliters of lake water were passed through a 2.4-cm-diameter Whatman GF/C filter and frozen until analysis. Filtered Chl *a* was extracted in methanol overnight at 4°C. Extract fluorescence was measured before and after acidification using a Turner 111 fluorometer fitted with a Corning CS 5-60 filter for the excitation light and a Corning CS 2-64 filter in combination with a 10% neutral density filter for

the emitted light. The fluorometer was calibrated as described by Strickland and Parsons (1972; Holm-Hansen 1978). In addition to periodic calibration using purified Chl *a* standards, fluorometer response has been checked routinely in recent years using coproporphyrin tetramethyl ester as a secondary standard.

Suspended particulate matter—Monthly averages of both streamflow and suspended sediment discharge were obtained for tributaries of Lake Tahoe from the U.S. Geological Survey's water quality monitoring program (U.S.G.S. WATSTORE daily value files). These averages cover the period from 1961 to the present. Routine in-lake measurements of total suspended solids (TSS; Greenberg et al. 1992) at the Index and Midlake Stations began in June 1995 and have continued approximately on a monthly basis. Measurements were made on a composite sample representing the upper 25 m and accompanied by determination of total chlorophyll (uncorrected for phaeophytin).

Data-analytical methods—Data aggregation: Secchi depth data at the Index Station were binned by month using averages determined by trapezoidal integration over time. Secchi depth data at the Midlake Station were too sparse for aggregation by monthly averages and instead were binned by month using medians. For comparison with the Midlake Station, the Index Station data were also sometimes binned using medians. For comparison with Secchi depth, Chl *a* was averaged over 0–30 m by trapezoidal integration and then binned by month using averages.

Estimating the seasonal component: We extracted seasonal patterns by seasonal and trend decomposition using loess (STL; Cleveland et al. 1990). STL is a filtering procedure for seasonal time series that estimates the seasonal component. STL involves a sequence of smoothing operations based on locally weighted regression (loess). The process consists of two recursive procedures: an inner loop nested inside an outer loop. In the inner loop, the seasonal component and then the trend component are updated, both by loess smoothing. To fit the seasonal component, loess is applied separately to each cycle subseries (e.g., the subseries of January values) of the residuals from the current trend component. Then the 12 smoothed fits are combined to form the complete seasonal component. In the outer loop, residuals from the seasonal and trend components are used to calculate robustness weights. These weights are used in the next pass of the inner loop to weigh down the otherwise distorting effects of outliers on the smoothing.

The analyst must specify several parameters for any particular application, the most important of which is the seasonal smoothing parameter, n_s , which represents the number of years included in the smoothed estimate for any given year in each cycle subseries. We chose this parameter by a diagnostic graphical method called a seasonal diagnostic plot (Cleveland et al. 1990). The subseries for each individual month over the entire record is compared with the smoothed fit for that month, and n_s is adjusted to exclude noise as much as possible. We used $n_s = 15$ but found little change in the results over a wide range of values.

Table 1. Comparison of combined Secchi depth measurements (in meters) made by two independent observers at the Index and Midlake Stations ($n = 217$).

Measurement	Mean	SD
Difference between down and up for observer 1	1.26	0.61
Difference between down and up for observer 2	1.05	0.54
Difference between observer 1 and 2 going down	0.40	1.24
Difference between observer 1 and 2 coming up	0.32	1.20
Average precision of measurement	0.027	0.028
Median precision of measurement	0.020	—

Modes of interannual variability: The use of principal component analysis (PCA) for analyzing interannual variability is described in detail by Jassby (in press). PCA reveals the number of independent underlying modes of variability, the time of year in which they are most important (represented by component coefficients), and their relative strength from one year to the next (represented by the amplitude time series). These features often provide strong constraints on the underlying mechanisms while also providing clues for their identity. When analyzing a monthly time series such as the Secchi depth series, an n by p data matrix is first formed in which $p = 12$ columns, each representing a specific month for the n years of record. Each row should begin at the month of the year in which serial correlation is minimal (Craddock 1965); a given row of 12 months does not therefore necessarily represent a calendar year. In the case of Secchi depth, serial correlation is lowest for September–October. Each row of the data matrix therefore corresponds to a California water year, which extends from October of one calendar year through September of the next. Principal components (PCs) were estimated by singular value decomposition of the covariance matrix of the data matrix. The number of significant PCs must be chosen by the analyst; if at least two significant PCs are found, the subset of significant PCs should be rotated (Richman 1986). We used a Monte Carlo technique known as Rule N (Overland and Preisendorfer 1982). Rule N involves computing the eigenvalues of a large number of uncorrelated n by p data sets. Each experimental eigenvalue is then compared with the 0.95 quantile of the corresponding simulated eigenvalues. Rule N is conservative in the sense that it may not identify all significant modes; it will identify the most important ones. We retained these PCs and rotated them using both the varimax and promax algorithms (Richman 1986); thus, we calculated the new component coefficients and the amplitude time series.

Results

Secchi depth—Precision: The difference between the depth of Secchi disc disappearance and reappearance averaged somewhat over 1 m for both observers (Table 1). For both observers combined, this difference amounted to $5 \pm 1\%$ of the Secchi depth. The difference between the two observers averaged 0.3–0.4 m for both Secchi disc disappearance and reappearance. Based on the 217 occasions when two observers independently measured Secchi depth,

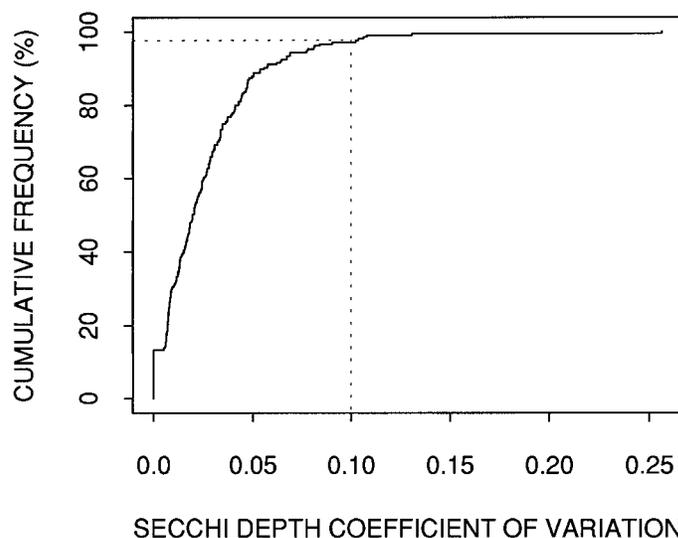


Fig. 2. Cumulative distribution for the precision of Secchi depth based on 217 occasions when two observers made independent measurements.

the average precision (as coefficient of variation) was 0.027 ± 0.028 and the median precision was 0.02. The cumulative distribution of precision shows one extreme value of over 0.25, but in almost every other case, the precision was much better than 0.1 (Fig. 2).

Index Station time series: The monthly time series of Secchi depth at the Index Station exhibits much variability at the seasonal scale (Fig. 3, thin line). In order to filter out seasonal effects and accentuate variability at longer scales, a centered 13-term moving average was calculated (Shumway 1988; Fig. 3, thick line). The filtered data are dominated by a long-term decreasing trend, due mostly to change before 1985. This overall trend is a significant one, according to the seasonal Kendall test ($p = 0.0025$; Helsel and Hirsch 1992), and has a Thiel slope of -0.25 m yr^{-1} .

The trend for each individual month is also negative, and, except for July, significantly so, according to Kendall's tau (Fig. 4). Trends during June–October (the more stratified time of year) are small compared to the remaining months.

The mean seasonal pattern and its variability are summarized in Fig. 5. The pattern is bimodal, with a strong Secchi depth minimum in June and a weaker local minimum in December. The overall maximum is in February, with a secondary local maximum in October. The minimum individual measurement of 8.5 m was measured on 1 June 1983, and the individual maximum of 43 m was measured on 8 February 1968 (the values in Fig. 5 are monthly averages, not individual measurements). Note that the distribution for each month is approximately symmetric around the median, therefore implying that the means and medians exhibit much the same pattern.

Secchi depth measurements at the Midlake Station were less frequent, particularly before 1980, but the time series for both stations was similar at all scales (not shown).

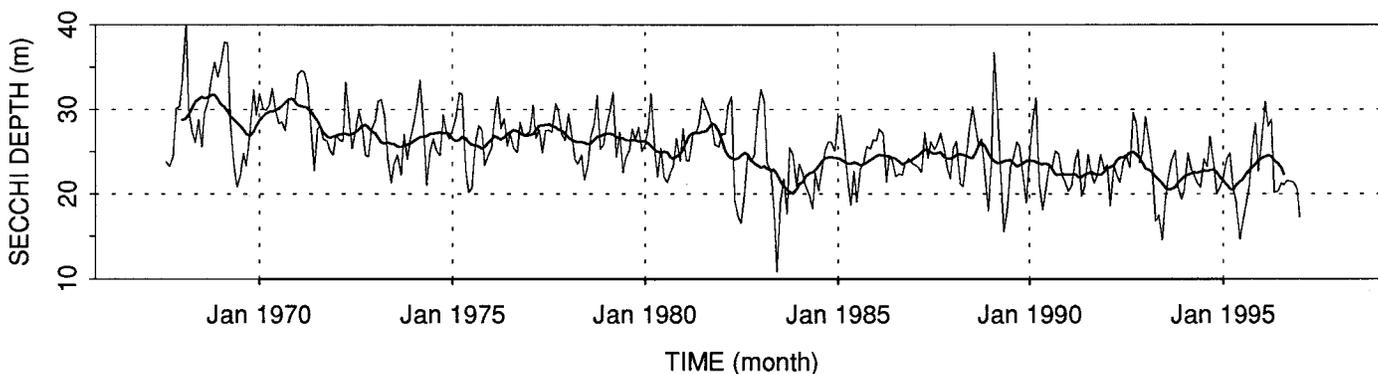


Fig. 3. Monthly average time series of Secchi depth at the Index Station.

STL decomposition: The STL decomposition of the Secchi depth series reveals a strong trend in the seasonal effects (Fig. 6). The seasonal pattern is essentially unimodal in early years with a midwinter maximum (usually in February) and a late spring–early summer minimum (usually in June). A late fall–early winter secondary minimum (usually in December) gradually develops, which now results in a strongly bimodal distribution; the development of the bimodal pattern was temporarily reversed in the early 1980s. Another obvious feature in the time course of seasonal effects is a long-term decrease in amplitude. Other less prominent changes can be observed in the seasonal series but are only a small part of the variability and were not further considered in our study.

PCA decomposition: According to Rule N, only the first two eigenvalues are significantly higher than expected. These two eigenvalues together account for 71.4% of the total variance of the monthly series.

We calculated the principal components of these Secchi depth data, retained the first two as suggested by Rule N, and rotated them using both the varimax and promax algorithms. As the results were essentially the same, we present data only for the varimax rotation (Fig. 7). The first rotated principal component (mode 1) accounts for 39.4% of the

variance. It is characterized by high component coefficients, particularly during the time of the winter maximum (February). The corresponding amplitude time series for mode 1 is dominated by a long-term decrease, especially before 1985. Interannual variability is secondary; the long-term trend alone accounts for most of the variance ($R^2 = 0.56$). The second rotated component (mode 2) accounts for a smaller but comparable variance of 32.0%. It is characterized by high component coefficients during the late spring–early summer minimum (June). Although a long-term trend is present, its amplitude time series is dominated much more by interannual variability than the trend ($R^2 = 0.24$).

Chlorophyll—The period during which both Secchi depth measurements and Chl *a* were collected (1987–1996) is not long enough for an adequate test of their long-term correspondence; the variability in these records is dominated by shorter time scales (Fig. 8). Note that we have used inverse Secchi depth for this and subsequent comparisons because of the approximate linearity between inverse Secchi depth and concentrations of materials contributing to the contrast attenuation coefficient (Eq. 1). In each of the years for which data were available throughout the year (1988–1995), the linear relationship between inverse Secchi depth and Chl *a* was insignificant (depending on the year, $p = 0.053$ – 0.770)

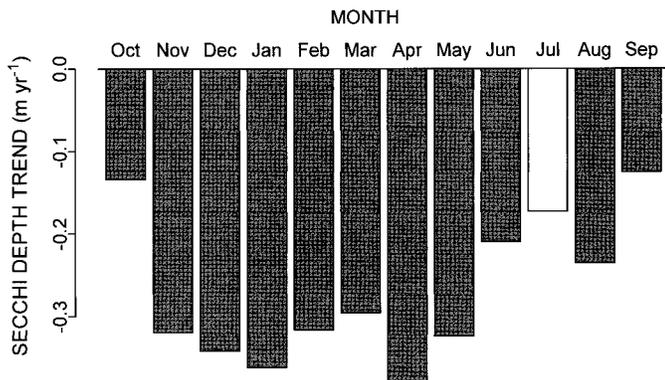


Fig. 4. Trends in Secchi depth at the Index Station for individual months (water years 1968–1996). Shaded bars are significantly different from zero according to Kendall's tau ($p < 0.05$).

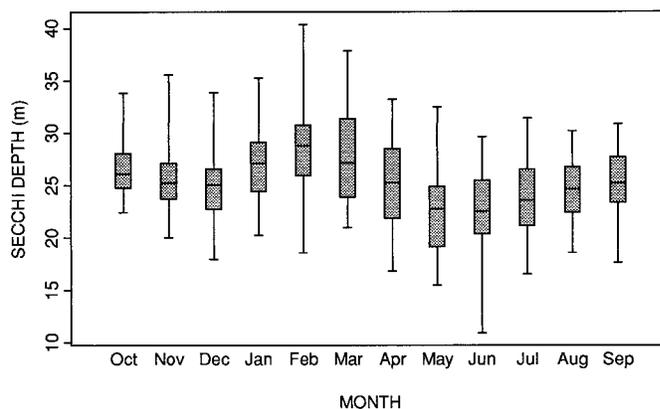


Fig. 5. Boxplots illustrating seasonal pattern of Secchi depth at the Index Station (water years 1968–1996).

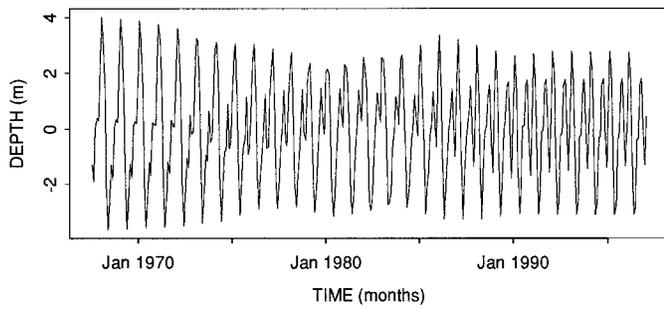


Fig. 6. Seasonal component of Secchi depth at the Index Station as determined by the STL procedure. Values are plotted as departures from the long-term mean.

and $n = 10-13$). A comparison of the mean seasonal patterns for these years further illustrates the lack of correspondence: inverse Secchi depth has relatively narrow maxima in December and from May–June, whereas Chl *a* has a broad maximum from December–April (Fig. 9).

These data also provide information at the interannual scale. Specifically, for each month of the year, the linear relationship between inverse Secchi depth and Chl *a* was insignificant (depending on the month, $p = 0.074-0.990$ and $n = 7-10$).

Chlorophyll measurements (uncorrected for phaeophytin) were also taken in conjunction with recent TSS measurements of composite samples representing the 0–25-m layer. These results are described below.

Suspended particulate matter—Blackwood Creek has the most complete flow record of tributaries in the Tahoe Basin (Fig. 10A). It is also the tributary closest to the Index Station (Fig. 1). The data for suspended sediment discharge are not as complete as the flow record (Fig. 10B) but are still sufficient to obtain a reliable summary of the seasonal pattern (Fig. 10C). The seasonal pattern exhibits a strong peak in May, but high values are also observed during the early winter of many years. This is true both in wet years such as 1980, and in dry years such as 1988, although there is much variability in the relative importance of the early winter peak.

The simultaneous measurements of Secchi depth, TSS, and total chlorophyll in the upper layer from mid-1995 through mid-1997 enable us to estimate the relative light-attenuating effects of chlorophyll-associated and other materials. First, we have to partition the TSS between chlorophyll-associated biomass and other substances, which in turn requires an assumption about the chlorophyll:dry weight (DW) ratio for phytoplankton and phytoplankton-derived materials. For the purpose of this discussion, we take this ratio as 0.005 (which could arise, for example, from a carbon:chlorophyll ratio of 60 and a carbon:DW ratio of 0.3 for diatoms, the dominant phylum in Lake Tahoe). Second, we need to assume a form for the dependence of Secchi depth on light-attenuating materials. Based on Eq. 1, which holds well for actual measurements from Lake Tahoe (Smith et al. 1973),

$$Z_s = \frac{1}{\alpha + \alpha_p P + \alpha_m M}, \quad (2)$$

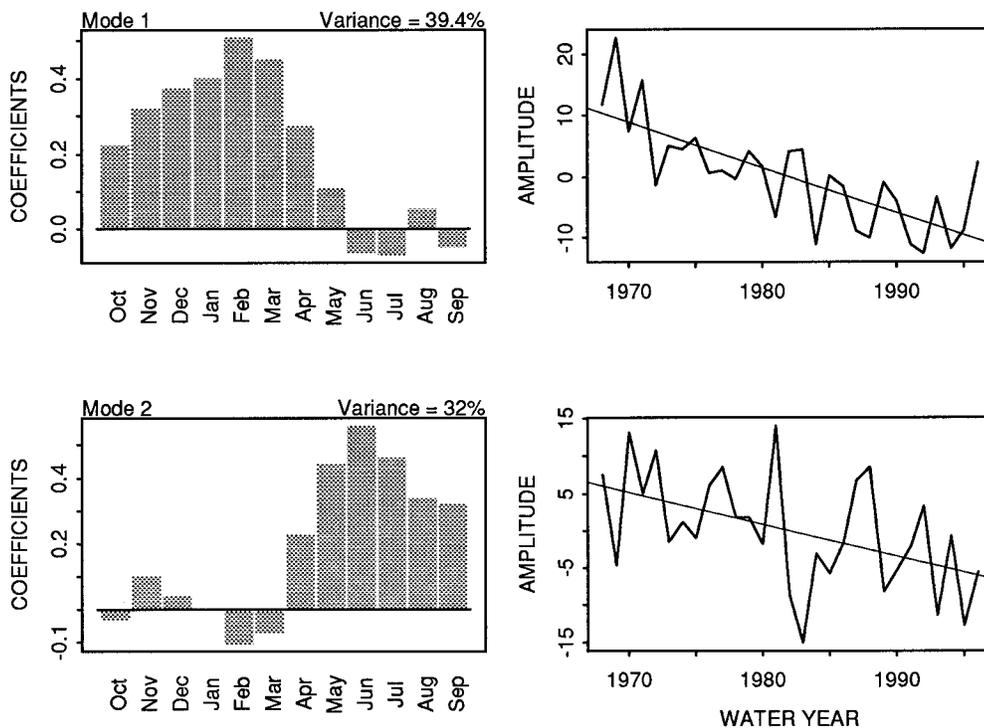


Fig. 7. Component coefficients and amplitudes for the first two principal components of Secchi depth at the Index Station (water years 1968–1996).

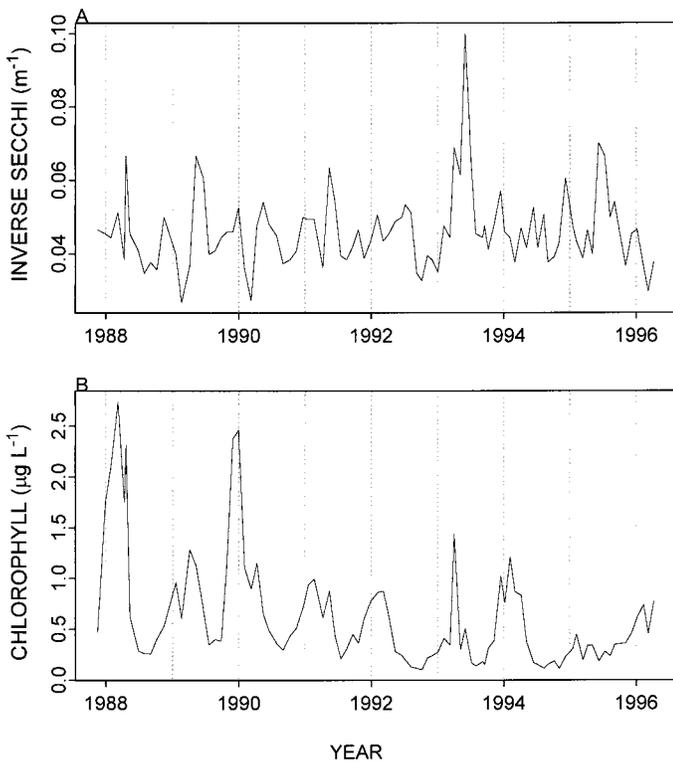


Fig. 8. (A) Inverse Secchi depth at the Index Station; (B) same for Chl *a* (averaged over 0–30 m).

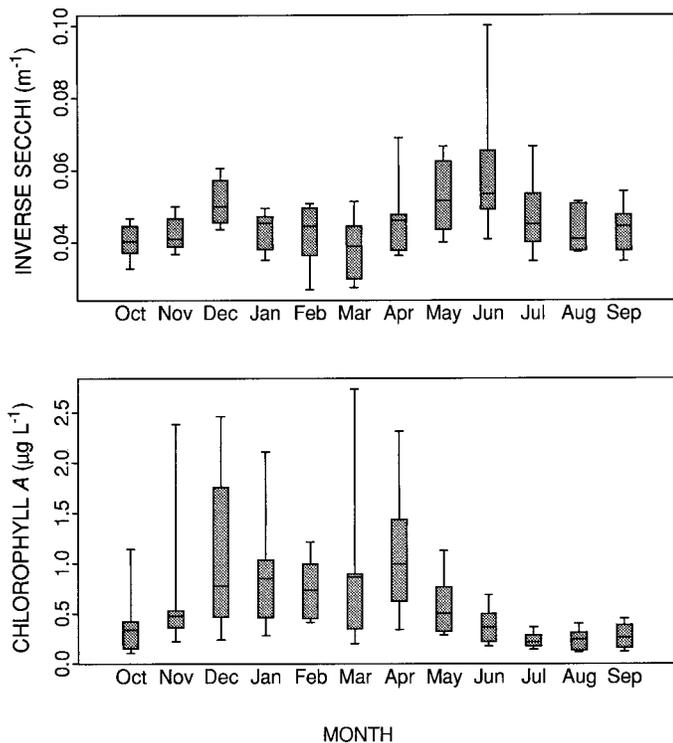


Fig. 9. Boxplots illustrating seasonal pattern of inverse Secchi depth and Chl *a* (averaged over 0–30 m) at the Index Station (water years 1988–1996).

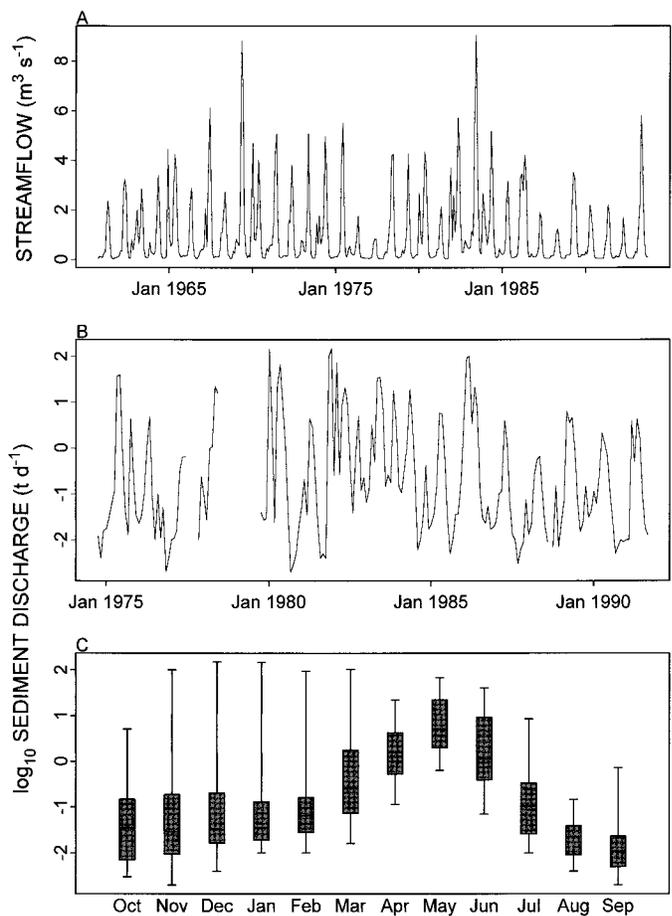


Fig. 10. (A) Blackwood Creek streamflow; (B) suspended sediment discharge (\log_{10}); and (C) seasonal pattern of suspended sediment discharge (\log_{10}).

where P is chlorophyll-associated (phytoplankton-derived) biomass (mg liter^{-1} DW), M is autochthonous and allochthonous particulate material (mg liter^{-1} DW) not associated with chlorophyll, a_p and a_m are effective attenuation cross sections for these two categories, and a describes background attenuation. Although the model is crude (cf. Buitveld 1995) and additive partitioning of apparent optical properties is not theoretically defensible, the model does reflect the availability of relevant data. P and M are functionally defined by the $1\text{-}\mu\text{m}$ filters used for total chlorophyll and TSS analysis. Background attenuation therefore includes water molecules, dissolved materials, and small particles such as viruses, smaller bacteria, smaller nonliving organic and clay particles, and probably fragments of diatom frustules. The linear regression estimate for this model, combining data for the Index and Midlake Stations, is summarized in Table 2. The partial residual plots for this model are provided in Fig. 11. Note that the partial relationship with P , although statistically significant, is based on a few large values, whereas that with M is much more robust.

Discussion

Secchi depth precision and representativeness—Because Secchi depth is not an inherent optical property and depends

Table 2. Summary of linear model for inverse Secchi depth (m^{-1}) as a function of chlorophyll-associated biomass (P) and non-chlorophyll-associated biomass (M) ($mg\ liter^{-1}$ dry weight).

Variable	Predictor	Value	Standard error	t -statistic	$Pr(> t)$
$Secchi^{-1}$ $R^2 = 0.61$	Intercept	0.0290	0.0037	7.94	0.000
	P	0.0790	0.0187	4.23	0.000
	M	0.0800	0.0118	6.76	0.000

on ambient light, it has sometimes been characterized as a crude measurement. Ambient light, however, affects Secchi depth only weakly as long as measurements are taken around midday, surface reflection is minimized, and wave action is not excessive (Davies-Colley et al. 1993); these conditions were accounted for in this study. Wave action is of course seasonal, which leads to the possibility of a bias in annual averages because measurements are not taken in rough conditions. The Lake Tahoe data set, however, has good coverage throughout the year: measurements were missed in only 7 of the 356 months of record at the Index Station. Regardless of the interpretation of Secchi depth in terms of

inherent optical properties, it is of intrinsic value as an appropriate endpoint for management of water clarity.

Secchi depth is also sometimes criticized as being too subjective, depending on the visual acuity of the observer. In fact, Secchi depths measured by different observers usually agree to within 10% (Højerslev 1986). Our own data confirm this conclusion, which suggests that 10% can be considered an upper limit to the precision of the measurement in almost all cases (Fig. 2).

The Index Station location was chosen originally because of both its relative accessibility and because of its representativeness for lakewide primary productivity (Goldman and de Amezaga 1975). A comparison of data from the Index and Midlake Stations revealed a striking similarity in nutrient concentrations, providing further evidence that the Index Station is an appropriate guide to lakewide conditions (Jassby et al. 1995). It is therefore not surprising that the Secchi depth time series at the Midlake Station also resembles that of the Index Station on the decadal, interannual, and seasonal scales.

Seasonal variability—Phytoplankton variability, at least insofar as it is represented by chlorophyll, does not appear to have a major impact on the seasonal pattern. For example, inverse Secchi depth exhibited no significant relationship to Chl a for any of the years in which their records overlapped (1987–1996). Similarly, seasonal composites illustrate that the late spring–early summer maximum in inverse Secchi depth has no counterpart in the chlorophyll pattern (Fig. 9). Seasonal composites do show both a local maximum in inverse Secchi depth and occasionally high Chl a values in December. However, no significant relationship exists between December inverse Secchi depth and chlorophyll a . The simple linear model (Eq. 2; Table 2) suggests some role for phytoplankton in the seasonal pattern, but only at high chlorophyll concentrations and only after the effect of other materials contributing to TSS is taken into account (Fig. 11).

What then can account for the seasonal pattern in Secchi depth? We propose that the following mechanism underlies the spring–summer portion of the pattern: the snowmelt in spring results in increasing streamflow and increasing suspended sediment discharge to the lake (Fig. 10). Enough of this material accumulates in the upper layer (0–30 m) to result in decreasing visual clarity throughout the spring. As the sediment load diminishes in June and thermal stratification intensifies, the balance between watershed inputs to the upper layer and outputs from this layer by sedimentation begins to shift. Consequently, Secchi depth is minimal in May–June and increases through the summer (Fig. 5). This view is consistent with the seasonal pattern of suspended

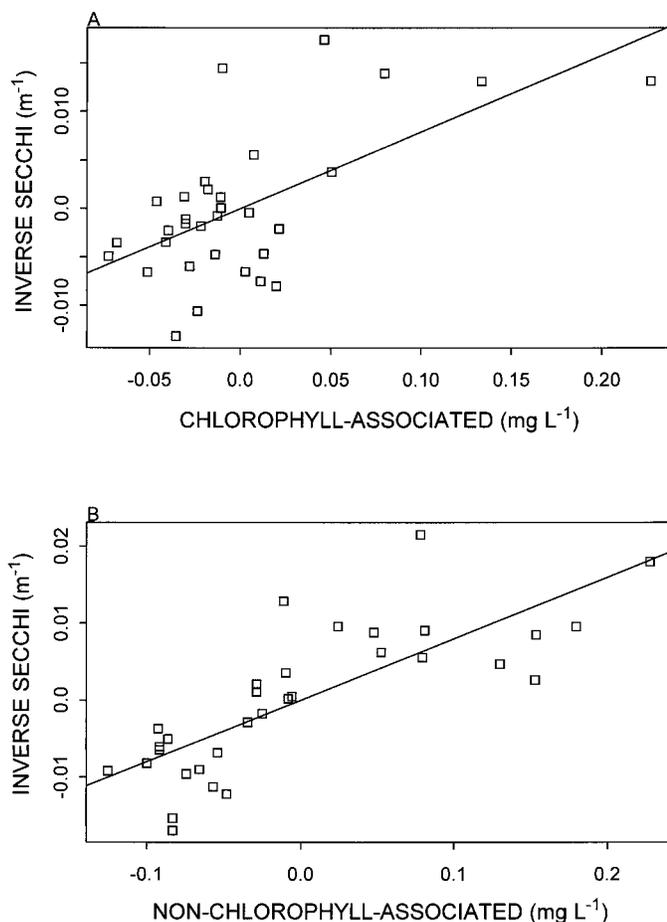


Fig. 11. Partial residual plots for the linear model (see Eq. 2) relating inverse Secchi depth to (A) chlorophyll-associated materials P ; and (B) other materials M . In (A), the residuals for each variable are plotted against each other, after first regressing each variable on M . Similarly, in (B), the variables have first been regressed on P .

Table 3. Summary of linear models for the amplitude time series (ATS) of Secchi depth, modes 1 and 2. Mixing depth (m) refers to the annual maximum depth of mixing. Streamflow ($\text{m}^3 \text{s}^{-1}$) refers to the average spring quarter discharge from Blackwood Creek.

Variable	Predictor	Value	Standard error	<i>t</i> -statistic	Pr(> <i>t</i>)
ATS1 $R^2 = 0.63$	Intercept	1000	236	4.25	0.000
	Trend	-0.509	0.118	-4.29	0.000
	Mixing depth	0.0247	0.0070	3.51	0.002
ATS2 $R^2 = 0.74$	Intercept	1046	179	5.85	0.000
	Trend	-0.522	0.090	-5.80	0.000
	Streamflow	-4.09	0.58	-7.08	0.000

sediment discharge (Fig. 10) and with visual observations of sediment plumes moving out into the lake from tributary streams (Goldman et al. 1974). The actual magnitude of suspended sediment discharge to the lake is also consistent with mineral suspensoid concentrations. The Upper Truckee River, which is the largest tributary of Lake Tahoe and accounts for ~19% of its runoff (Marjanovic 1991), averaged a suspended sediment discharge of 8.85 t d^{-1} during the period 1972–1988. Even if distributed over the entire lake in the 0–30-m stratum, this rate is equivalent to $0.23 \text{ mg liter}^{-1}$ in a single year. As discussed below, a change of only $0.1 \text{ mg liter}^{-1}$ could easily account for a 5–10-m change in Secchi depth, which is the magnitude of seasonal change (Fig. 5).

A secondary increase in suspended sediment discharge often happens in early winter; the wet season produces increasing runoff until precipitation begins to fall in the form of snow rather than rain (Fig. 10B). It is tempting to attribute the December minimum in Secchi depth to this runoff, in analogy to the June minimum. This view cannot be supported, however. A unique and important advantage of the STL procedure is its ability to identify long-term changes in the seasonal pattern. Other methods assume the seasonal pattern is unchanged and thereby relegate changes at this scale to the residual series. Such changes are obvious in many ecological series and turn out to be important for our understanding of the Secchi depth series. The STL results demonstrate a transition from a unimodal pattern to a bimodal pattern over the years (Fig. 6). Although the seasonal component has obviously undergone much smoothing, this intensification of a secondary minimum over the years is a large and significant feature. If this feature were due to runoff and suspended sediment discharge prior to freezing conditions, then one would expect a similar intensification of these variables as well. No such phenomenon occurs, and, in fact, autumnal suspended sediment discharge was at least as high in earlier as in later years (Fig. 10A,B).

A more likely explanation is that this transition is due to processes within the lake. Thermal stratification usually peaks in August, and the thermocline begins to deepen in September. As it penetrates to the 60–120-m region around December, it encounters the deep chlorophyll maximum (DCM), a characteristic feature of Lake Tahoe and other deep water bodies (Abbot et al. 1984). The subsequent upwelling of phytoplankton from this maximum can, in some years, contribute momentarily to a phytoplankton increase in surface waters. Further erosion of the thermocline below the DCM then gradually dilutes phytoplankton in the upper layer (e.g., 1989; Fig. 8). Although Fig. 8 shows that upwelling

of the DCM cannot account for the concurrent decrease in Secchi depth by itself, it also illustrates how a particle maximum at intermediate depths could produce a local Secchi depth minimum in late fall–early winter. Total suspended particulate matter, both organic and inorganic, does in fact reach a maximum at intermediate depths in Lake Tahoe (based on sediment trap data; A. Heyvaert pers. comm.). By contrast, resuspension in more shallow lakes can enrich particle concentrations in the deepest waters (Weyhenmeyer 1996). Mineral particles that have fallen out of the mixed layer during summer may also upwell during erosion of the thermocline. Furthermore, mineral suspensoids have probably accumulated over the years (*see below*) and therefore could account for the long-term intensification of the bimodal pattern observed in the STL analysis (Fig. 6). The long-term increase in primary production at the lake (Goldman 1988) suggests that chlorophyll levels have also increased in the DCM, which may be an additional factor intensifying the December Secchi depth minimum.

Interannual variability—The principal component analysis provides insight into the longer-term variability of Secchi depth. Each mode exhibits a decadal-scale trend as well as year-to-year variability about this trend line. Mode 1 represents the autumn–winter period of weak thermal stratification, during which time the thermocline erodes and deepens, sometimes resulting in complete mixing. The extent of mixing during this period has a profound effect on interannual variability of primary production because of variable upwelling of nutrients from the depths (Goldman et al. 1989; Goldman and Jassby 1990). We propose that mixing also controls interannual variability in this mode, although through a different mechanism. According to linear regression analysis, the amplitude time series for this mode is related to both a linear trend and maximum depth of mixing. In other words, mixing depth has a significant influence on year-to-year variability about the trend line (Table 3, Fig. 12A). Note that the coefficient for mixing depth is positive, implying that deeper mixing results in higher Secchi depth during this season, contrary to what would be expected if nutrient upwelling and phytoplankton production underlay this variability. However, deeper mixing dilutes phytoplankton in the DCM and can be expected to have a similar impact on total suspended particulate matter, which reaches a maximum at intermediate depths. The effect of mixing can therefore be understood as a dilution of light-attenuating particles.

Mode 2 represents variability during the spring–summer months when the lake is more strongly stratified. As the

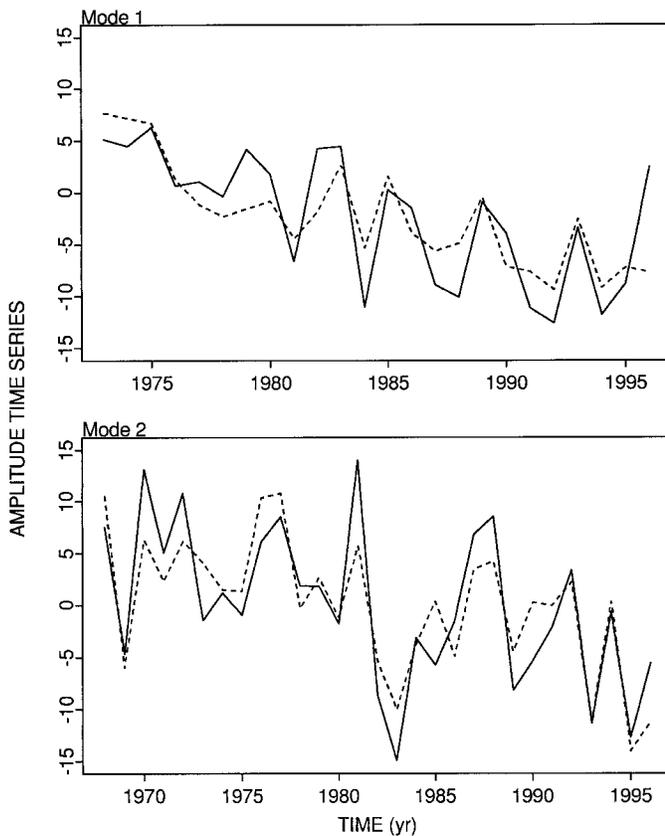


Fig. 12. (A) Amplitude time series for mode 1 (solid line); predicted values based on a linear trend and maximum mixing depth (dashed line). (B) Amplitude time series for mode 2 (solid line); predicted values based on a linear trend and spring quarter streamflow (dashed line).

seasonal minimum this time of year is probably due to suspended sediment discharge into the lake (*see above*), a natural hypothesis is that interannual variability in discharge causes interannual variability in clarity at this time. Indeed, this appears to be the case. Again using linear regression analysis, the amplitude time series for mode 2 can be related to both a linear trend and to streamflow (Table 3, Fig. 12B). Here we use Blackwood Creek spring quarter streamflow as the index of sediment discharge. Streamflow is used instead of sediment discharge because the record is longer and more complete. The influence of streamflow is clearly significant. Note that the sign for streamflow is also consistent with the claim that years of high streamflow, and therefore high sediment discharge, are also times in which spring–summer Secchi depth is suppressed below the long-term trend. Further evidence for a nonphytoplankton effect is provided by the major El Niño–Southern Oscillation (ENSO) event of 1982–1983. Watershed precipitation and lakewide runoff were unusually high for 1982 and 1983, and Secchi depth experienced a striking short-term downturn in spring–summer of both years, followed by a partial recovery in succeeding years (Fig. 3, Fig. 12B). As mentioned above, the depth of spring mixing at Lake Tahoe strongly affects primary production. Upwelled nutrients are far in excess of

nutrients from runoff, even in high runoff years. In 1982, however, the lake mixed only to 250 m, compared to the maximum depth of 505 m. Primary production during 1982 was therefore unremarkable, suggesting that chlorophyll was also unremarkable and thus unable to account for the extreme Secchi depth measurements. The ENSO evidence is therefore completely consistent with the effect of mineral suspensoid inputs from the watershed but not at all consistent with phytoplankton changes.

Much variability remains unaccounted for in both modes. Nevertheless, it is gratifying that linear analyses—both for the decomposition of Secchi depth variability into separate modes and for the relationship with environmental variables—can be so consistent with simple and plausible explanations. Indeed, the analysis provides further justification for this novel approach to the use of PCA in time series analysis (*cf.* Yajima 1996). The unaccounted variability in part reflects the inadequacy of a model specified solely in linear terms; it does not necessarily play a major role in additional environmental factors. The zooplankton record is not long enough to assess top-down influences, but we noted that zooplankton effects on Secchi depth could not be detected for the similarly ultraoligotrophic Crater Lake, Oregon (Larson *et al.* 1996*b*; *cf.* Stramski *et al.* 1992).

Long-term trend—The long-term (decadal-scale) change in Secchi depth appears to be due to an accumulation of materials in the lake. Secchi depth tends to be at a maximum when the lake is circulating most deeply, namely in late winter just before shallow stratification sets up again (Fig. 5). In a sense, Secchi depth at this time is an index of average particle concentrations in the lake. It is highly variable because of frequent occurrence of incomplete mixing and because of the change in attenuation cross sections as particle composition and size change. In the long term, though, the trend in this maximum annual value is also downward (Fig. 4) and implies a long-term accumulation of particles.

Can we deduce anything further about the nature of the accumulating particles? In particular, can we distinguish between accumulation of chlorophyll-associated materials and accumulation of other materials? The simultaneous measurements of Secchi depth, TSS, and total chlorophyll in the upper layer during 1995–1997 provide some insight conditional to the validity of several assumptions presented above (*see results*). The linear regression model for inverse Secchi depth is well behaved (Eq. 2, Table 2) and suggests that P and M in Lake Tahoe have approximately the same effect on clarity per unit dry weight. Using other ratios for Chl:DW changes the relative value of these coefficients, but no significant difference can be observed between these two coefficients when the precision of the estimates is taken into account. The imprecision for the chlorophyll-associated coefficient is at least in part because of the different ways that chlorophyll is packaged in cells of different taxa (Edmondson 1980; Figueroa *et al.* 1997) but also because of changes in C:Chl content (Cloern *et al.* 1995; Geider *et al.* 1997). Similarly, a given level of mineral suspensoids will attenuate differently depending on derivative soil type and size distribution (Bhargava and Mariam 1996). Moreover, we have been forced to assume constant contributions by gelbstoff

(dissolved organic material) and small particles passing through the filters. These implicitly group with water molecules in the constant term of Eq. 2 and contribute to the unexplained variability. Nonetheless, theoretical and laboratory results demonstrate a large overlap between the scattering cross sections for phytoplankton and mineral particles of the expected size in lakes (Davies-Colley et al. 1993). As scattering dominates Secchi depth transparency in lakes, this result is at least consistent with the interpretation of category *P* as mostly phytoplankton and category *M* as mostly mineral suspensoids.

Assuming Eq. 2 and Table 2 are appropriate descriptions of Secchi variability, we can ask whether *P* or *M* can account for the long-term loss of clarity. This loss amounts to approximately 7.5 m over the last 30 yr using the Thiel slope of -0.25 m yr^{-1} . Using a Chl:DW ratio of 0.005, the mean values for *P* and *M* during the 1995–1997 measurement period were 0.134 and 0.108 mg liter⁻¹ DW, respectively, corresponding to a predicted Secchi depth of 20.7 m. Without *P*, the Secchi depth would be 26.6 m; without *M*, the Secchi depth would be 25.3 m. Although these differences are somewhat lower than 7.5 m, we can obtain differences as high as 7.8 and 8.2 m, respectively, using other values within the 95% confidence limits for the estimates of a_p and a_m . A buildup of either phytoplankton-derived materials or mineral suspensoids, or of both, could therefore explain the drop in clarity.

Based on physical considerations, a significant role for mineral suspensoids seems likely. In Tahoe, with an average depth of 313 m, particles settling out at less than $10 \mu\text{m s}^{-1}$ (315 m yr^{-1}) could easily be retained by the annual mixing or even by other forms of vertical exchange. Assuming the density of quartz as 2.65, this includes all clay ($<2 \mu\text{m}$) and many silt particles ($2\text{--}50 \mu\text{m}$) (Davies-Colley et al. 1993). Clay particles also tend to be platelike and therefore settle even more slowly than would be indicated by these estimates for spheres. Mineral particles with high scattering efficiency are usually $0.5\text{--}2 \mu\text{m}$, and these will tend to be retained in Lake Tahoe. They can settle faster through coagulation with algae, detritus, and bacterial polyelectrolytes, but the least flocculation will occur in an ultraoligotrophic lake with low particle concentration and low ionic strength. Organic particles settle even more slowly, but they are presumably more subject to grazing by zooplankton and to packaging in larger fecal particles, as well as, of course, decomposition, so it is not as clear a priori that they will accumulate.

The cumulative loading of suspended sediments to the lake is also consistent with a role for mineral suspensoid concentrations. Recall that the Upper Truckee River (Fig. 1), which accounts for $\sim 19\%$ of the runoff into Lake Tahoe (Marjanovic 1991), averaged a suspended sediment discharge of 8.85 tons d^{-1} during the period 1972–1988. Distributed over the entire lake volume, this rate is equivalent to $0.021 \text{ mg liter}^{-1}$ in a single year, or $0.62 \text{ mg liter}^{-1}$ in 30 yr. As pointed out above, just $0.1 \text{ mg liter}^{-1}$ could account for a 5–10 m Secchi depth decrease. Accordingly, only a small fraction of cumulative suspended sediment from just this one source needs to be retained in the water column to account for loss of clarity. Note that the Upper Truckee River used to drain into Lake Tahoe through Pope Marsh, once the

largest wetland in the Sierra Nevada mountain range. The marsh was largely destroyed in the late 1950s by a marina development. The enormous dredging operations necessitated diverting the Upper Truckee away from the development and into a straight channel that connects directly with the lake. The large tributary drains the developed, eroded uplands of the south basin, and sediment plumes are visible each spring (Goldman et al. 1974).

Further studies are required to delineate the relative roles of different light-attenuating categories. Specifically, the relative contributions of phytoplankton and other particles need to be described more clearly. This requires lowering the uncertainty in effective attenuation cross sections (Table 2), but it also may involve using a more appropriate index of phytoplankton scattering than chlorophyll. Chlorophyll is a good index for absorption by phytoplankton, hence its effect on the vertical attenuation coefficient for downward irradiance (Kirk 1984). However, total biovolume and mean cell volume derived from microscopy may be a better indicator of scattering and its effect on Secchi depth transparency. Related issues are the relative importance of autochthonous contributions (such as that of biogenic silica) to mineral suspensoids, as well as the role played by gelbstoff. The latter may be especially important in transparency variability of oligotrophic lakes such as Lake Tahoe (Lind 1986). In addition, the size and density distribution of particles entering and within the lake need to be determined. Long-term clarity losses due to mineral particles are dependent on the fraction of particles that will be retained in the lake and contribute to a buildup of light-attenuating particles. Because of the analyses reported here, all of these issues are now under active study at the lake.

In addition to their ecological implications regarding the scales and mechanisms of variability in lakes, our results have resource management implications. First, by understanding the mechanisms for seasonal and interannual variability, we can judge whether a shift in transparency is a shorter-term phenomenon or represents a longer-term change that requires a management response. Second, in deep lakes such as Tahoe, it is not enough to institute erosion control measures that target total suspended sediment discharge if the relevant-sized particles continue to get through unhampered. Indeed, the larger, less important particles are the most likely to be removed by watershed management practices, and the resulting improvements to the lake may be far less than anticipated. Finally, we previously demonstrated that the residence times for nitrogen and phosphorus, which limit phytoplankton biomass at the lake, are on the order of decades (Jassby et al. 1995). The time scale for recovery from abatement of nutrient loading is therefore also on the order of decades. If, however, the residence time for the appropriate fraction of mineral suspensoids is much shorter, it may be possible to achieve a quicker recovery of optical water quality by emphasizing small particle rather than nutrient management. The time scale of recovery from the 1982–1983 ENSO event does in fact suggest a shorter residence time for mineral particles and offers some hope in this regard.

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