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OBSERVATIONS ON THE ECOLOGY AND TROPHIC STATUS OF LAKE TAHOE (NEVADA AND CALIFORNIA, USA) BASED ON THE ALGAE FROM THREE INDEPENDENT SURVEYS (1965–1985)

Sam L. VanLandingham1

Abstract—Numerous physical, chemical, and biological criteria evidently confirm that Lake Tahoe is oligotrophic. However, detailed examination of the ecology and trophic status of algae (mostly diatoms) from Lake Tahoe taken from three independent, long-term sampling programs aided in interpretation of plankton and periphyton algal communities by spectral analysis (supported by computerized data synthesis) and suggested that the prevailing trophic disposition of this deep, subalpine lake no longer can be described as “ultra-oligotrophic” or typically oligotrophic. Although at various places in recent years there has been some increase in oligotrophic species that seems to correspond with recent sewage export from the Tahoe basin, there was a marked tendency toward mesotrophy and/or eutrophy over most of the lake from April 1965 through October 1985. This study posits the speculation that there may be other “ultra-oligotrophic” lakes over the world from which future studies may reveal algal communities that may be described as more mesotrophic and/or eutrophic than oligotrophic. Lake Tahoe probably is not as oligotrophic as is generally believed, and the indicator algae in it are not as accurate as is generally believed.

There have been few American lakes that have inspired such curiosity, commentary, lore, and interest among scientists as Lake Tahoe. From the time of Ehrenberg (1871), there has been considerable controversy and speculation in connection with the limnology of Lake Tahoe. Statements describing Lake Tahoe as “a remarkably unproductive subalpine environment” (Mahood et al. 1984) and as “still one of the most oligotrophic lakes in the world” (Goldman 1974) seem misleading, on the other hand, such comments as “heavy periphyton growth” and “alarm increase in primary productivity” (Goldman and De Amezaga 1975) and “it is beginning to show signs of the earliest stages of eutrophication” (Mahood et al. 1984) are equally perplexing. In addition, Goldman (1981) reported that the annual productivity of the pelagic water of Lake Tahoe has more than doubled in the past two decades. Moreover, I find the terming of Lake Tahoe as “extremely oligotrophic” (Goldman and Armstrong 1969) and “ultra-oligotrophic” (Tilzer and Horne 1979) enigmatic in view of the obvious enrichment of the littoral areas. Indications of mesotrophy and eutrophy demonstrated by the algae in the lake are conspicuous, and Tahoe no longer can be considered “one of the most oligotrophic lakes in the world.”

The California–Nevada–Federal Water Pollution Control Administration (FWPCA) survey confirmed that Lake Tahoe was oligotrophic mainly on the basis of low zooplankton and phytoplankton counts, low periphyton densities, and low P (5 μg l⁻¹) and N (100 μg l⁻¹) concentrations. A large number of species in Lake Tahoe was described as eutrophic, although their presence was not considered to be indicative of eutrophic conditions (California Department of Water Resources 1966). Total P at many stations in the last 10–15 years seems excessive for an oligotrophic lake and probably has enhanced the growth of many eutrophic diatoms and other algae. Why are so many of the typical or cosmopolitan oligotrophic diatoms, such as Melosira distans (Ehr.) Kütz., Cyclotella ocellata Pant., Frustulia rhomboides (Ehr.) De Toni, Navicula radiosa Leu.d.-Fort., Pinnularia biceps Greg., Tabellaria flocculosa (Roth) Kütz., and Tetracyclus lacustris Ralfs, infrequent or rare in Lake Tahoe? All of these taxa are common in both ancient and modern lakes in this region. Melosira distans, for example, is a dominant or subdominant species in oligotrophic Suttle and Woahink lakes, Oregon, in a Pleistocene oligotrophic diatomite.

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deposit about 500 m from the shore of Lake Tahoe at Tahoe City, and in several oligotrophic dry lakes nearby in Nevada. The rarity of the above-mentioned diatoms can be explained partially by the observation that most of these taxa prefer acidic waters and that Lake Tahoe nearly always has a pH above 7. Only a very few oligotrophic diatoms, such as *Cyclotella stelligera* (Cl.) V.H., *Achnanthes minutissima* Kütz., and *Anomoeoneis exilis* (Kütz.) Cl., ever attain noteworthy prominence in Lake Tahoe. Weber (1970) used plankton counts of less than 500 cells/ml as one of many criteria for determining oligotrophic lakes. In recent years cell counts for the planktonic algae occasionally have exceeded 500 cells/ml in littoral areas.

Problems associated with interpreting trophic or inorganic nutrient categories in lakes are numerous. Whiteside (1983) contends that the oligotrophy-eutrophy concept is best interpreted in its original sense, namely, referring to nutrient levels (or community structure) in lakes, and is inappropriately used when referring to the aging process, morphometry, etc. It follows that it may be possible for a lake to be deep or in the youthful stages of ontogeny but have relatively high nutrient levels. Or, a lake may be shallow or in the oldest stages of ontogeny but have lower nutrient levels. Sometimes lakes defy assignment to a definite trophic status as La Perriere et al. (1975) demonstrated in respect to a deep, subareic lake. The occurrence of certain diatoms, which generally are considered eutrophic, seems to be influenced more by such factors as temperature than by trophic levels. For instance, Weber (1973) pointed out that *Melosira islandica* O. Müll. is considered eutrophic in northern Europe, but in North America it is found only in cold, oligotrophic water both in higher latitudes and higher altitudes at lower latitudes. *Fragilaria pinnata* Ehr. and *F. crotonensis* Kitt. are examples of diatoms that generally are considered eutrophic but that occur commonly in oligotrophic lakes (California Department of Water Resources 1966). No matter what the descriptive or semantic status of Lake Tahoe may be, there is good evidence that its algae frequently indicate relatively moderate to high nutrient levels, and they apparently have done so for many years.

Computers Data Synthesis

Continuous algal ecological spectral analysis reference system (CAESARS) is a comprehensive, computerized retrieval plan based on approximately 3,000 publications from which about 500,000 bits of information concerning over 4,000 common and widely occurring algae taxa are categorized into nine physical, chemical, and occurrence spectra, each of which is subdivided into four or more categories (Figs. 1–4). Categories of each spectrum are based on theoretical and natural observations found in Kisseleva (1939), Foged (1963), Reimer (1965), Round (1965), De Smet and Evens (1972), Schoeman (1973), Friedrich (1973), Lowe (1974), and Temnikova-Topalova and Misaleva (1982). Important expoundings on each of the nine spectra are: pH (Hustedt 1937, Meriläinen 1967, Cholnoky 1968), saprobian (Kolkwitz and Marsson 1908, Caspers and Schulz 1960, Fjerdingstad 1964, 1965a, 1965b, Caspers and Karbe 1967, Sládeček 1967, 1969, 1973, Schoeman 1979, Lange-Bertalot 1979a, 1979b), nutrient (Rawson 1956, Sparling and nalewajko 1970), halobion (Kolbe 1927, Legler and Krasske 1940), current (Shirshov 1933, Zelinka and Marvan 1961, Blum 1963), general habitat, specific habitat, and seasons (Schröder 1939, Whitford and Schumacher 1963, Hutchinson 1967, Symons 1970, Staker 1976, Pudo 1979, Moore 1981), and temperature (Louis and Aelvoet 1969, Friedrich 1973). Information from new references is used continuously to update CAESARS. Most terminology used in the categories of the spectra is self-explanatory or in common use, but Lowe (1974) and VanLandingham (1982) give detailed descriptions of each category and spectrum. A series of histograms can be made (Figs. 1–4) by calculating the percentage of each taxon in each sample and totaling the percentages of all taxa in each category. These spectral categories and/or histograms have proven to be ideal as a standard of ecological comparison for various algal samples from all over the world (Collingsworth et al. 1967, Dutchie and Bani 1967, VanLandingham 1968, 1970, 1972, 1976, 1982, Messina-Allen and VanLandingham 1970, Robbins and Hohn 1972, VanLandingham and Jossi 1972, Abbott and VanLandingham 1972, Lowe
Fig. 1. Spectral histograms based on diatom species percentages from plankton grab samples on 6–8 February 1967 by the California-Nevada–FWPCA survey.
Fig. 2. Spectral histograms based on diatom species percentages from California-Nevada-FWPCA survey periphyton samples taken during intervals designated under each station.
Fig. 3. Spectral histograms of diatom species percentages from averages of 15 fall 1967, 10 winter 1967–1968, 13 spring 1968, and 13 summer 1968 plankton samples at index station (Tahoe Pines) of Goldman (1974).
Fig. 4. Spectral histograms of diatom species percentages from the VanLandingham survey of 1967–1985, all stations were planktonic except Logan Shoals, which was periphytic.
1974). One of the advantages of a comprehensive algal data synthesis like CAESARS is that the general and specific habitat spectra in conjunction with the nutrient and saprobion spectra can be helpful in determining if an alga is absent from an assemblage because of lack of suitable physical habitat or because of adverse water chemistry. Any artificial, comprehensive system of data synthesis involving the classification of ecological tendencies of algae is bound to have conspicuous deficiencies. Stoermer (1984) presents an excellent and objective discussion of some of these difficulties.

SAMPLES

California–Nevada–FWPCA Survey

PLANKTON.—Plankton grab samples were taken during this cooperative investigation from the following five stations on 27–30 April, 17–19 August, 28–30 September 1965; 25–27 January, 27–29 April, 16–18 August, 14–17 November 1966; and 6–8 February 1967 (California Department of Water Resources 1966, 1967). Histograms were made from diatom species percentages for the 6–8 February 1967 samples (Fig. 1).

Station 1 is about 1 km north of the mouth of the Upper Truckee River and at the edge of the southerly shelf of Lake Tahoe, El Dorado Co., California. The station is representative of conditions in shallower waters near an extensively developed residential and resort area and is responsive to surface inflow from tributary streams. Bottom depth is 7.5 m. Magnetic bearings from Station 1 are N 4° E to Cave Rock and S 86° E to the building on Glen’s Pier at Al Tahoe (Fig. 5).

Station 2 is about 1.3 km northeast of the buoy at the mouth of Emerald Bay in El Dorado Co., California. The station is representative of conditions in deep waters and may be affected by inflows through Emerald Bay. Bottom depth is 345 m. Magnetic bearings from station are S 30° W to buoy “2” at the mouth of Emerald Bay and S 86° E to the building at Glen’s Pier in Al Tahoe (Fig. 5).

Station 3 is 8.5 km south of Stateline Point and due west from Secret Harbor. The station is representative of waters in the deepest part of the lake and is at the eastern boundary of Placer Co., California. Bottom depth is 471 m. Magnetic bearings from Station 3 are N 8° W to Cal-Neva Lodge and S 67° W to Deadman Point on the Nevada shore (Fig. 5).

Station 3A (alternate station) is 5 km southwest of South Point, near the confluence of the Placer–El Dorado county line (California) with the Nevada state boundary. The station is representative of waters in the deepest part of the lake. Bottom depth is 465 m. Magnetic bearings from Station 3A are N 15° W to Cal-Neva Lodge and S 64° E to the Sahara Hotel at Stateline (Fig. 5).

Station 4 is 180 m from shore at a point 1.3 km west of Incline Creek, Washoe Co., Nevada. The station is representative of shallow waters in Crystal Bay and is responsive to inflow from Incline Creek. Bottom depth is 6 m (Fig. 5).

Station 5 is 1.3 km easterly from the dam at the lake outlet on the Truckee River at Tahoe City, Placer Co., California. The station is representative of shallow waters at the northwest corner of the lake and of the water flowing out of the lake. Bottom depth is 9 m. Magnetic bearings from Station 3 are N 38° W to the Chevron sign at Tahoe City Boat Works and N 20° E to the United States Coast Guard radio tower (Fig. 5).

PERiphyton.—Station 5 also was used for periphyton sampling. The bottom sample from this station, representing 20 October 1965–25 January 1968, was selected for comparison with four surface periphyton samples that were taken from the pier at the United States Coast Guard Station (2.9 km northeast of Tahoe City) at Lake Forest, Placer Co., California. Surface samples represented the time intervals of 2–20 December 1966, 20 December 1966–4 January 1967, 4–12 January 1967, and 13 January–13 February 1967. Spectral histograms were compiled from diatom species proportional counts from these five periphyton samples (Fig. 2). Permanent hyrax slides of both periphyton and planktonic samples from the stations mentioned above have been deposited at the United States National Museum of Natural History, Washington, D.C.

Goldman (1974) Survey

PLANKTON.—In Goldman’s (1974) comprehensive study of the eutrophication of Lake Tahoe from 1967 through 1971, samples were taken on 115 different days from the designated index station at Tahoe Pines (in the Blackwood Creek–Madden Creek interfluve
Fig. 5. Map of Lake Tahoe showing sites mentioned in this paper. Circled numbers represent sample stations of the California-Nevada-FWPCA survey.
area, Placer Co., California) (Fig. 5). Appendix C of that publication gave a tabulation of the average number of individuals (cells/ml) of each phytoplankton species for the entire 105-m water column at this station. The fall 1967 through summer 1968 sequence, represented by 51 sampling days, was used for plotting histograms (Fig. 3). Results from fall 1968 through fall 1971 sequences of samples were very similar and therefore were not figured. The fall 1967 spectra were plotted by totaling the average number of individuals of each diatom species for the entire 105-m water column for the 15-day fall 1967 sequence and then calculating the percentage of each diatom species in the total diatom community for that season. In the same manner, spectral histograms were generated for the 10 samples from the winter of 1967–1968, the 13 samples from the spring of 1968, and the 13 samples from the summer of 1968 (Fig. 3).

Periphyton.—Goldman (1974) showed the relative proportions of periphyton (mostly diatoms) for the intervals of 24 June–30 September 1970 and 1 October 1970–2 May 1971 from several stations around Lake Tahoe in the vicinity of the following localities: General Creek, Emerald Bay, and Tahoe Keys in El Dorado Co., California; Zephyr Cove and Cave Rock in Douglas Co., Nevada; Skunk Harbor in Carson City, Nevada; Incline Creek and Crystal Bay in Washoe Co., Nevada; and Dollar Point (Lake Forest), Ward Creek, and Tahoe Pines in Placer Co., California (Fig. 5). These samples are discussed below under Observations.


Plankton.—My own survey of the diatoms of Lake Tahoe began with plankton samples from Tahoe City (Station 5) on 28 March 1967 and continued with samples at irregular times from this and three other stations until 28 October 1985. Because of possible differences in species interpretations in the California–Nevada–FWPCA joint survey, several samples were sent to various investigators and laboratories for determinations, comparisons, and verifications. The Academy of Natural Sciences of Philadelphia laboratory and I examined the 16 May 1967 plankton sample from Station 5 (Fig. 4). Our species determinations were very similar. Permanent hyrax slides are deposited at the Geology Department, California Academy of Sciences, San Francisco. The samples were prepared for microscopic examination and species proportional analysis following VanLandingham (1976). Since July 1973, sampling has been restricted to three stations in the southeast portion of the lake:

Station A (South Lake Tahoe) is about 1 km west of the boat harbor near the South Lake Tahoe Recreation Area, El Dorado Co., California (Fig. 5). This station was chosen for its close proximity to the most densely populated and highly developed region of the lake. Spectral histogram results from two samples separated by a 12-year span from this station can be compared (Fig. 4).

Station B (Zephyr Cove) is 1.5 km northeast of Zephyr Point at the Zephyr Cove pier, Douglas Co., Nevada (Fig. 5). Although there are some recreational and commercial facilities in the area, it is not heavily populated. A series of histograms was plotted for the 27 October 1985 sample from this station (Fig. 4).

Periphyton.—Station C (Logan Shoals) is 2.5 km north of Cave Rock and near the mouth of Logan House Creek in Douglas Co., Nevada (Fig. 5). This is one of the few remaining, relatively unspoiled areas on Lake Tahoe. It is the only station encountered in this study that I have found to be oligotrophic more often than mesotrophic and/or eutrophic on the basis of indicator algae. At this station periphyton was scraped at irregular intervals from plants and large boulders at the water’s edge. The spectral histograms were composed for a recent sample from 27 October 1985 (Fig. 4).

Observations

California–Nevada–FWPCA Survey

Phytoplankton.—The 27–30 April 1965 and 25–27 January 1966 plankton diatoms from samples of the California–Nevada–FWPCA joint investigation indicated a pronounced mesotrophic character for the entire lake. The prominence of Synedra nana Meist., an indicator of mesotrophy (Cody 1978), was responsible for the strong mesotrophic nature of these samples. The remaining dominant species, all of which were euphotic (and/or mesotrophic) indicators except Cyclotella bodanica Eul. ex Grun. and Stephanodiscus invistatus Hohn & Hell.,
accounted for a less pronounced but conspicuous eutrophic character. The percentages of the most dominant species from the 27–30 April 1965 samples were as follows: Station 1, Fragilaria crotonensis 52, Synedra nana 21, Stephanodiscus invissutatus 4, and Nitzschia acicularis (Kiitz.) W. Sm. 3; Station 2, S. nana 39, Asterionella formosa Hass. 29, F. crotonensis 20, and N. acicularis 6; Station 3, F. crotonensis 47, S. nana 37, N. acicularis 4, and A. formosa 3; Station 4, S. nana 31, F. crotonensis 30, F. construens (Ehr.) Grun. 3, and Amphipora (Entomoneis) paludosa W. Sm. 3; and Station 5, S. nana 41, N. acicularis 11, and F. crotonensis 4. The dominant species from the 25–27 January 1966 samples were as follows: Station 1, F. crotonensis 48, S. nana 33, F. construens 4, and Melosira italica (Ehr.) Kütz. 4; Station 2, S. nana 53, F. crotonensis 15, M. italica 8, and F. pinnata 5; Station 3A, S. nana 59, F. crotonensis 21, A. formosa 6, and N. acicularis 3; Station 4, F. crotonensis 43, S. ñana 35, F. construens 6, and A. formosa 5; and Station 5, F. crotonensis 48, S. nana 23, C. bodanica 8, and M. italica 3. Eutrophic and/or mesotrophic diatoms prevailed at all five stations in the plankton samples collected on 17–19 August and 28–30 September 1965. Only Station 2 (at the August sampling) showed any marked tendency toward oligotrophy.

A similar trend toward mesotrophy in the winter can be seen in the first three stations on 6–8 February 1967 (see nutrient spectrum, Fig. 1). Station 4 (Fig. 1) was anomalous and showed an oligotrophic nature that was found rarely in the plankton. In all of these samples Cyclotella bodanica was dominant, but Synedra nana, Fragilaria crotonensis, and many other mesotrophic and eutrophic indicators were important. The nutrient spectra of all stations (Fig. 1) correlate well with both the saprobion and pH spectra. Mesotrophic waters usually are concomitant with oligosaprobic and/or saproxenous conditions in the saprobion spectrum and with indifference in the pH spectrum. Oligohalobous indifference in the halobion spectrum is to be expected in subalpine lakes. The prominent limnophilous element in the current spectrum and the prominent lake and pond category in the general habitat spectrum suggest that the plankton at this time of the year is mostly indigenous to the lake and not carried in from streams. The specific habitat spectrum confirmed the planktonic nature of the samples. Because the seasonal distribution of most of these planktonic diatoms is imperfectly known, the seasonal spectrum gave inconclusive results. VanLandingham (1964) and others have pointed out that temperature and nutrients are more important in diatom distribution than seasonal influence. The strong oligothermal character of the temperature spectrum is normal and reflects the cold-water characteristics which would be expected in the plankton of a large, subalpine lake in the winter. On the other hand, samples from all of the periphyton stations from cold times of the year (late fall–winter) were eurythermal (widely tolerant of temperature changes) (Fig. 2).

Eutrophy in the nutrient spectrum normally is correlative with oligosaprobic to weak mesosaprobic conditions in the saprobion spectrum and with alkaliophilous conditions in the pH spectrum. Spring plankton samples of 27–29 April 1966 demonstrated this very well as did periphyton samples (Fig. 2) and the Tahoe Pines plankton samples (Fig. 3). Fragilaria crotonensis was the most abundant diatom at all stations (composing 98% of the assemblage at Station 2) in the 27–29 April 1966 plankton samples. Although F. crotonensis was less important (becoming more subdominant to Fragilaria construens and F. pinnata) in the summer (16–18 August) samples and the fall (14–17 November) samples, the conspicuous eutrophic conditions remained. A sample from a depth of 25 m was taken at Station 2 in the summer to supplement the regular 3-m sample from that station. The two most dominant diatoms, Cyclotella meneghiniana Kütz. and C. atomus Hust., from the deep sample were prominent eutrophic indicators and accounted for 39% and 30%, respectively, of the total diatom community.

PERIPHITYON.—It is noteworthy that the mesotrophic trend found in diatoms of the plankton samples of 6–8 February 1967 (Fig. 1), 25–27 January 1968, and 27–30 April 1965 did not occur in any of the periphyton samples (Fig. 2). Fragilaria construens, F. pinnata, Synedra vaucheriae Kütz., and Nitzschia kuertzingiana Hilsie (all of which are characteristic of eutrophic waters) accounted for most of the prominent eutrophic aspect of all of these
periphyton samples; the last of these species is a diagnostic eutrophic indicator (Krieger 1927, Jørgensen 1948, Cleve-Euler 1953, Kolbe 1953, Van der Werff and Huls 1957–1974, Cholnoky 1968, Schoeman 1973, Moghadam 1976, Caljon 1983). In large lakes it is not unusual to find planktonic taxa composing a large part of the periphyton assemblages, hence the large proportion of plankton in the specific habitat spectrum of all the periphyton samples (Fig. 2). This phenomenon also can be seen in the specific habitat spectrum of the Logan Shoals periphyton sample of the VanLandingham survey (Fig. 4).

Goldman (1974) Survey

**Phytoplankton.**—Goldman (1974) stated in his conclusions,

*Cyclotella bodanica* and *Melosira crenulata* are dominant centric diatoms while *Fragilariopsis crotonensis* is the most important pennate. These three oligotrophic forms account for about 80% of the phytoplankton biomass throughout the year.

It is likely that only one of these, *C. bodanica*, is an oligotrophic form (Hustedt 1930, Van der Werff and Huls 1957–1974, Tamás 1964, Hutchinson 1967, Dutich and Sreenivasa 1971, Sreenivasa and Dutich 1973, Almer et al. 1974, Rosén 1981). However, there are many reports of it in eutrophic or mesotrophic waters, such as Lipscomb (1966). On the other hand, Hillard (1959) noted that a slight pulse in *C. bodanica* corresponds with eutrophy. Recent taxonomic research suggests that *C. bodanica* may grade into *C. comta* Fricke. The report on centric diatoms of Lake Tahoe by Mahood et al. (1984) discussed *C. comta* in detail but did not mention *C. bodanica*. There is no clear consensus in the numerous references in CAESARS that shows *C. comta* to be correlative with any particular trophic status. It is probably eurytrophic (indifferent to inorganic nutrient content).

*Melosira crenulata* is a junior synonym of *M. italica*, which most authorities consider to be a eutrophic indicator. Mahood et al. (1984) state that *M. italica* is alkaliphilous and mesotrophic. Reynolds (1984) is one of the few references that gives it a distinct mesotrophic designation. Although Van der Werff and Huls (1957–1974) and Bradbury (1972a) indicated that *M. italica* is mesotrophic, they also implied that its range extended into the oligotrophic and/or eutrophic zones. However, it is indeed mesotrophic, the probability of its being alkaliphilous is subject to serious question. It is more likely that it is not mesotrophic but alkaliphilous and eutrophic. If there is any propensity for mesotrophic diatoms to correlate with a position in the pH spectrum, it is with indifference (occurrence around pH 7), which is to be expected if one follows the explanations of Fjerdingstad (1965a), Sparling and Nalewajko (1970), and VanLandingham (1976). Although there have been indications that *M. italica* may be acidophilous (Niessen 1956, Round 1961), 17 CAESARS references categorize it as alkaliphilous (Foged 1958, 1959, 1976, 1980a, Maillard 1959, Liebmann 1962, Cholnoky 1968, 1970a, VanLandingham 1970, Ehrlich 1973, Gasse 1975, Kaczmarska 1976, Reháková 1976, Moreira and Moreira 1982, 1984, Gasse and Tekaia 1983, Dixit and Dickman 1986; 4 as alkaliphilous to indifferent (Hustedt 1957, Gasse 1972, Lowe 1974, Foged 1978); and 5 as indifferent (Foged 1954, 1957, 1970, Haworth 1969, Messina-Allen and VanLandingham 1970, Baudrimont 1974, Khursevich 1976, Del Prete and Schofield 1981). If *M. italica* is conceded to be alkaliphilous, it is much more likely to have the associated eutrophic correlation found with over 100 commonly occurring diatoms. Only Round (1960), Cholnoky (1970a), Stockner (1971), and Weber (1973) indicated that *M. italica* might be characteristic of oligotrophic waters, while there is much more agreement concerning its correlation with eutrophic waters (Krieger 1927, Hustedt 1930, 1942, Brockmann 1935, Frenguelli and Cordini 1937, Foged 1951, 1959, Bourrelly and Manguin 1952, Järnefelt 1952, Guermeur 1954, Messina-Allen and VanLandingham 1970, VanLandingham 1970, Baudrimont 1974, Planas 1975, Gasse 1975, and Negoro 1981). Mesohalobous (characterized by brackish water, 0.5–3.0% salt) organisms are very rare in alpine and subalpine lakes. The statement of Mahood et al. (1984) that *M. italica* is mesohalobous seems doubtful in view of the evidence that only Van der Werff and Huls (1957–1974) reported it from the weak mesohalobous zone (but also in the oligohalobous zone). If *M. italica* is truly mesohalobous, why would it be so common in a high, subalpine lake, such as Lake Tahoe? There is even some consensus that *M. italica* has a negative correlation with salt content since Cleve-Euler
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In the examination of over 4,000 references, no indication was found that *Fragilaria crotonensis* was clearly diagnostic of oligotrophic waters, although it is sometimes found in large numbers in those waters. Beeton (1965), Stoermer and Yang (1970), Stoermer et al. (1974), Stoermer and Ladewski (1976), and Grimes et al. (1984) suggested that it ranged from oligotrophic to eutrophic. Van der Werff and Huls (1957–1974) gave a dystrophic to eutrophic (and/or hypertrophic) range. Teiling (1955), Rawson (1956), Patrick and Reimer (1966), Tarapchak and Stoermer (1976), and Gerrath et al. (1980) considered it to be most prominent in mesotrophic waters. It has been described as mesotrophic-eutrophic by Cleve-Euler (1953), Round and Brook (1959), and Lowe (1974). But the greatest agreement is in favor of its eutrophic tendency: Krieger (1927), Hustedt (1930), Jørgensen (1948), Margalef (1957), Hutchinson (1967), Stockner and Benson (1967), Leh (1969), Frey (1969), Vollenweider (1970), Stockner (1971), Stoermer et al. (1971), Stadelmann (1971), Bradbury (1972a, 1972b), Haworth (1972a), Niko1oyev and Petrova (1978), Burns and Mitchell (1974), Planas (1975), Gorham and Sanger (1976), Holtan (1978), Bailey and Davis (1978), Cassie (1979), Cassie and Freeman (1950), Rosén (1981), Negoro (1981), Mason (1981), Brugam and Patterson (1983), Reynolds (1984), Haffner et al. (1984), and Engstrom et al. (1985). In addition, Stockner (1972) stated that it correlates well with domestic sewage discharge into lakes. Stoermer et al. (1974) and Bradbury (1975) advocate that it is eurytopic, as do Duthie and Sreenivasan (1971), but with acknowledgment of its eutrophic character. *Fragilaria crotonensis* requires for optimal growth more than 20 µg P 1⁻¹ (Fogg 1973). Løvstad (1984) indicated a sharp drop in the development of *F. crotonensis* at concentrations of less than 16 µg P 1⁻¹ in eutrophic Lake Jaren in April and May 1976. Goldman (1974: 72) stated that *F. crotonensis* "is now the dominant type in Lake Tahoe, both in biomass and numbers." Such a diatom (which, according to 21 references supplied by CAESARS, is found only in the oligosaprobic and/or weak mesosaprobic zones) seems out of place in such large numbers in a body of water so oligotrophic as Lake Tahoe is alleged to be.


According to Goldman (1974: 131), the five most dominant species of phytoplankton at the index station (Tahoe Pines) for 1967–1969 (in order of importance) were *Fragilaria crotonensis*, Melosira circumulata (= *M. italica*), *Fragilaria pinnata*, Stephanodiscus astraea (Ehr.) Grun., and Cyclotella bodanica. Although the trophic disposition of *F. pinnata* is considered to be oligotrophic or mesotrophic through eutrophic (Van der Werff and Huls 1957–1974, Stoermer et al. 1971) and oligotrophic (Beeton 1965, Baudrimont 1974), the greatest number of authorities deem it to be eutrophic (Hustedt 1937, 1938, Jørgensen 1948, Foged 1951, 1959, Bourrelly and Mangin 1952, Ross 1952, Cleve-Euler 1953,

Stephanodiscus astraea and its varieties are some of the most diagnostic of all indicators of eutrophy. According to CAESARS, apparently no authorities judge S. astraea to be exclusively oligotrophic. Cleve-Euler (1951), Patrick (1956), and Werff and Huls (1957–1974) consider the trophic range to be oligotrophic and/or mesotrophic through eutrophic, but most investigators agree that it is eutrophic (Krieger 1927, Hustedt 1930, 1942, 1949, Jørgensen 1948, Foged 1948, 1951, 1953, 1959, Bourrelly and Manguin 1952, Kolbe 1953, Guermer 1954, Brockmann 1954, Round and Brook 1959, Hutchinson 1967, Gasse 1969, 1972, 1974b, 1975, Haworth 1972b, Moreira 1975, Stoermer and Ladewski 1976, and Mason 1981). Mahood et al. (1984) did not mention S. astraea but did comment on Stephanodiscus alpinus Hust., a closely related form. It is highly unlikely that S. alpinus is alkalibiontic, as they claim. Alkalibiontic species are rare among the diatoms. Out of a total of 2,900 diatom taxa, CAESARS reveals that no more than two dozen are definite alkalibionts, none of which are centrics except Stephanodiscus dubius (Fricke) Hust. Stephanodiscus alpinus may be eutrophic as Hohn (1969) and Mahood et al. (1984) imply. However, Ayers et al. (1967) indicate that it might be oligotrophic, and Tarapchak and Stoermer (1976) note maximum abundance in the mesotrophic zone. Although it occurs in very oligotrophic lakes, it seems to become more abundant with moderate degrees of eutrophication (Stoermer 1978, Håkansson and Stoermer 1984).

Goldman (1974: appendix) shows very conspicuous pulses of Synedra radians Kütz. (= Synedra acus var. radians) at the index station in summer 1969, spring 1970, and winter, spring, and fall 1971. Apparently only Whitford and Kim (1971) found S. radians to be oligotrophic. It is thought to be mesotrophic (Ayers et al. 1967), mesotrophic through eutrophic (Cleve-Euler 1953, Van der Werff and Huls 1957–1974), and eutrophic (Jørgensen 1948, Lowe 1974).


Dinobryon sertularia Ehr. made up a considerable portion of the total algae community on at least three occasions at Tahoe Pines, having a total of 38.34, 18.99, and 21.42 individuals/ml for the entire 105-m water column on 9 and 16 May 1968 and 24 July 1969, respectively (Goldman 1974). On these three occasions, D. sertularia was an important subdominant, composing 18.10, and 28.8% respectively, of the total population. In the same publication (Goldman 1974: Fig. 2), apparently D. sertularia is referred to as Dinobryon sociale Ehr. Both of these taxa are eutrophic. Such investigators as Krieger (1927), Huber-Pestalozzi (1941), Meyer and Brook (1969), and Gerrath et al. (1980) believe that D. sertularia occurs under eutrophic conditions, while Krieger (1927) and Huber-Pestalozzi (1941) hold the same opinion for D. sociale.

Sphaerocystis schroeteri Chod. was the dominant algal species on nine different occasions in the fall of 1967 at the Tahoe Pines station (Goldman 1974). In spite of the fact that it is occasionally found in oligotrophic lakes (Almer et al. 1974), many such writers as Meyers and Brook (1968) describe S. Schroeteri as eutrophic, whereas Reynolds (1984) contends that it is mesotrophic.
There is good evidence that in some areas of Lake Tahoe the algae display an oligotrophic tendency at certain times. Goldman (1974: 131) found *Cyclotella stelligera* to be uncommon at the index station (Tahoe Pines) in 1967–1971 but to be present in large numbers in midlake plankton samples in 1972–1973. CAESARS provides a strong opinion that *C. stelligera* is typical of oligotrophic waters: Jørgensen (1948), Cleve-Euler (1951), Hutchinson (1967), Stockner (1971), Schnitzler (1971), Holland and Beeton (1972), Croome and Tyler (1973), Burns and Mitchell (1974), Lowe (1976), Bailey and Davis (1978), Cassie and Freeman (1980), Smol et al. (1983), Schelske (1984), and Engstrom et al. (1985). Smedman (1969), Bradford (1972b), and Tarapchak and Stoermer (1974) advocate dystrophic-oligotrophic, oligotrophic-mesotrophic, and mesotrophic categories, respectively, while Dutchie and Sreenivasa (1971) suggest it is "eurytopic-eutrophic." Only Cholnoky (1968, 1970b), Lowe (1974), and Moghadam (1976) support the contention of Mahood et al. (1984) that it is eutrophic. Sewage export from the Tahoe basin in recent years may be responsible for the increase of such oligotrophic indicators as *C. stelligera* at various places in the lake. On the other hand, most of the evidence supplied by the Van Landingham survey of the years 1967–1985 suggests that the propensity toward mesotrophy (or even eutrophy) displayed by the most dominant diatoms is still strong over much of the lake.

**Periphyton.** —In spite of the fact that the littoral zone contributes a small portion of the total primary productivity and that the lake has great area and depth, the importance of the littoral areas and periphyton cannot be overlooked in a comprehensive evaluation of the lake’s trophic characteristics. The seven most dominant species in the periphyton from 11 stations around Lake Tahoe between 1 October 1970 and 2 May 1971 were: *Synedra actinastroides* Lemm., *Fragilaria crotonensis*, *Gomphonema parvulum* Kütz., *Cyclotella bodanica*, *Synedra ulna*, *Gomphonema herculeana* (Ehr.) Cl., and *Melosira culmata* (Goldman 1974: Fig. 55). CAESARS indicates that only *C. bodanica* is predominantly oligotrophic; all of the rest are eutrophic, except *G. herculeana*. The six most important diatoms in the periphyton from 10 stations around Lake Tahoe between 24 June and 30 September 1970 were: *Epithemia argus* (Ehr.) Kütz., *Rhopalodia gibba* (Ehr.) O. Müll., *Synedra ulna*, *Cymbella ventricosa* Ag., *Navicula aurora* Sov., and *Fragilaria capucina* Désm., none of which clearly indicates oligotrophic conditions and most of which are eutrophic indicators. Goldman (1974) notes that *F. capucina* was a dominant species in the periphyton of the summer of 1971 only off the Upper Truckee River mouth and in Emerald Bay, both of which are noted for high productivity. Many authorities think that *F. capucina* is a good enrichment indicator. However, Schröder (1939) states that it is not particularly sensitive to pollution. Only Rawson (1956) and Beeton (1965) place it directly in the oligotrophic zone. Cleve-Euler (1953) and Van der Werff and Huls (1957–1974) assign it to the dystrophic through mesotrophic and/or eutrophic zones. The range given by Round and Brook (1959) is mesotrophic-eutrophic. However, nearly all authorities regarded it as eutrophic: Krieger (1927), Hustedt (1930, 1935, 1942), Jørgensen (1948), Foged (1951, 1959), Bourrelly and Manguin (1952), Holland (1965), Gasse (1969), Bradford (1972b), Stoermer et al. (1974), Lowe (1974), Stoermer and Ladewski (1976), Tarapchak and Stoermer (1976), and Bailey and Davis (1978).


**Phytoplankton.** —Many of my own samples from Tahoe City (station 5 of the California-Nevada-FWPCA survey) demonstrated marked fluctuations in the histograms of all spectra at different times of the year. However, mesotrophic and/or eutrophic conditions always predominated in the nutrient spectrum. In the 16 May 1967 plankton sample from station 5 (Fig. 4), *Synedra ulna* (25% of the total) was responsible for most of the mesotrophic manifestation, and *Fragilaria crotonensis* (20% of the total) accounted for most of the eutrophic manifestation. This sample, which comes from the northeastern portion of the lake, is included for comparison with samples from the three stations (South Lake Tahoe, Zephyr Cove, and Logan Shoals) in the southeastern portion of the lake and with other results from station 5 (Figs. 1–2). Spectral histograms of diatom species percentages from plankton samples at the South...
Lake Tahoe station on 3 July 1973 and 27 October 1985 can be compared in Figure 4. Other samples were taken at South Lake Tahoe during the long interval represented by these two samples, but their histograms were not figured because of their great similarities. After a period of over 12 years, one can see the similarity of the spectra in these two samples and the eutrophic aspects of both. The diminishing of the eutrophic category in the 1985 sample in relation to the 1973 sample may be a result of sewage export from the Tahoe basin in recent years. The planktonic assemblage from Zephyr Cove on 27 October 1985 was very typical of that station and exhibited the usual eutrophic characteristics (Fig. 4); counts for the diatoms were about 20 cells/ml. Cyclotella glomerata Bach., Achnanthes lanceolata, Nitzschia linearis (Ag.) W. Sm., and Cocconeis diminuta Pant. were the dominant taxa, the last of which is a diagnostic mesotrophic to eutrophic indicator (Hustedt 1938, Jørgensen 1948, Cleve-Euler 1953, Foged 1957).

PERIPHYTON.—After studying hundreds of samples over a period of 18 years from many stations in the three independent surveys of Lake Tahoe, I have found Logan Shoals to be the only station (planktonic or periphytonic) in which the indicator algae suggest general oligotrophic conditions more often than mesotrophic and/or eutrophic (Fig. 4).

Conclusions

The slight increase in recent years in oligotrophic algae, such as Cyclotella stelligera and Achnanthes minutissima, and the corresponding slight decrease in the dominant mesotrophic and eutrophic algae at various places in the lake seem to correlate well with the export of sewage from the Tahoe basin. This situation bears testimony to the sensitivity of the algae as indicators. However, the strong mesotrophic-eutrophic trend, which was indicated by the algae from about 1965 until about 1973 or 1974, still continues today, although probably to a lesser degree. Moreover, repeated spills of raw and partially treated sewage have been indicated adequately by the microalgae populations and other modes of observation to such an extent that the United States Environmental Protection Agency and California's regional water quality control board have duly noted that the Lake Tahoe water reuse system for recycling sewage into drinking water is no longer feasible (U.S. Water News 1956). It could be claimed that the persistence and prominence of a whole suite of characteristically eutrophic (and/or mesotrophic) diatoms in a lake traditionally thought to be oligotrophic attests to the admonition that we should reexamine either the lake or the validity of the algal indicator concept (or both). Can algal communities be valid indicators of the trophic status of a lake or do physical and chemical factors provide the only reliable clues to deciphering trophic status? If the former is true, then our traditional opinions about Lake Tahoe will have to change. If the latter is true, then there should be dynamic changes in limnological thought. In either case, it seems prudent to maintain philosophical objectivity and consider all aspects of biological, physical, and chemical factors in trophic assessment, even if they seem to be contradictory. If it is granted that Lake Tahoe is not highly anomalous, then undoubtedly it is somewhat less "ultra-oligotrophic" than the water chemists and physical limnologists would advocate, and probably the indicative diatoms and other algae are somewhat less accurate than the diatomists and aquatic biologists would advocate.

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