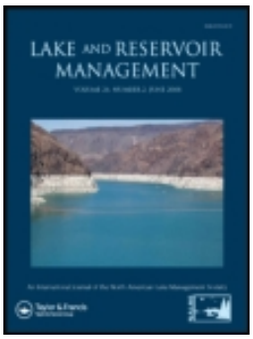

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Evaluation of Phytoplankton–Limiting Factors in Lake Chapala, México: Turbidity and the Spatial and Temporal Variation in Algal Assay Response

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ABSTRACT

Laboratory algal bioassays using both cultures of Ankistrodesmus bibraianus and natural phytoplankton, and large, in-lake, container assays with natural populations, were used to determine the factor most limiting phytoplankton production in Lake Chapala, México. Both types of laboratory culture assays showed that nitrogen was the principal limiting nutrient at each station across this very large lake in all seasons. The growth response of natural phytoplankton was similar to that of A. bibraianus. However, management practices to regulate the lake's productivity based solely upon this laboratory information would be inappropriate because the natural population assays showed that the ultimate limiting factor in situ is illumination controlled by the high clay turbidity. Rarely, if ever, was phytoplankton production controlled by the laboratory-determined limiting nutrient, nitrogen, expressed in the lake.The importance of performing algal assays extensively through time and space also was demonstrated. The nitrogen-augmented increase over controls in A. bibraianus biomass ranged from less than 50 percent at the end of the dry season to greater than 1,000 percent in the middle of the rainy season. The average annual percent response at different sampling stations ranged from 438 percent to 541 percent. Also, the sample to sample variation was different for different stations. The variation coefficient was only 35 percent for the mid-lake station, but greater than 84 percent for the station nearer the source of river inputs.

Introduction

Algal bioassays are widely used valuable tests to determine the factors governing algal production of aquatic ecosystems (Maloney and Miller, 1975). This procedure is based on Liebig's law of the minimum which says that the maximum production that can be reached is proportional to the quantity of the biologically available nutrient present in the minimum concentration relative to the organism's requirements. Determining the limiting nutrient allows one to predict the impact of influents upon water quality and changes in the watershed use, and evaluate synergistic effects in a way not possible with other assay procedures (Miller et al. 1978).

Algal bioassay techniques for measuring nutrient limitation vary greatly. Methods include: laboratory procedures using small samples of filtered, sterile lake water inoculated with a standard test organism (U.S. Environ. Prot. Agency, 1978); very large *in situ* enclosures of natural populations (Schelske and Stoermer, 1972); and open cylinders isolating a column of lake water (Goldman, 1962; Lund, 1972). There are advantages and disadvantages to each of these techniques. Using standard algal species, such as *Ankistrodesmus bibraianus* (Reinsch) Korshikov (formerly *Selenastrum capricornutum*), under controlled light and temperature laboratory conditions allows interlaboratory comparisons because the test organism is readily available, its physiological requirements and responses are known, and its growth

is accurately and easily measured. This species is widely used under the U.S. Environmental Protection Agency prescribed conditions, but has not been used in México. *In situ* assays using natural phytoplankton populations more closely approximate natural environmental conditions including interspecies interactions. Thus they are more suited to answering questions about specific ecosystem-level responses (Komarkova, 1979).

In this study of Lake Chapala, México, both types of procedures were used—a choice subsequently found to be fortunate— and thus led to identifying both the proximate and ultimate production-governing factors. This paper will illustrate both results of algal assay analyses for the largest and most economically important lake in México and three potential errors of interpretation that may occur in algal assay studies. These errors arise from inadequate sampling through time and through space, failure to identify the important non-nutrient regulators of algal production, and laboratory culture conditions that differ from the natural environment (i.e., illumination intensity, temperature, etc.).

Lake Chapala belongs to the Río Lerma–Lake Chapala–Río Santiago hydrological system, one of the most important in México (Fig. 1). The Río Lerma is the lake's principal water source. Outputs are via the Río Santiago and evaporation. Loss to groundwater has not been measured. The physical and chemical limnology and the hydrology of Lake Chapala have been described in detail by Limón et al. (1989). A summary is presented in Table 1. Although the lake is the largest in México, during this study the mean depth was only 4.5 m. The water is the principal source, via the Río Santiago, for the Guadalajara metropolitan area with a population of nearly 4.5 million and a water demand growing at 5.6 percent annually. In addition, the lake is important for commercial fisheries, tourism, and irrigation.

An unusual aspect, regarding elements normally limiting productivity, is the high mean inorganic phosphorus concentration (705 μg/L) relative to the inor-

Table 1.—Summary of Lake Chapala's physical limnology, mean chemical limnology, and mean phytoplankton production and biomass (data from Subdirección de Estudios, 1981, Limón et al. 1989.)

Volume ($10^6 m^3$)	4667
Area (km^2)	1039
Maximum length (km)	75
Maximum width (km)	22.5
Perimeter (km)	209.5
Mean depth (m)	4.5
Total hardness (mg/L $CaCO_3$)	148
pH	8.4–8.9
Total dissolved solids (mg/L)	387
Inorganic phosphorus (μg/L)	705
Ammonia nitrogen (μg/L)	145
Nitrate nitrogen (μg/L)	367
Primary production (g C m^{-2} year)	76
Chlorophyll *a* (mg m^{-3})	5.4

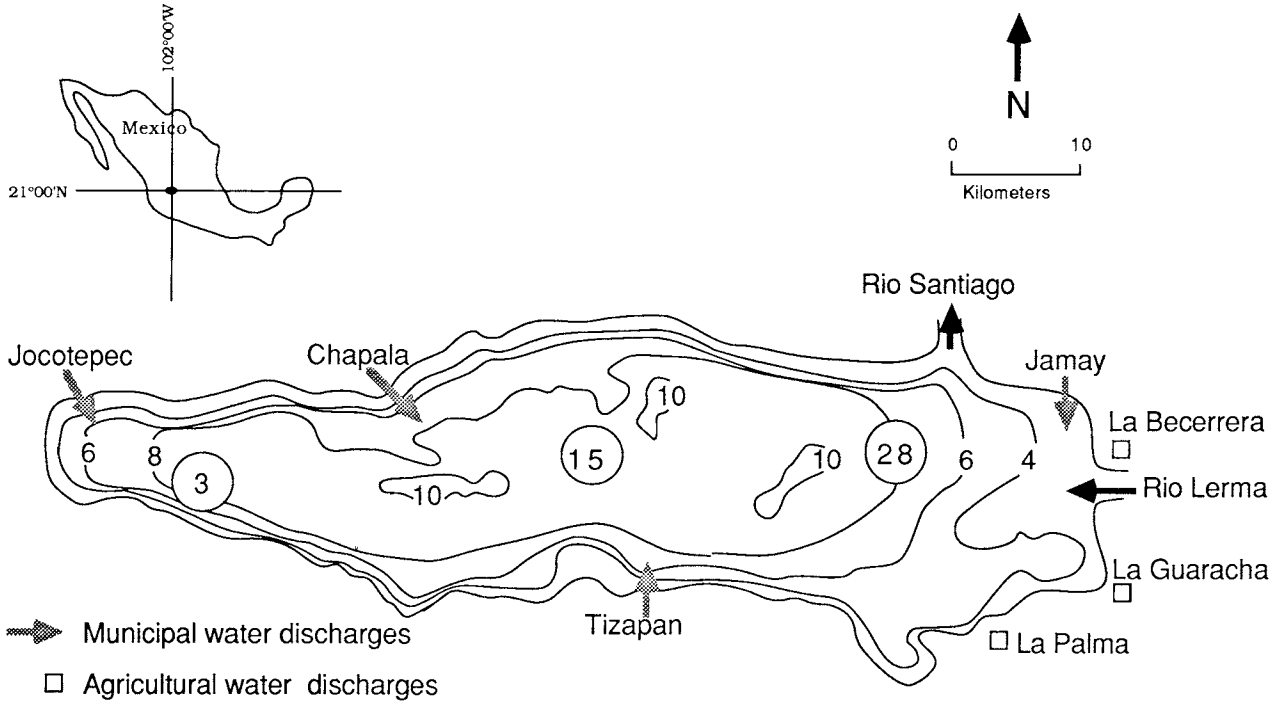

Figure 1.—Morphometric map of Lake Chapala, Mexico showing sampling stations (circled numbers) used in this study. Depth contours are in meters.

ganic nitrogen concentration (145 and 367 μg/L as NH_3-N and NO_3-N, respectively). The nitrogen to phosphorus ratio for any station was always less than one. Also important was the very high inorganic turbidity. Average Secchi transparency varied from 0.2 m at the east end of the lake to 0.8 m at the west end with a lake-wide average of 0.5 m. The mean photic depth, as measured by photometer, at the east and west ends was 0.6 and 2.1 m, respectively.

Methods

For the laboratory assays, sample water was collected from Lake Chapala on eight dates between July 1983 and July 1984. Integrated water samples of the photic zone were collected from three stations – mid-lake (15), east end (28), and west end (3) (Fig. 1). The U.S. Environmental Protection Agency (1978) prescribed conditions were followed as closely as possible. Each sample was filtered (0.45 μm) and sterilized (autoclave). The bioassays were done in triplicate in 50 ml test tubes. Three nutrient addition treatments and a control from each station were used (Table 2). Each tube was inoculated with *A. bibraianus* and incubated under cool white fluorescent lights (4,300 lumens) on a 12 h/12 h light-dark cycle. Each tube was gently shaken twice daily for a 12-day incubation period. Algal growth was determined daily by measuring *in vivo* chlorophyll fluorescence using a Turner Designs fluorometer. Fluorescence is preferred over microscopic cell counting (U.S. Environ. Prot. Agency, 1978). Cell counts that were made at the beginning of the investigation correlated with chlorophyll fluorescence. The fluorescence values at the day of maximum fluorescence, usually day seven to nine, were used for comparative evaluation of algal growth response. Fluorescence always was declining by the 12th day.

Table 2.—Treatments used for the *Ankistrodesmus bibraianus* algal assay procedure on Lake Chapala, México

TREATMENT	FORM	CONCENTRATION (MG/L)
Control		
Nitrogen	$NaNO_3$	1
Phosphorus	K_2PO_4	0.5
Nitrogen + Phosphorus	as above	as above

Additional algal assays were performed on three dates using the above procedure. These used natural phytoplankton from the three lake stations. Zooplankton were first removed by filtration of the lake water through plankton netting (0.64 μm).

A third type of assay was performed on two dates – a natural lake community assay. In these assays, a large volume of water was collected from the lake and returned to the laboratory. This sample was siphoned into 3.8 1-polyethylene bottles. Each bottle was spiked with either nitrate nitrogen, ammonia nitrogen, inorganic phosphorus, or a micronutrient solution. An additional bottle was an unmodified control. Initial nutrient concentrations and algal biomass (chlorophyll fluorescence) were determined. These bottles were incubated at lake temperature and a light intensity equal to 60 percent of surface daylight intensity at the time of sample collection. These bottles were gently shaken daily. After six days of incubation the algal biomass was again measured by chlorophyll fluorescence. The final concentration of inorganic nutrients in each bottle was measured.

Results and Discussion

The growth of *A. bibraianus* in water from each region of Lake Chapala at any time of the year was stimulated by inorganic nitrogen (Table 3). Growth by natural phytoplankton populations also was stimulated by nitrogen (Table 4) and for comparable periods the response generally was greater than for *A. bibraianus*. The purpose of this discussion is to show that: (1) the extent of this stimulation could not be predicted on the basis of region, season, or nitrogen or phosphorus content of the lake water (Fig. 2); and (2) more importantly, the growth of the lake's phytoplankton was not governed by any nutrient. In the lake the phytoplankton growth was governed by the low light conditions produced by turbidity. The large container assays provided with adequate illumination illustrated this. These findings were consistent with the vertical and horizontal patterns of phytoplankton photosynthetic production – the most turbid region of the lake had the highest nutrient concentrations but the lowest phytoplankton production (Doyle, 1985).

The spatial difference in response to nitrogen was in the west region of the lake where the mean response was somewhat greater than the other two regions. There the ambient inorganic nitrogen concentration was consistently low through the year (Fig. 2), yet there was considerable sample to sample variation in algal growth response. For these west region samples the ambient nitrogen content was very small in proportion to the nitrogen added (1 mg/L) in the assay. The ambient concentrations in the other regions were highly variable seasonally. On average, ambient concentrations increased in laboratory additions by approximately 20 percent. Therefore, at the central and east stations, seasonality in ambient nitrogen concentrations should have elicited variable growth response. For these regions, a distinct reciprocal relationship of ambient inorganic nitrogen to growth response existed.

Table 3.—Percent growth response of *Ankistrodesmus bibraianus* relative to controls by the different treatments for three regions of Lake Chapala, México for eight dates, 1983–84.

DATE	REGION	TREATMENT		
		NITROGEN	NITROGEN + PHOSPHORUS	PHOSPHORUS
July	East	1171	1085	43
	Central	750	850	67
	West	620	1060	60
August	East	990	890	100
	Central	296	287	156
	West	1100	900	150
September	East	273	269	96
	Central	283	358	117
	West	725	825	75
November	East	173	64	100
	Central	500	920	100
	West	267	300	83
January	East	620	640	140
	Central	462	450	137
	West	740	700	140
February	East	147	200	100
	Central	309	264	100
	West	267	325	83
May	East	214	257	114
	Central	464	509	109
	West	380	470	100
July	East	230	230	110
	Central	442	450	92
	West	225	300	100
Mean (±s)	East	477 (±403)	454 (±371)	100 (±27)
	Central	438 (±153)	511 (±246)	110 (±27)
	West	541 (±309)	610 (±310)	99 (±31)

If there was any seasonal response to nitrogen (Fig. 2) it was a reduced response late in the dry season (February and May) when ambient nitrogen concentrations were low. This seasonal algae growth response was less evident in the central region. Although a large response occurred during the rainy season of July 1983 for all regions of the lake, no comparable response occurred in July of 1984. The responses of *A. bibraianus* and natural phytoplankton were not in good agreement with regard to seasonality. For example, in February, the *A. bibraianus* response was one of the lowest whereas the natural phytoplankton response was the greatest.

The fact that nitrogen was important in laboratory assays, but unimportant in the lake would not have been known without the natural population large container assays. During the six days of incubation under enhanced illumination conditions, changes in the phytoplankton occurred in both experimental and control bottles—each had significant increases in algal biomass. However, increases in the phosphorus- or micronutrient-augmented containers were similar to the controls (Table 5).

Table 4.—Percent growth response of natural phytoplankton relative to controls by the different treatments for three regions of Lake Chapala, México for three dates, 1984.

DATE	REGION	TREATMENT		
		NITROGEN	NITROGEN & PHOSPHORUS	PHOSPHORUS
February	East	800	700	133
	Central	467	767	67
	West	600	450	100
March	East	175	575	125
	Central	360	300	60
	West	625	700	150
June	East	281	262	90
	Central	188	206	88
	West	450	630	140
Mean (±s)	East	419 (±334)	512 (±226)	116 (±23)
	Central	338 (±115)	424 (±300)	72 (±14)
	West	558 (±95)	593 (±129)	130 (±26)

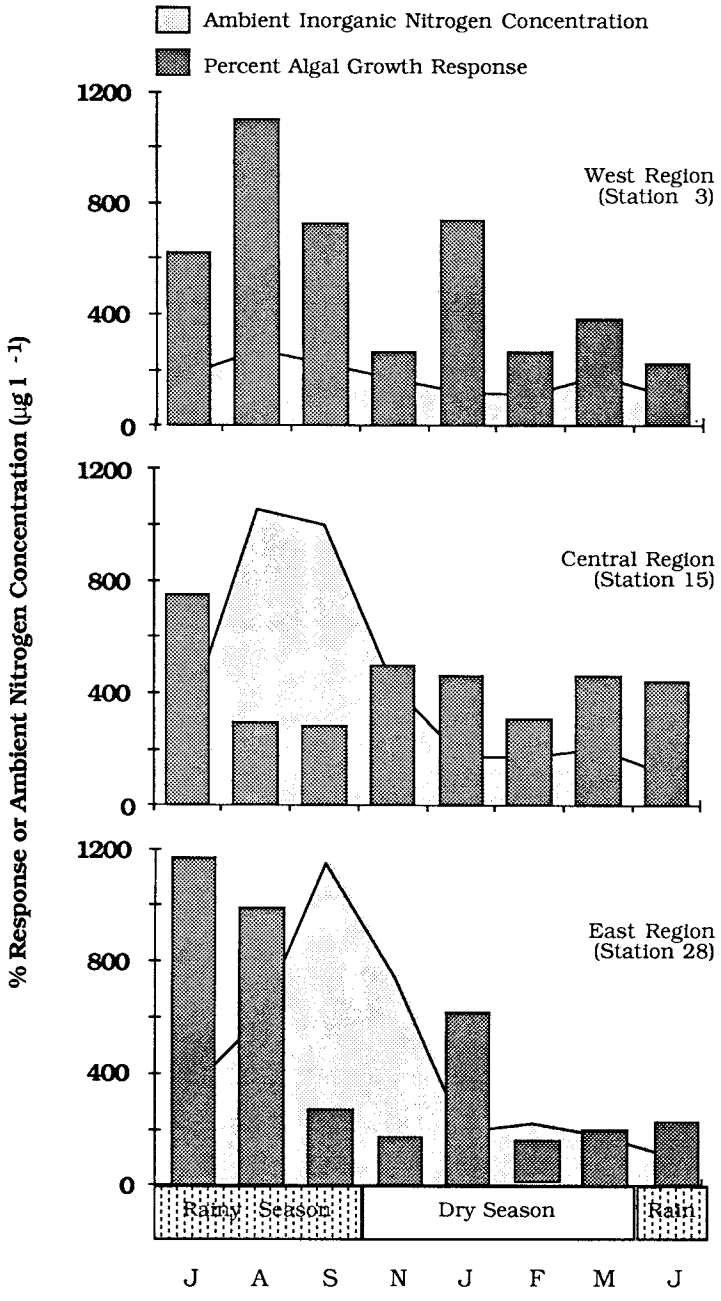

Figure 2.—Percent algal (Ankistrodesmus bibrianus) growth response (bars) relative to controls for additions of inorganic nitrogen by sampling station from July 1983 to July 1984. Ambient inorganic nitrogen concentrations are shown in the background. The rainy seasons are shown in the horizontal bar below the lower panel.

Adding either nitrate or ammonia nitrogen caused a significant increase over the controls. An important point is that the increased algal growth in the control bottles led to almost total exhaustion of inorganic nitrogen during incubation in all bottles – even those with supplemented nitrogen. In the controls, the ambient nitrogen concentration initially was relatively high. Given ambient nitrogen levels and additional light to overcome the turbidity present in the water, the natural populations were capable of significant growth – growth that was not realized in the lake because of light limitation. Thus, irrespective of *A. bibraianus* algal assays results, *in situ* nitrogen limitation for the Lake Chapala phytoplankton probably occurs rarely. One would expect nitrogen limitation only at the end of the dry season when ambient nitrogen concentrations are lowest. However, during this dry season, the water is at maximum turbidity caused by wind-driven resuspension of the sediments (Limón et al. 1989) and the phytoplankton are almost always light limited.

Nutrient concentrations are important to determining the water quality in lakes and reservoirs. Knowing the relative importance of the different potential growth limiting elements often is essential to the proper management of a lake. This knowledge is important both to the manager concerned with eutrophication problems and to the manger concerned with increasing biological productivity for human use. Thus lake surveys of ambient nutrient concentrations and/or evaluations by algal bioassays have become standard management practices. However, indiscriminate use of either type of information for Lake Chapala would have led to misinterpretation of the factors controlling algal growth. The extremely high nutrient concentrations should indicate severe eutrophication problems. The low nitrogen to phosphorus ratio should indicate nitrogen limited productivity – an indication clearly confirmed by the laboratory algal assay results. In this case watershed management practices to alter the inputs of nitrogen and phosphorous or in-lake practices to control their bioavailability would have little effect. However, in reality any management practices that lessened the lake's inorganic turbidity would have serious adverse consequences. Lake Chapala is unlike Lake Mead, where a close coupling existed between the lake's phosphorus and silt loads such that reducing silt sedimentation and increasing transparency depleted the lake of this essential nutrient (Axler et al. 1988). Approximately 90 percent of the phosphorus in Lake Chapala is soluble and free from the suspended clays (Limón et al. 1989). The "eutrophic" increase in algal biomass seen in the large container assays indicates what would happen to Lake Chapala following reduction in turbidity. If greater transparency occurred, findings show that control of nitrogen sources will be neces-

Table 5.—Percent growth response of natural phytoplankton community during a six day incubation period by the different treatments for the central region of Lake Chapala, México, and decline in concentration (μg/L) of inorganic nitrogen during this period.

	OCTOBER	NOVEMBER
Ammonia Nitrogen		
Growth response (%)	497	590
Initial NH_3-N	440	430
Final NH_3-N	43	26
Initial NO_3-N	420	150
Final NO_3-N	<10	23
Nitrate Nitrogen		
Growth response (%)	442	500
Initial NH_3-N	40	30
Final NH_3-N	36	37
Initial NO_3-N	820	550
Final NO_3-N	<10	185
Phosphorus		
Growth response (%)	223	213
Initial NH_3-N	40	30
Final NH_3-N	30	14
Initial NO_3-N	420	150
Final NO_3-N	<10	16
Micronutrients		
Growth response (%)	197	No data
Initial NH_3-N	40	
Final NH_3-N	32	
Initial NO_3-N	420	
Final NO_3-N	<10	
Control		
Growth response (%)	226	215
Initial NH_3-N	40	30
Final NH_3-N	35	14
Initial NO_3-N	420	150
Final NO_3-N	<10	20

sary to prevent eutrophication problems. Such control is difficult. Fortunately, nitrogen fixation by cyanobacteria does not occur in this lake (Glass, 1987). This lack of nitrogen fixation is currently unexplained. If it is resulting from a lack of photosynthetic energy for the energy-demanding process, then greater transparency may permit nitrogen fixation, and cyanobacterial blooms—with their other associated problems—may become a feature of this lake.

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