

PHYTOPLANKTON PRODUCTIVITY
OF
TROPICAL LAKE CHAPALA,
MEXICO

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ABSTRACT

Phytoplankton productivity and other environmental variables were measured for one year (June 1983 - June 1984) at five stations on Lake Chapala, Mexico. Contrary to expectations, productivity in this shallow, tropical lake was low. Phytoplankton productivity, estimated from ^{14}C data, was $76.4 \text{ g C m}^{-2} \text{ year}^{-1}$ ($209 \text{ mg C m}^{-2} \text{ day}^{-1}$). Phytoplankton productivity at the depth of optimum light intensity averaged $320 \text{ mg C m}^{-3} \text{ day}^{-1}$, and always occurred within the top 70 cm of the water column. Light extinction due to inorganic turbidity was the principal limiting factor of areal phytoplankton productivity. Nutrient limitation was less important, although nitrogen may have become limiting during the dry season. Among stations, areal phytoplankton productivity varied inversely with turbidity and was decidedly seasonal. It was highest during the rainy season (June - September), when the water was most transparent.

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INTRODUCTION

What are the consequences of low latitude on the limnology of lakes? The answer remains largely unresolved for many important aspects of phytoplankton ecology. For example, some feel that tropical lakes are universally more productive than their temperate counterparts (Lewis 1974). Brylinsky and Mann (1973) analyzed data from many lakes at different latitudes and found a significant negative correlation between annual phytoplankton production and latitude. Thus, they conclude that tropical lakes, which annually receive higher inputs of solar energy, have higher phytoplankton production. However, Schindler (1978a) and Hammer (1980) performed similar analyses and found no correlation between annual production and latitude.

It is generally regarded that phytoplankton populations in lakes at lower latitudes have less seasonal fluctuations than populations in temperate lakes (Ganf and Viner 1973, Goldman and Horne 1983, Robarts 1979). Melack (1979a) examined seasonal patterns of phytoplankton productivity and biomass for numerous lakes. He concludes that tropical phytoplankton populations are less variable seasonally, both

in terms of productivity and biomass. However, exceptions abound. Lake Tanganyika, a large tropical lake, has considerably more seasonal variation in phytoplankton biomass than most large temperate lakes (Hecky and Kling 1981).

Finally, tropical phytoplankton populations are often limited by nitrogen (e.g., Lewis 1974, Moss 1969, Talling 1965a, Wurtsbaugh et al. 1984), whereas temperate populations are usually limited by phosphorus (Wetzel 1983). These findings have reinforced the idea that tropical ecosystems are usually deficient in nitrogen (Odum and Pigeon 1970, cited by Goldman and Horne 1983, Viner 1975). However, further studies show that phosphorus significantly limits productivity in many tropical lakes and reservoirs (Kalff 1983). In fact, Schindler (1978a) showed that the phosphorus input models for temperate lakes also predict annual phytoplankton production in tropical lakes. Thornton and Walmsley (1982) had similar success using these phosphorus models in several African reservoirs.

Apparently, the only general agreement concerning tropical phytoplankton ecology is that more studies are needed. Serruya and Pollinger (1983) note that limnological studies of lakes at lower latitudes largely have been ignored until recently. This lack of information on tropical lakes impedes a synthetic understanding of their processes and dynamics.

This investigation examined the phytoplankton productivity and related environmental parameters of Lake Chapala, Mexico. Five stations were monitored from June 1983 to June 1984. There are no published data of primary production rates of Mexican lakes. A literature search of several data bases (BIOSIS, NTIS, SIE, Pollution Abstracts, Aquatic Science), found no publication of community or ecosystem level limnology for Mexico. This study helps fill a serious gap in our understanding of tropical lakes in general, and Mexican lakes in particular. The results are also interpreted in comparison to temperate lake dynamics.

My objectives in studying this tropical lake were threefold: (1) to determine the spatial and temporal variability of phytoplankton productivity, (2) to establish which environmental parameters most likely limit phytoplankton productivity, and (3) to mathematically model phytoplankton productivity in terms of such environmental variables as light penetration, nutrient concentration, phytoplankton biomass, and phytoplankton productivity at optimum light. This research tested three hypotheses:

- 1) Ho: Annual net phytoplankton production is the same at all stations on the lake
- 2) Ho: Daily phytoplankton productivity does not vary seasonally
- 3) Ho: Nitrogen availability is the limiting factor of phytoplankton productivity.

For the purposes of this paper, the following terms and abbreviations are defined:

Net phytoplankton production is the accumulation of organic material over a period. This does not include such losses as respiration, excretion, death, or grazing.

Phytoplankton productivity is the rate at which this organic matter is accumulating (Wetzel 1983).

Phytoplankton biomass is the weight of all living phytoplankton at a given time (Wetzel 1983).

In this study, biomass was always estimated by extraction of chlorophyll pigments.

NPP Net daily phytoplankton productivity
($\text{mg C m}^{-2} \text{ day}^{-1}$)

NPP(eu) Net daily phytoplankton productivity
within the euphotic zone ($\text{mg C m}^{-3} \text{ day}^{-1}$)

NPP(mix) Net phytoplankton productivity
within the entire mixing zone ($\text{mg C m}^{-3} \text{ day}^{-1}$)

NPP(max) Maximum net phytoplankton productivity
($\text{mg C m}^{-3} \text{ day}^{-1}$)

Z(eu) Euphotic depth. The depth of 1% of surface illumination.

Z(mix) Mixing depth. In the absence of any stable thermal stratification on Lake Chapala, the mixing depth was assumed to be equal to the lake depth.

LITERATURE REVIEW

Historic Perspective

The allegation of a poor understanding of tropical lakes is not new. Seventy-five years ago, Wesenbourg-Lund (1910, cited by Talling 1965b) called for immediate action to fill the deficiency in our knowledge of tropical freshwaters. Over the years, interest in tropical lakes has grown. Recently, the goal of the International Biological Program to measure global productivity stimulated work in tropical freshwater systems. One of the goals of its Freshwater Program was to systematically compare phytoplankton production of lakes at various latitudes (Rzoska 1980). Also, the 1980 Societal Internationalis Limnologiae (SIL) sponsored workshop on the Promotion of Limnology in Developing Countries held in Kyoto, Japan, dealt largely with tropical limnology (Mori and Ikusima 1980).

Even so, few tropical lakes have been studied comprehensively. Exceptions are Lake George, Uganda, and Lake Chad, Chad. Lake George was subject to comprehensive investigations by the Royal Society African Freshwater

Biological Team. Ganf (1972, 1974a, 1974b, 1974c, 1974d, 1975) investigated phytoplankton production. Others studied the zooplankton, fish, water chemistry, hydrology and zoobenthos. Burgis (1978) provides a bibliography of Lake George papers. Lake Chad was intensively investigated by a research team from the 'Office de la Recherche Scientifique et Technique Outre-mer' (ORSTOM). Carmouze et al. (1983) compiled contributions on all major aspects of this project and provide a comprehensive bibliography of work done on Lake Chad. Lemoalle (1983) studied phytoplankton production.

While the limnology of few tropical lakes has been as intensively investigated as that of Lake George or Lake Chad, information on phytoplankton production exists for many others. In Southeast Asia, for example, Lake Lanao, Philippines, was originally surveyed by Frey (1969). Later, Lewis made intensive investigations of the phytoplankton community (Lewis 1974, 1978a, 1978b).

African lakes studied include Lake Tanganyika (Coulter 1963, 1968, Hecky et al. 1981, Hecky and Fee 1981, Hecky and Kling 1981, Melack 1980), Lake Victoria (Talling 1966, Talling and Talling 1965), Lake McIlwaine (Robarts 1979, 1982, Robarts and Southall 1977), and many others (e.g., Belay and Wood 1984, Melack 1979b, Talling 1965a, Talling et al. 1973).

Phytoplankton production studies in the neotropics are less numerous. Some of the best information comes from the riverine lakes of the Amazon (Fisher 1979, Fittkau et al. 1975, Schmidt 1973a, 1973b, 1976, 1982, Sioli 1975, Zaret et al. 1981). However, the most comprehensively investigated lake is Lake Titicaca, Peru (Richerson et al. 1977, Carney 1984). Phytoplankton production studies on other South American lakes and reservoirs include those of Barbosa and Tundisi (1980), Hartman et al. (1981), Miller et al. (1984), Tundisi et al. (1978). Although a few limnological studies have been made in Central America (Deevey et al. 1980, Gliwicz 1976, Lewis and Weibezahn 1976, Loffler 1972, Vaux et al. 1984), few have attempted studies of phytoplankton productivity.

Published reports of tropical limnology are not only few, but also poorly organized. Many potentially important papers are scattered in various international and local journals. Serruya and Pollinger (1983) have compiled much of the published information for many tropical lakes. Their efforts were largely successful (Melack 1984a).

Mixing Patterns in Tropical Lakes

Probably the only all-embracing definition of a tropical lake is the geographic one: that it lies between the Tropics of Cancer and Capricorn. Included in that definition are warm, shallow lakes; large, deep ones; riverine lakes; and small, ice-bound lakes of high altitude, to name a few (Burgis 1978). All of these lakes are subject to high solar irradiance. In comparison with the temperate zone, this irradiance is almost invariant through time. This constant solar regime, as modified by lake depth, lake morphometry, and altitude each has important implications for the normal mixing patterns of tropical lakes.

Because of the relatively invariant solar regime, tropical lakes are characterized by small variations in temperature, both in vertical profile and from season to season (Hill and Rai 1982, Serruya and Pollinger 1983). This temperature is generally high, but the same holds true for the colder waters of high altitude tropical lakes (Serruya and Pollinger 1983, Taylor and Aquise 1984). This very small temperature difference in vertical profile, in conjunction with the insignificant influence of the Coriolis force at this latitude (Lewis 1973), results in the stratification of tropical lakes being significantly less stable than temperate ones (Hill and Rai 1982, Lewis 1973, 1974). This decreased stability makes wind mixing more

effective. Consequently, tropical lakes generally have deeper thermoclines than temperate ones (Lewis 1973, Serruya and Pollinger 1983). This deeper thermocline probably allows more regeneration in the epilimnion and retards nutrient losses to the hypolimnion (Hecky and Fee 1981).

Many tropical lakes are polymictic. A lake will be polymictic if it is deep enough to stratify, but not deep enough for the thermocline to be in equilibrium with the strongest winds of the stratification period (Lewis 1973). While this statement is equally true of tropical and temperate lakes, the greater depth of the thermocline makes polymixis more likely in the tropics.

Tropical lakes are more likely to have multiple thermoclines than temperate lakes (Lewis 1973). For example, in his work on Lake Victoria, Talling (1966) was able to document the existence of two thermoclines during part of the year. The upper one was subject to displacement by changing winds, while the lower one was more seasonally stable. Newell (1960) felt that the open water of this lake was stratified throughout the year into three layers. Baxter et al. (1965) report that several African lakes show two forms of thermoclines. One thermocline is always deep-seated and stable while the other is superficial and more ephemeral. Lake Valencia, Venezuela, also has several thermoclines during the stratification period (Lewis 1983).

Lewis (1973) described three distinct thermoclines on Lake Lanao, Philippines. Their depths correspond to the mixing depth of three types of meteorological disturbances. The first thermocline is weak and usually forms between 5-20 meters. Its depth is determined by the relative strength of the daily breezes. Frequent squalls destroy this "breeze thermocline" and establish or reinforce a deeper one between 20-30 meters. The "squall thermocline" is disrupted only by violent storms. These very strong winds establish the depth of the most stable or "storm thermocline" at about 40-60 meters. The layers often become chemically heterogeneous due to differing metabolic processes occurring in each layer. Lewis calls the mixing of these epilimnetic layers "atelomixis."

Tropical lakes also tend to undergo a diel cycle of stratification and de-stratification in the upper portion of the water column. This cycle consists of three stages. The first stage is early morning isothermy. Nevertheless, by mid-morning the upper layer begins to warm and become thermally isolated from the rest of the water column. The second stage of complete thermal stratification is usually well established by noon. During the third stage, the thermal stratification is destroyed. In the late afternoon or early evening, the upper mixed portion begins to cool and deepen. This process, often assisted by the onset of evening winds, soon re-establishes isothermy in the upper

layer of the lake. Practically identical cycles have been reported for a variety of African lakes (Ganf 1974d, Ganf and Horne 1974, Talling 1966, Baxter et al. 1965), riverine lakes of the Amazon (Hill and Rai 1982, MacIntyre and Melack 1984), lakes of high altitude (Powell et al. 1984), and Indian ponds (Saunders et al. 1975). In lakes too shallow to support stable thermoclines, this may be the only type of stratification evident. This phenomena is not limited to the tropics (e.g., Frempong 1983) or to freshwaters (Howe and Tait 1969, Strommel et al. 1969, cited by Powell et al. 1984). However, it seems to be of greater ecological importance in the tropics because it is often the major limnological cycle (Ganf and Horne 1974).

Tropical lakes have traditionally been classified according to the frequency of deep circulation into warm monomictic, polymictic, and oligomictic (Hutchinson 1957). While this classification scheme retains some usefulness, it has proved impossible to establish specific geographic bounds on these lake types (Lewis 1973). That is because a tropical lake's morphometry (e.g., Baxter et al. 1965), its exposure to wind (e.g., Macintyre and Melack 1984, Wood et al. 1976), and local aperiodic meteorological disturbances (e.g., Lewis 1973) become as important as the seasonal temperature changes in determining the specific circulation patterns (Serruya and Pollinger 1983).

A classification system incorporating these other factors has yet to be proposed. Therefore, I will simply review the thermal characteristics of some of the more common lake types found in the tropics.

Shallow Lakes and Ponds These lakes are characterized by being too shallow to develop a thermocline that is stable for extended periods (Baxter et al. 1965). Most of these lakes have diel thermal patterns (Serruya and Pollinger 1983). That is, they undergo a diel cycle of stratification and de-stratification. Lake George (Ganf and Horne 1974), Lake Chad (Carmouze et al. 1983), and some ponds of India (Saunders et al. 1975) are examples of lakes showing this pattern. Because there are no seasonal patterns of stratification, hydrological changes are often important in determining seasonal limnological cycles (e.g., lake Chad). However, in cases of invariant hydrological regimes, lakes may show a surprising degree of ecological stability (Ganf and Viner 1973).

Deeper Lakes These lakes are characterized by stable thermoclines. While lake depth is critical, it is not the only important factor in determining whether a lake will stratify for extended periods. Two lakes of identical depths may or may not show a seasonally stable thermocline depending upon the lake's shape and exposure to wind (Baxter et al. 1965). Lakes with a stable thermocline may be

classified into warm monomictic, oligomictic, or meromictic, depending upon whether circulation occurs annually, rarely, or never.

Most tropical lakes are warm monomictic (Talling 1969). This means that the lake mixes only one time each year at a temperature above 4 C. However, the annual cycle of stratification is generally controlled not by solar radiation and temperature, but by rainfall and wind patterns (Burgis 1978, Talling 1969). Examples of such lakes includes Lake Lanao, Philippines, (Lewis 1973) and Lake Victoria, East Africa, (Talling 1966).

Other tropical lakes are oligomictic. That is, circulation occurs irregularly at long intervals. Few good examples of such lakes exist, although Lake Pawlo, Ethiopia, is probably one (Baxter et al. 1965).

Finally, some of the very deep tropical lakes never completely mix. These lakes have both a seasonal thermocline and a deeper, permanent one below which the water is always anoxic (Serruya and Pollinger 1983). Examples include Lake Malawi (Eccles 1974), Lake Tanganyika (Coulter 1968), and Lake Kivu (Damas 1937, cited by Serruya and Pollinger 1983, Degens et al. 1971 cited by Serruya and Pollinger 1983). Evidence suggests, however, that some exchange occurs between the seasonally mixed layers and the permanent anoxic zone, although the mechanism of the

exchange is not understood (Serruya and Pollinger 1983).

High Altitude Lakes Tropical lakes of high altitude have both low temperature and small vertical thermal gradients. They are, therefore, the least stable of all tropical lakes (Serruya and Pollinger 1983). Löffler (1972) distinguishes between two types of high altitude tropical lakes. The "Paramos" type is found in the wet high mountains where the diel variation in temperature is very small. The "Puna" type is located in dry mountain areas and is characterized by relatively large diel temperature fluctuations. The Paramos, with their low and constant temperatures, are especially unstable and subject to frequent mixing. The Puna type has a more distinct pattern of stratification.

Floodplain Lakes Associated with the major rivers in the tropics are numerous floodplain lakes. In the Amazon basin, these lakes are generally less than 15m deep and most have permanent connections to the river. The most important limnological event in these lakes is the annual 10 m fluctuation in water level (Hill and Rai 1982, Rai and Hill 1980, Schmidt 1972, 1973b).

These lakes stratify on both a seasonal and diel basis (Hill and Rai 1982). Diel stratification of the surface waters can be observed most of the year (Schmidt 1973a,

Melack and Fisher 1983). However, the frequency of holomixis varies with the changing water levels (MacIntyre and Melack 1984). During the low water period the lakes do not have stable thermoclines, although diel stratification and de-stratification is common. With rising waters, the lakes stratify on a more permanent basis. This stratification usually sets in when the lake becomes more than 5 to 6 m deep (Macintyre and Melack 1984, Melack and Fisher 1983, Tundisi et al. 1984). However, even during this period of more persistent stratification, the thermocline is fairly unstable (Hill and Rai 1982). Therefore, individual lakes, or given areas within larger lakes, may deviate from this normal pattern, depending on their shape and relative exposure to wind (Melack 1984b, Melack and Fisher 1983).

Horizontal Variability in Phytoplankton Productivity and Biomass

Lakes are often horizontally heterogeneous in phytoplankton productivity and biomass. The differences may be due to patterns imposed by water currents, winds, or predation (Wetzel 1983). For example, the phytoplankton and zooplankton of Lake George are usually arranged in concentric circles with the greatest density at the very center of the lake. This pattern seems to be caused by circular water currents in the lake (Ganf 1974b), although

heavy grazing by planktivorous fish near the shore may also be important (Burgis et al. 1973). Zooplankton predation may affect horizontal distributions as well. In Lake Naivasha, Kenya, differences of up to 100% between stations along a single transect are apparently related to different predation pressures by Daphnia pulex (Harper 1984). Finally, the unusually high horizontal variation in phytoplankton biomass in Hartbeespoort Dam, South Africa, is attributed to local wind patterns (Robarts 1984).

Horizontal variations might also be caused by localized differences in the nutrient concentrations or underwater light climate. These differences often result in particularly good environments for phytoplankton growth (Fisher and Parsley 1979). Inflowing rivers sometimes bring in large amounts of nutrients, which stimulate phytoplankton growth (e.g., Melack 1979b). In extreme cases, the areas receiving these nutrient inputs may be properly classified as eutrophic, although the rest of the lake is oligotrophic (Henry et al. 1984). Lakes which receive water from several rivers that drain different types of soils may show dramatic heterogeneity in water chemistry and in the phytoplankton community (Brinson and Nordlie 1975).

The littoral zone also may be nutrient rich with respect to the rest of the lake. This enrichment may be due to resuspension of nutrients from wind or wave action, or to release of nutrients by rooted macrophytes (Howard-Williams

and Lenton 1975). In tropical lakes which experience drastic fluctuations in water level due to the pronounced cycle of wet and dry seasons, another type of near shore enrichment may be important. During the dry season, the shoreline can be enriched with nutrients by an accumulation of plant material and animal dung. Upon the flooding of this area during the rainy season, the nutrients are released into the lake (Gaudet and Muthuri 1981, MacLachlan 1971).

While areas near river inflows often are rich in nutrients, they also may be turbid, and therefore, poor habitats for phytoplankton growth. Such is apparently the case in a number of South African reservoirs (Walmsley 1978) and in Lake Izabel, Guatemala, (Brinson and Nordlie 1975). The littoral zone is also sometimes more turbid than the rest of the lake (e.g., Melack 1980), presumably due to increased resuspension of sediments.

Morphometric differences from one area of the lake to another may cause horizontal variability in phytoplankton biomass (Wetzel 1983). An excellent example is Lake Chad, where four morphologically distinct areas of the lake show marked differences in phytoplankton productivity, biomass, and species composition (Carmouze et al. 1983, Lemoalle 1983). In Lake Tanganyika, different basins have different mixing depths. This has been used to explain the spatial variability of phytoplankton biomass on this lake (Hecky and

Kling 1981).

While no concrete examples seem to exist, horizontal variations may also result from localized breakdown in a lake's stratification. Such destratifications might be due to localized cooling (Baxter et al. 1965) or localized wind action on more exposed areas of the lake (Melack 1984b).

Temporal Variability in Phytoplankton Productivity and Biomass

There are very few exclusively tropical species of phytoplankton (Kalff and Watson 1984). Therefore, one should not expect tropical phytoplankton populations to differ markedly from temperate ones in their response to changes in environmental factors. Phytoplankton, whether from a tropical or temperate lake, may generally be regarded as being principally limited by two resources: sunlight and nutrients (Lewis 1974). Changes in these resources will produce changes in the phytoplankton population. Such changes may occur on aperiodic, diel, or seasonal bases.

Diel Variations As one moves from higher to lower latitude, the predominant limnological cycles tend to be short (Ganf and Horne 1974). In the tropics, seasonal cycles are often muted and diel cycles are more important (Ganf 1974b, 1975, Goldman and Horne 1983). Because

tropical lakes have little variation in solar irradiance or temperature throughout the year, other factors such as wind and rain usually dominate the limnological cycles. In lakes where even these variables are constant, the entire range of environmental variations may occur during one day. In some lakes, the characteristic annual pattern of lake stratification is compressed into 24 hr (Burgis 1978, Ganf and Horne 1974). Lake George clearly exemplifies three major consequences of this diel pattern of stratification (Ganf 1975, Ganf and Viner 1973).

First, diel stratification may lead to very complex patterns of phytoplankton distribution within the water column. On Lake George, the phytoplankton are usually evenly distributed in the early morning. However, with the onset of stratification, complex vertical patterns are soon evident (Ganf 1974b). The changing vertical patterns through the day, and the large changes seen from day to day, make an accurate estimate of phytoplankton productivity impossible (Ganf 1975).

Second, this diel pattern of stratification may result in an unusually stable species composition. In most temperate lakes, the length of the predominant limnological cycle is usually much greater than the mean generation time of the phytoplankton. This allows sufficient time for the species composition to change with changing environmental factors. On Lake George, the diel cycle, which is the

dominant limnological cycle, is less than the generation time of most species. Therefore, it's unlikely that the species composition of the lake will change unless the diel cycle is disrupted for a long enough period to allow the phytoplankton to respond to that change (Ganf and Horne 1974). The high biotic stability in Lake George has been noted by many (Ganf 1975, Ganf and Viner 1973, Burgis et al. 1973, Burgis and Walker 1972).

A third consequence of complete daily mixing is the absence of an anoxic hypolimnion. Under aerobic conditions, the exchange equilibrium of nutrients between the water column and the oxidized sediments is largely unidirectional towards the sediments (Wetzel 1983). Therefore, the sediments of these lakes function as nutrient sinks.

Aperiodic Variation Many tropical lakes are polymictic (see above). That is, they stratify and mix several times a year. The breakdown and reforming of this thermocline has important ecological consequences. In some lakes, mixing may significantly alter the light climate of the phytoplankton. An important parameter in determining the underwater light climate is the ratio of $Z(\text{mix})$ to $Z(\text{eu})$ (Talling 1971, see below). A sudden change in $Z(\text{mix})$ by the formation or destruction of a thermocline will obviously change this ratio. This change may impose light limitation upon a community previously not light limited, or release a

community from light limitation (e.g., Melack and Kilham 1974).

In cases where the stratification persists long enough for an anoxic hypolimnion to develop, mixing will result in injection of nutrients such as phosphorus or nitrogen into the epilimnion (Melack and Fisher 1983). Lewis (1973) points out that complete anoxia is not necessary for aperiodic mixing to be important. Atelomixis, the mixing of chemically non-homogeneous layers of a lake, can result in significant changes in the chemical composition of the epilimnion.

Seasonal Variation The idea that tropical ecosystems are more seasonally stable than temperate ones has become almost axiomatic. However, some evidence shows that while tropical environments are indeed more stable, tropical populations are not (Leigh 1975). Although data upon which to make comparisons are limited, tropical populations of insects (Wolda 1978), birds (Fogden 1972, Karr 1976), herbivorous mammals (Leigh 1975), and arthropods (Tanaka and Tanaka 1982) appear to undergo seasonal fluctuations in number comparable to temperate populations. These cycles are generally associated with changes in rainfall rather than changes in solar radiation or temperature.

What about phytoplankton populations in tropical lakes? Solar radiation is of critical importance in determining the dynamics of freshwater systems. It not only is the direct supply of energy for photosynthesis, but also the indirect determinant of water temperature, thermal stratification, and all associated chemical changes (Talling 1969, Wetzel 1983). In temperate lakes, the seasonal changes in the limnology of a lake are usually dominated by seasonal changes in solar irradiance and temperature (Goldman and Horne 1983). In tropical lakes, solar irradiance varies little throughout the year and, in most lakes, the temperature never falls to physiologically inhibiting levels (Burgis 1978). Are the phytoplankton populations of such lakes more seasonally stable than temperate ones? The answer seems to be a qualified yes.

As one leaves the temperate zone and moves towards the equator, seasonal fluctuations in the limnology of lakes tend to be muted (Ganf and Horne 1974, Goldman and Horne 1983, Hill and Rai 1982). However, in only a few lakes, such as Lake George (Ganf and Viner 1973) and Lake Titicaca (Richerson et al. 1984), are seasonal fluctuations of little or no importance. Talling (1965b) cautions that, while fluctuations in phytoplankton biomass and productivity of tropical lakes are often small, they are usually seasonal. It is therefore important to interpret data in terms of the overall seasonal patterns.

Melack (1979a) has statistically examined data from a number of tropical, temperate, and arctic lakes in order to discern general patterns of temporal variability of phytoplankton productivity and biomass which may be attributed to latitudinal differences. He found that tropical lakes, as a whole, are significantly less variable than temperate ones. However, there is no latitudinal trend evident among tropical lakes. That is, equatorial lakes are no more stable than other tropical lakes.

Melack (1979a) also proposed three patterns for temporal change in abundance and/or photosynthetic rates of tropical phytoplankton populations. These patterns are based on the annual coefficient of variation (CV, standard deviation as a percentage of the mean) for phytoplankton productivity or biomass. The first and most common pattern, consists of lakes whose phytoplankton populations show decided seasonal fluctuations. These fluctuations generally correspond to changes in environmental parameters such as rainfall, river flow, or vertical mixing patterns within a lake. These populations have a CV greater than 25%. The second pattern consists of lakes whose phytoplankton populations show little seasonal variability. They have CV's less than 20%. In these lakes the diel variations are often as great as the seasonal ones. The last pattern is characterized by a few lakes whose phytoplankton populations made abrupt changes from one persistent assemblage to

another.

Talling (1984) has summarized what is now known about phytoplankton seasonality in four types of African lakes and what underlying mechanism could be responsible for the observed patterns. First, African lakes at higher latitudes often function much like temperate ones in that seasonal patterns of phytoplankton productivity or biomass accompany annual cycles in temperature and solar irradiance. Second, the patterns found in deep tropical lakes are often more closely associated with changes in thermal stratification, which, in turn, are often dependent upon seasonal wind patterns. Third, patterns on shallow tropical lakes which do not stratify seasonally are often dominated by hydrological changes. These changes may affect phytoplankton productivity by altering turbidity, nutrient inputs, or water retention time. Finally, shallow tropical lakes with invariant hydrological regimes can be exceptionally stable and show practically no seasonal variations.

To understand the seasonal patterns, it is instructive to think of the phytoplankton being in a dynamic equilibrium with such essential factors as light and nutrients. A major change in any one factor will have a significant effect on the whole community.

As noted above, changes in phytoplankton biomass are often associated with the seasonality of rainfall, river discharge, and vertical mixing. However, the specific mechanism by which these changes affect the phytoplankton is quite varied. For example, the onset of the rainy season often affects phytoplankton biomass or productivity (e.g., de Emiliani and Depetris 1982, Rai 1978). A positive correlation is often explained by increased nutrient loading to lakes (Fittkau et al. 1975, Ganesella-Galvao 1985, Hammer 1981, Henry et al. 1984, Melack 1979b, Rai and Hill 1980). Other studies show that the rainy season is a time of greater water transparency (Cheng and Tyler 1976, Hare and Carter 1984), which may be of importance in light limited systems. Increased transparency is apparently the reason for high areal productivity in some Amazonian lakes during the flood stage (Schmidt 1973b).

However, the increased river flow characteristic of the rainy period may cause a decrease in phytoplankton productivity or biomass by increasing the turbidity (Duthrie and Stout 1984, Fisher 1979, Hartman et al. 1981, Talling and Rzořka 1967). In the riverine lakes of the Amazon, the nutrient-rich flood waters serve first to lower productivity due to increased turbidity. However, once the suspended sediments settle out, productivity and biomass increase dramatically (Fisher and Parsley 1979, Forsberg 1984).

The phytoplankton of some tropical lakes undergo seasonal fluctuations due to the changing conditions associated with wind patterns (e.g., Robarts 1984). During windy periods, stratified lakes often become isothermal and redistribute nutrients from the hypolimnion or sediments to the entire water column. This is often followed by increased productivity (Coulter 1968, Hecky and Kling 1981, Melack and Fisher 1983, Tundisi and Tundisi 1984, Tundisi et al. 1978). On other lakes, windy periods are the times of least productivity due to the high turbidity stirred up from the sediments (Gianesella-Galvao 1985, Walker and Tyler 1984).

Production Models

In an effort to simplify the estimation of phytoplankton production, many authors have offered mathematical models relating phytoplankton production to one or more biologically meaningful variables (Baly 1935, cited by Iwakuma and Yasuno 1983, Cabrera and Montecino 1984, Fee 1973, Ryther 1956, Ryther and Yentsch 1957, Steel 1962, Talling 1957). Some variables which have been used are incident solar irradiation, underwater light penetration, phytoplankton production at optimum light intensity, mixing depth, and phytoplankton biomass.

Reviews of these and other models are provided by Jassby and Platt (1976), Talling (1971), and Vollenweider (1965). However, because these models are often derived from experimental observations from narrow ranges of ecological habitats, they should be critically examined under varied environmental conditions before widespread acceptance (Ganf 1974c). Iwakuma and Yasuno (1983) and Jassby and Platt (1976) attempt to verify some of these models by testing them against data collected for Lake Kasumigaura, Japan, and off the coast of Nova Scotia, respectively. Lemoalle (1983) verifies that phytoplankton production data from Lake Chad is described well by the model proposed by Talling (1957).

Factors Controlling Phytoplankton Production and Biomass

The concept of a single factor regulating or limiting phytoplankton growth is best defined by Liebig's law of the minimum (Liebig 1849). This law simply states that the essential factor which is found in the lowest amount relative to need, will limit the growth of an organism. In limnology, this concept has led to a vast number of studies to try to identify which factor most commonly limits phytoplankton growth. This work has centered around the availability of necessary macro- and micronutrients and assumes that physical environmental factors such as light and temperature are at acceptable levels. In tropical

systems, solar radiation and temperature are rarely found to limit phytoplankton growth (Lund 1965, cited by Moss 1969).

While, theoretically, any essential nutrient could become limiting, phosphorus is usually the one found in such critical supply (Goldman and Horne 1983, Hutchinson 1957, Wetzel 1983). Studies in the temperate zone show that annual phosphorus loading or environmental concentrations of phosphorus can be used to predict phytoplankton biomass in lakes (Dillon and Rigler 1974, Schindler 1978b, Vollenweider 1968, cited by Wetzel 1983). Some evidence suggests that this same relationship may not be true in many tropical systems. Studies by Talling (1966) and Talling and Rzoska (1967) suggest that nitrogen is limiting in the African lakes they studied. Other studies of tropical lakes also show nitrogen to be limiting (Henry et al. 1984, Lewis 1974, Moss 1969, Wurtsbaugh et al. 1984, Zaret et al. 1981). Talling (1965a) suggests that nitrogen may limit phytoplankton growth in African lakes due to the low levels of inorganic nitrogen relative to phosphorus. Because phytoplankton tissues contain, by weight, about seven times more nitrogen than phosphorus in their tissues (Vallentyne 1974, cited by Wetzel 1983), environmental concentration ratios less than this are thought to indicate that nitrogen may become limiting before phosphorus.

The mechanisms controlling the ratio of available nitrogen to phosphorus are not well understood. In areas not impacted by humans, phosphorus becomes available to phytoplankton primarily through the physical weathering of rocks. Nitrogen, on the other hand, becomes available through nitrogen fixation by prokaryotic organisms. Nitrogen fixation may occur in the lake itself by blue green algae or by bacteria in the soil around the lake, and be washed in by rains (Wetzel 1983). Apparently, the biotic process of nitrogen fixation occurs at a relatively faster rate than the release of phosphorus because most freshwater systems are phosphorus limited (Goldman and Horne 1983). However, some non-forested tropical areas seem to provide an exception to the generalization of phosphorus limitation. There the soils are usually poor in nitrogen. This lack of nitrogen may be due to nitrogen being washed from the soil during the heavy rains, or to an apparent paucity of nitrogen fixation. Also, because of the high temperature, these soils are subject to high rates of denitrification. The result is that tropical lakes often have low N:P ratios (Golterman and Kouwe 1980, see also Talling and Talling 1965, Talling 1966, Moss and Moss 1969, Sioli 1975). A clear example of the influence of the watershed soils upon phytoplankton productivity is seen in the riverine lakes of the Amazon. Lakes, that have watersheds with soils having low nitrogen to phosphorus ratios, are nitrogen limited. Those with soils having higher ratios are phosphorus limited

(Zaret et al. 1981).

Nitrogen is certainly not universally limiting in tropical freshwaters. Studies show phosphorus to be the primary limiting factor in several lakes (Dufour et al. 1981, cited by Kalff 1983, Hammer 1981, Melack et al. 1982, Peters and MacIntyre 1976). Kalff (1983) concludes that phosphorus, not nitrogen, most commonly limits phytoplankton production in Africa. Furthermore, he shows that phosphorus and chlorophyll data from two lakes fit the model developed for temperate systems by Dillon and Rigler (1974). Schindler (1978a) concludes that phosphorus input models developed in the temperate zone can be extended to lakes of all latitudes. That is, he found a significant correlation between annual phytoplankton production and annual phosphorus loading for tropical lakes.

Techniques for determining nutrient limitation of phytoplankton production are varied. Most involve some type of bioassay utilizing either a standard test organism such as Selenastrum capricornutum (United States Environmental Protection Agency 1978, Maloney et al. 1972), or natural phytoplankton populations (Komarkova 1979, Schelske et al. 1972, Setaro and Melack 1984). However, under some conditions, phytoplankton bioassays may be substituted by measurements of environmental nutrient concentrations. If a nutrient is present in measurable concentration it most likely does not limit phytoplankton growth (Schelske et al.

1978). Marvan et al. (1979) provide a review of bioassays for monitoring phytoplankton production.

Light is of obvious importance to any photosynthetic organism. Because light does not fall evenly at all latitudes, one might expect some correlation between latitude and phytoplankton production. Brylinsky and Mann (1973) have shown that such a relationship exists. They found that, on a global basis, a significant amount of the variation in annual phytoplankton production can be explained by latitudinal differences. Tropical lakes, which annually receive more solar energy, tend to be more productive. However, Hammer (1980), in making similar analyses, found no correlation between annual production and latitude. They conclude that, while the temperature and irradiance levels in the tropics favor high phytoplankton production, it is often not realized due to poor nutrient supply or excessive turbidity. In the end, if a correlation does exist between annual production and latitude, it may be due to higher nutrient inputs, not to higher solar irradiance. While the data available for such analysis are limited, it appears that annual nutrient inputs are negatively correlated with latitude (Schindler 1978a).

While latitudinal trends in phytoplankton production may correlate with solar irradiance, in any given lake the light regime actually experienced by the phytoplankton cells is the critical factor. Talling (1971) has described three

variables which modify the light conditions in a column of water: changes in surface irradiance, light penetration into the lake, and the ratio of $Z(\text{mix})$ to $Z(\text{eu})$.

Surface irradiance may vary due to changes in day length or cloud cover. In tropical systems, solar irradiance becomes limiting only in cases of extreme cloud cover during much of the year. For example, the persistent cloud cover over the rainforest of Ecuador limits the phytoplankton production of those lakes (Miller et al. 1984). Light limitation by cloud cover may be a general phenomena for Amazonian lakes, at least during part of the year (Hill and Rai 1982).

The reduction of light with depth is due to the absorption or scattering of light. Absorption may be due to the water itself, dissolved organic compounds in the water, or phytoplankton cells. Most scattering of light is due to suspended inorganics (Wetzel 1983). Lake George is a good example of a lake in which the high light attenuation is due to dense phytoplankton populations. Although nutrient levels are low (Viner 1973), the phytoplankton population is thought to be light limited due to extreme self-shading (Ganf 1974c). Talling et al. (1973) found very high photosynthetic rates in the soda lakes of Ethiopia. They considered this to be near the maximum possible under natural conditions, in view of the self-shading effect of dense phytoplankton populations.

Some tropical lakes may have very high light attenuation due to suspended sediments. Such lakes include Lake Chad (Lemoalle 1983), Lake Tapacura, Brazil, (Hartman et al. 1981), Lake Crescent, Tasmania, (Cheng and Tyler 1976), several small lakes in Australia (Walker and Tyler 1984), some Rift Valley lakes of Ethiopia (Wood et al. 1979), and a few South African reservoirs (Walmsley 1978). In some Amazonian lakes, the high light attenuation is due to organic stains (Miller et al. 1984, Schmidt 1976, Rai and Hill 1981). In any case, the inability of light to penetrate through the water column may limit further phytoplankton growth. Murphy (1962) notes that increasing non-phytoplankton turbidity drastically reduces net phytoplankton productivity by decreasing the efficiency of an individual photosynthesizer.

How the ratio of $Z(\text{mix})$ to $Z(\text{eu})$ can affect the underwater light regime is less obvious. An increase in this ratio lowers net phytoplankton production by first "diluting" the production over a deeper population, and, second, by increasing respiratory losses (Talling 1971). Respiratory losses increase due to the proportionally greater time a phytoplankton cell spends in the aphotic part of the water column (Murphy 1962). The high ratio of $Z(\text{mix})$ to $Z(\text{eu})$ explains the very low productivity of some Ethiopian Rift Valley lakes (Belay and Wood 1984).

Because tropical lakes generally have deeper thermoclines than temperate lakes (Lewis 1973, see above), the ratio of $Z(\text{mix})$ to $Z(\text{eu})$ will probably be greater. If so, tropical lakes may tend to be more light limited than temperate ones.

DESCRIPTION OF STUDY AREA

Lake Chapala was selected for this study of phytoplankton productivity in a tropical lake for two reasons. The first was because of its great economic importance to Mexico. The results of this study would be of immediate practical help to the Mexican government in formulating future management principles. The second was because the basic physical and chemical limnology of this lake are relatively well known.

Economic Importance

Lake Chapala, located 20 km southeast of Guadalajara, is the largest lake of Mexico. Its socio-economic importance to the region is difficult to overstate. The lake supplies 85% of the domestic and industrial water needs of Guadalajara, Mexico's second largest city with a metropolitan population of 3.3 million (Simons 1984). It also contributes to the regional economy through a large commercial fishery, irrigation, and as a principal tourist attraction (Chavez 1973, Simons 1984, Anon 1981). In a report concerning Lake Chapala's water quality in relation

to nearby municipalities, Amezcua recently estimated that some 7.5 million people depend directly upon the Rio Lerma-Lake Chapala-Rio Santiago water system (Amezcua n.d. [1978?])

The Mexican government, realizing the importance of this lake, organized the Comision Lerma-Chapala-Santiago in 1953 to begin gathering information on the lake's water quality. These activities were greatly expanded in 1972 with the creation of the Centro de Estudios Limnologicos (CEL) within the Secretaria de Agricultura y Recursos Hidraulicos (SARH). CEL is the national center for limnological studies and its principal responsibility is to maintain a monitoring program of Lake Chapala. For this reason, knowledge of the basic physical and chemical limnology of this lake is good relative to that of other lakes and reservoirs of Mexico. However, most of this information is found in unpublished reports.

Geology, Geography, and Climate

Lake Chapala (Figure 1) is located at 20 07' N and 102 25' W at an altitude of 1521 m above mean sea level. It is formed in a massive graben and is thought to be the remains of an extensive system of tertiary lakes. The soil is derived primarily from volcanic ash and is generally poor in nutrients (Anon 1981).

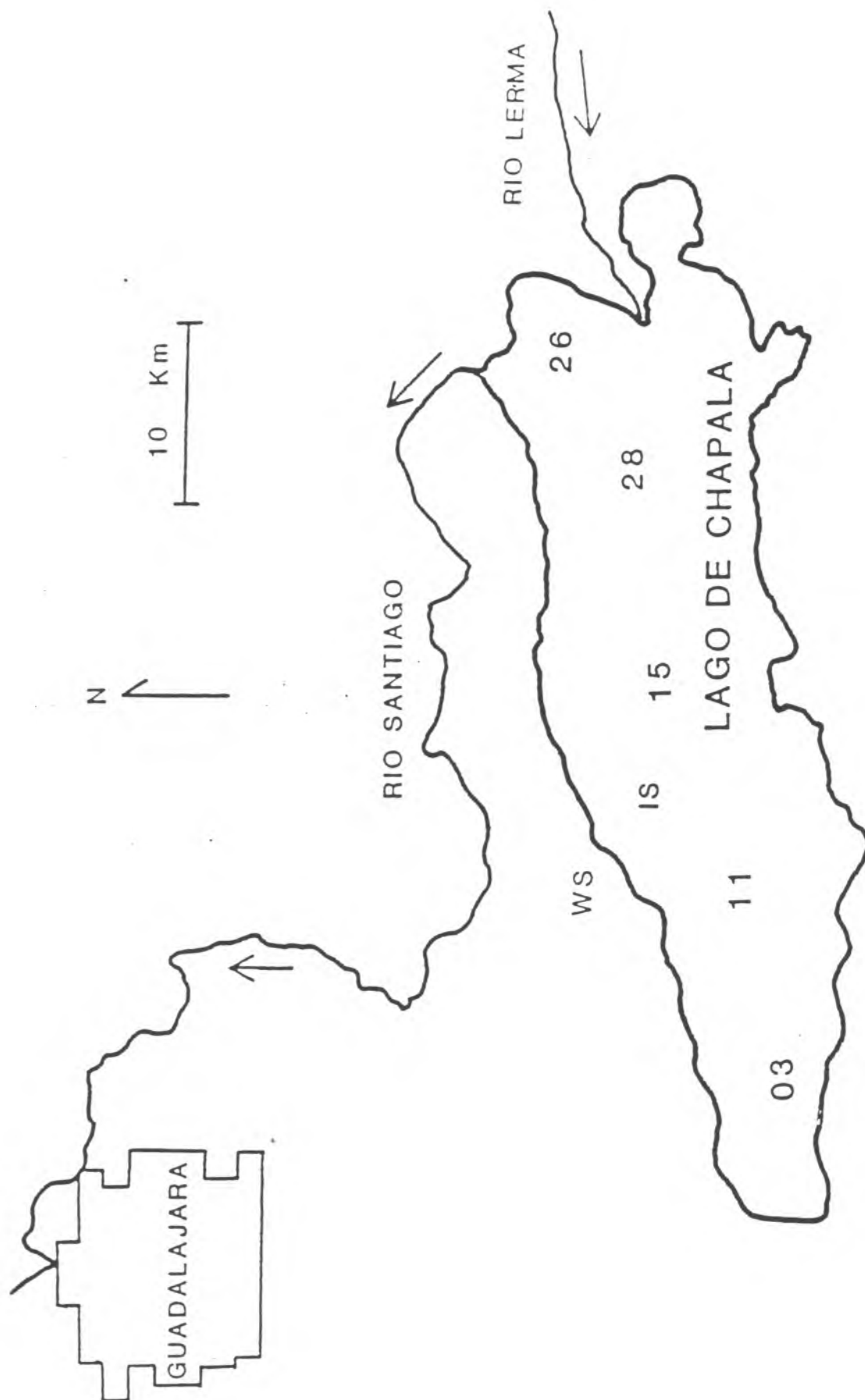


Figure 1. Location of the five sampling stations (03, 11, 15, 28, and 26) as well as the incubation station (IS) and on-shore work station (WS) on Lake Chapala.

The climate is mild and characterized by a four month rainy season between June and October, followed by a cool, dry winter. This rainy season accounts for 85% of the annual rainfall. Annual mean air temperature is 20 C with a range of 16.0 to 23.0 (Anon 1981). Dominant winds blow from the east for about eight months from the south or west at other times. These winds are often quite strong (Chavez 1973, Comision Lerma-Chapala-Santiago 1965, deBuen 1945).

Morphology and Hydrology

Lake Chapala is very large and very shallow. Principal morphologic and hydrologic characteristics of the lake are presented in Table 1. Figure 2 gives the relationship between water level, area, and volume.

The mean water balance for 1935-1970 (Table 1) shows that water losses due to evaporation were approximately balanced by water gains from precipitation plus direct runoff. Likewise, the Rio Lerma inflow was balanced by the Rio Santiago outflow (Limon and Quijano 1982). However, the more recent water balance of 1978-1983 is drastically different from that given above. For these years, water losses from evaporation have not been balanced by gains in precipitation and direct runoff. The result has been a significant reduction of total volume and surface area of the lake (Simons 1984).

Table 1. Principal morphometric and hydrologic characteristics of Lake Chapala.

I.	Location:	Latitude - 20 15" N
		Longitude - 103 W
		Elevation - 1525 m AMSL
		Mean temperature - 20.0 C
II.	Morphology:	Area - 1112 km ²
		Max. length - 76.6 km
		Max. width - 22.5 km
		Max. depth - 13.0 m
		Mean depth - 7.2 m
III.	Hydrology: *	Drainage area - 52,500 km ²
		Annual rainfall - 770 mm
		Water balance -
		Contributions
		Rio Lerma 49.11 (50%)
		Surface rainfall 25.81 (27%)
		Direct runoff 21.98 (23%)
		Extractions
		Rio Santiago 39.78 (42%)
		Evaporation 45.03 (47%)
		Other losses 10.85 (11%)

* = mean 1935 - 1970. Water balance is reported in units of m³ sec⁻¹ After Limon and Quijano (1982) and Simons (1984).

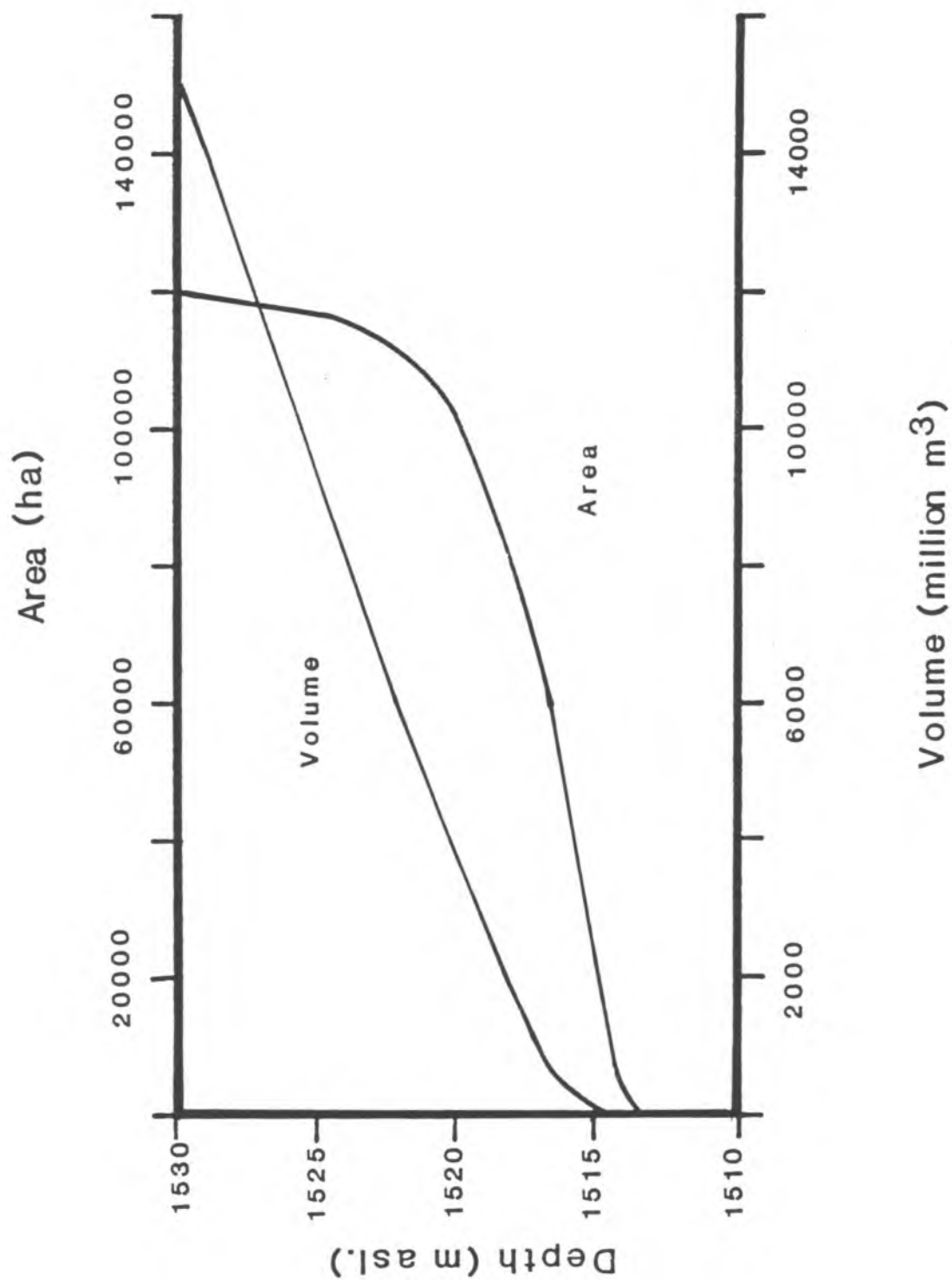


Figure 2. Relationship of depth, volume, and area on Lake Chapala

Although the lake's only major inflow and outflow are both at the East end (Figure 1), water flowing in from the Rio Lerma does not flow directly out the Rio Santiago. Instead, strong winds circulate the water to the rest of the lake (Figure 3) (Simons 1984). As might be expected from this circulation pattern, the lake is quite homogeneous during most of the year. However, during the rainy season, the east end is significantly different from the rest of the lake in terms of ambient concentrations of tritium and oxygen-18. This is probably due to the huge pulse of water flowing in from the Rio Lerma (Limon and Quijano 1982). About 77% of the Rio Lerma's annual input into the lake occurs during this rainy period (Simons 1984).

Limnology

Physical Limnology There are two profound consequences to Lake Chapala's shallow depth and constant exposure to the wind. The first is that the lake is not thermally stratified (Chavez 1983, deBuen 1945, Universidad Nacional Autonoma de Mexico 1974). Unpublished data provided by CEL confirms this reported thermal homogeneity and shows that it is equally true of dissolved oxygen and all forms of phosphorus and nitrogen. There are also no vertical differences in the concentrations of tritium or oxygen-18 (Limon and Quijano 1982). Ortiz (personal communication), in studying the benthic fauna, found no

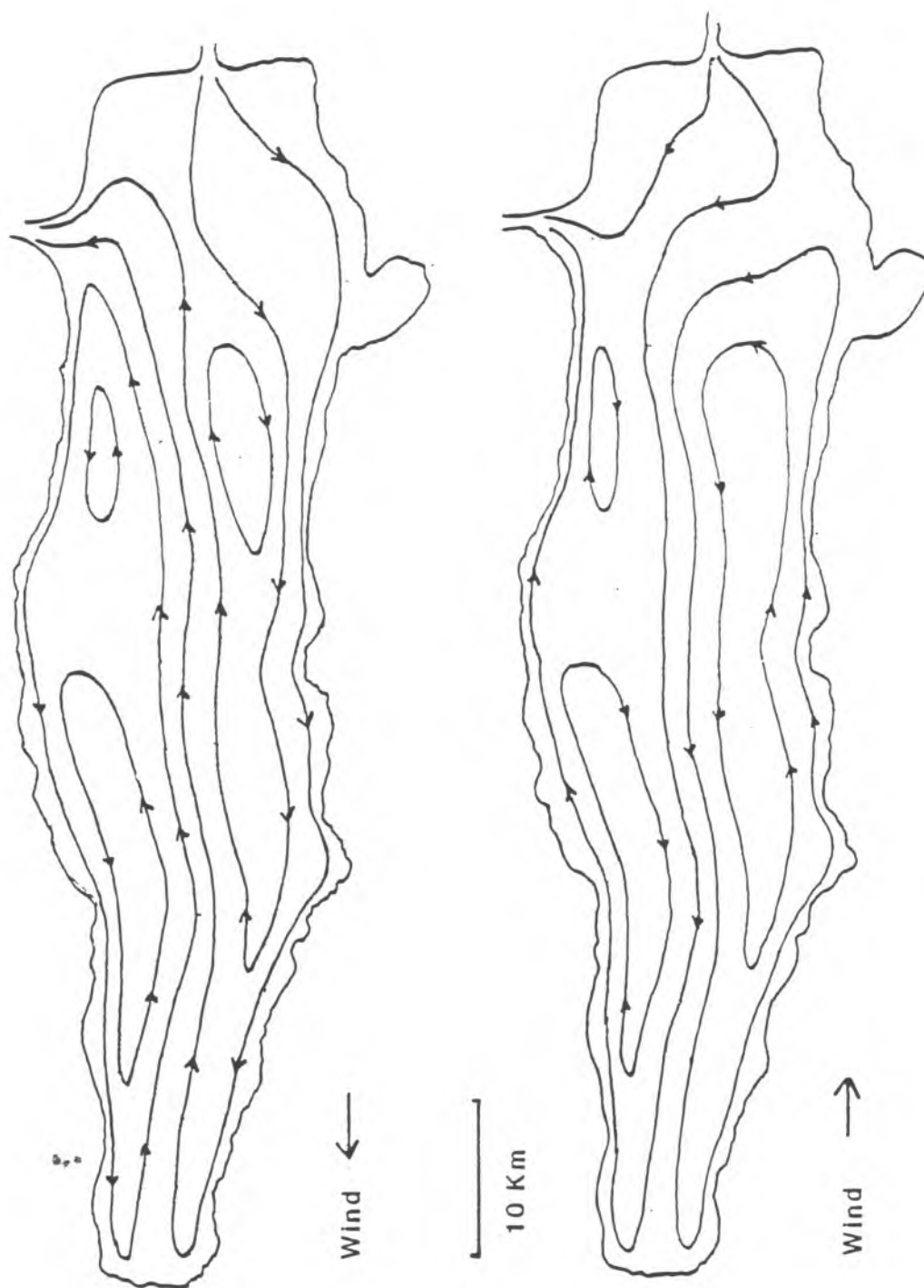


Figure 3. Water circulation patterns on Lake Chapala assuming a 9 km h⁻¹ wind (after Simons 1984).

evidence of oxygen deficiencies in the sediments, indicating a well mixed water column.

The second consequence is the high turbidity characteristic of the lake. deBuen (1945) reported Secchi transparencies of only about 0.25 m. This was apparently due to high levels of suspended solids in the water. Universidad Nacional Autonoma de Mexico (1974) shows an average concentration 324 mg/l total solids, 280 mg/l of which could be removed by filtration. Unpublished data from from 1977-1978 supplied to us by CEL show high turbidity on the lake with a corresponding low light penetration. However, there was a gradient of light extinction over the surface of the lak. Extinction was highest at the east end and lowest at the west end. Light penetration to one meter ranged from 2.7% to 13% of surface irradiance.

Chemical Limnology Physical and chemical data supplied by CEL for 1977-1978 are summarized in Table 2. These data show Lake Chapala to have relatively high concentrations of both inorganic nitrogen and phosphorus. About 88% of the phosphorus is in the form of orthophosphorus, and is presumably available to the phytoplankton populations. The N:P ratio is only 3.3, indicating that nitrogen should become limiting before phosphorus.

Table 2. Principal physical and chemical features of Lake Chapala.
Values are averages and observed ranges of 10 sampling dates
representing all seasons (data provided by the Centro de
Estudios Limnológico for 1977-1978).

	mean	range
Physical:		
Temperature (C)	21.4	17.4 - 25.1
Turbidity (JTU)	> 25	<25 - 230
Total Solids (mg l ⁻¹)	350	195 - 588
Chemical*:		
pH (pH units)	8.3 (median)	6.7 - 8.7
Total Alkalinity (mg l ⁻¹)	200	127 - 335
Nitrate Nitrogen (mg l ⁻¹)	0.60	0.22 - 1.35
Ammonia Nitrogen (mg l ⁻¹)	0.10	0.02 - 0.23
Total Nitrogen (mg l ⁻¹)	0.87	0.50 - 2.26
Total Phosphorus (mg l ⁻¹)	0.26	0.09 - 0.35
Orthophosphorus (mg l ⁻¹)	0.23	0.09 - 0.32

* = data from stations 03, 15, and 26 only

The east end of the lake, which is near the Rio Lerma inflow, shows considerably higher nutrient concentrations during the rainy season. During the rest of the year the nutrient levels are only slightly higher. This is the same pattern of nutrient distribution reported by Universidad Nacional Autonoma de Mexico (1974).

Little is known about the influence of heavy metals upon the lake, although they may be significant. Inputs of lead into the lake from the Rio Lerma are reported to be high, and the mean residence time is between 80-90 years (Caballero et al. 1982). High lead concentrations have been reported in both planktonic and benthic organisms (Universidad Nacional Autonoma de Mexico 1974).

Biological Limnology The net phytoplankton community of Lake Chapala is dominated by green algae such as Staurastrum sp and Closterium sp. This community is homogeneously distributed over the lake and reaches its peak between November and February, corresponding to an increase in light transparency (Ortiz et al. 1982). No estimates are available for phytoplankton production. Attempts by CEL to measure the production using the light and dark bottle oxygen technique were unsuccessful due to the low sensitivity of the method and the consequent inability to obtain statistically valid data (Limon, personal communication).

Although Lake Chapala is very shallow, the macrophyte community is probably not important in terms of the total organic matter input. The extreme west end of the lake is the only area with substantial populations of rooted macrophytes. These beds of Potamogeton sp are probably of only local significance. Also, the floating macrophyte Eichhornia sp may periodically become locally important. These floating mats are most often seen following the onset of the rains. Although they are usually not extensive, Chavez (1973) reports that, in 1962, they covered up to 25% of the lake's surface.

The zooplankton community is composed primarily of Diaptomus sp, Ceriodaphnia sp, and Keratella sp. These organisms reach their maximum densities from August to December (Ortiz et al. 1982).

The benthic community is quite sparse (Deevey 1957, cited by Serruya and Pollinger 1983). Vodopich (personal communication) estimates that the mean density of organisms is about 370 m^{-2} . About 50% of these being oligochaetes and the remainder distributed among four genera of Chironomids.

The fish community is composed of a number of species within the families Cyprinidae, Ictaluridae, Goodeidae, and Atherinidae. A number of genera within the atherinid genus Chirostoma are heavily fished to provide the area people

with a local delicacy, the dried "charall". Recently, the exotic genus Tilapia has been introduced in an effort to increase fisheries (Chavez 1973).

METHODS

Sampling Regime

Five stations were selected from a larger group of 28 stations used by CEL, to determine the physical, chemical, and biological characteristics of Lake Chapala. These stations were located about equidistant along the 76-km fetch of the lake (Figure 1). Water samples were taken and productivity measured every two weeks between June and November, 1983 and approximately every three weeks from December, 1983 to June, 1984.

Due to the size of Lake Chapala, it was impossible to sample all five stations on the same day. Therefore, three stations were sampled the first day of a sampling series and three were sampled on the second. The mid-lake station, Station 15, was sampled both days. This sampling scheme allowed us to estimate the variation in physical, chemical, and biological parameters on both a diel and seasonal basis. Twenty-three sampling series were carried out between June, 1983 and June, 1984. Each sampling series was usually completed in two consecutive days, but occasionally, due to bad weather, delays of up to four days occurred.

Water Sampling and Field Measurements

Stations were sampled between 6:30 and 9:30 A.M. The vertical temperature profile was measured using a YSI submersible thermister. An underwater light extinction coefficient was calculated from measurements using a Lambda¹ radiometer in the quantum mode or was estimated from Secchi depth according to the relationship in Figure 4.

At each station, three types of water samples were collected using an underwater pump. First, water samples were collected from four discrete depths through the euphotic zone. Where possible, these samples were always collected from the surface, 0.5 m, 1.0 m, and 2.0 m. When station 26 was less than 2.0 m deep, samples were taken from the surface and at approximately 30-40 cm intervals. Second, equal volumes from each of the four depths were mixed to form a composite sample. Third, a deep sample was taken during series 13 to 23. This sample was collected about 15 cm above the bottom.

Two separate sets of each type of water sample were always collected. The first was used for the determination on ammonia nitrogen ($\text{NH}_4\text{-N}$) and nitrate nitrogen ($\text{NO}_3\text{-N}$) concentrations while the second was used to measure phytoplankton productivity and all remaining physical and chemical analyses. All containers used for water collection

¹ Lambda Inst. Corp., Fullerton, California

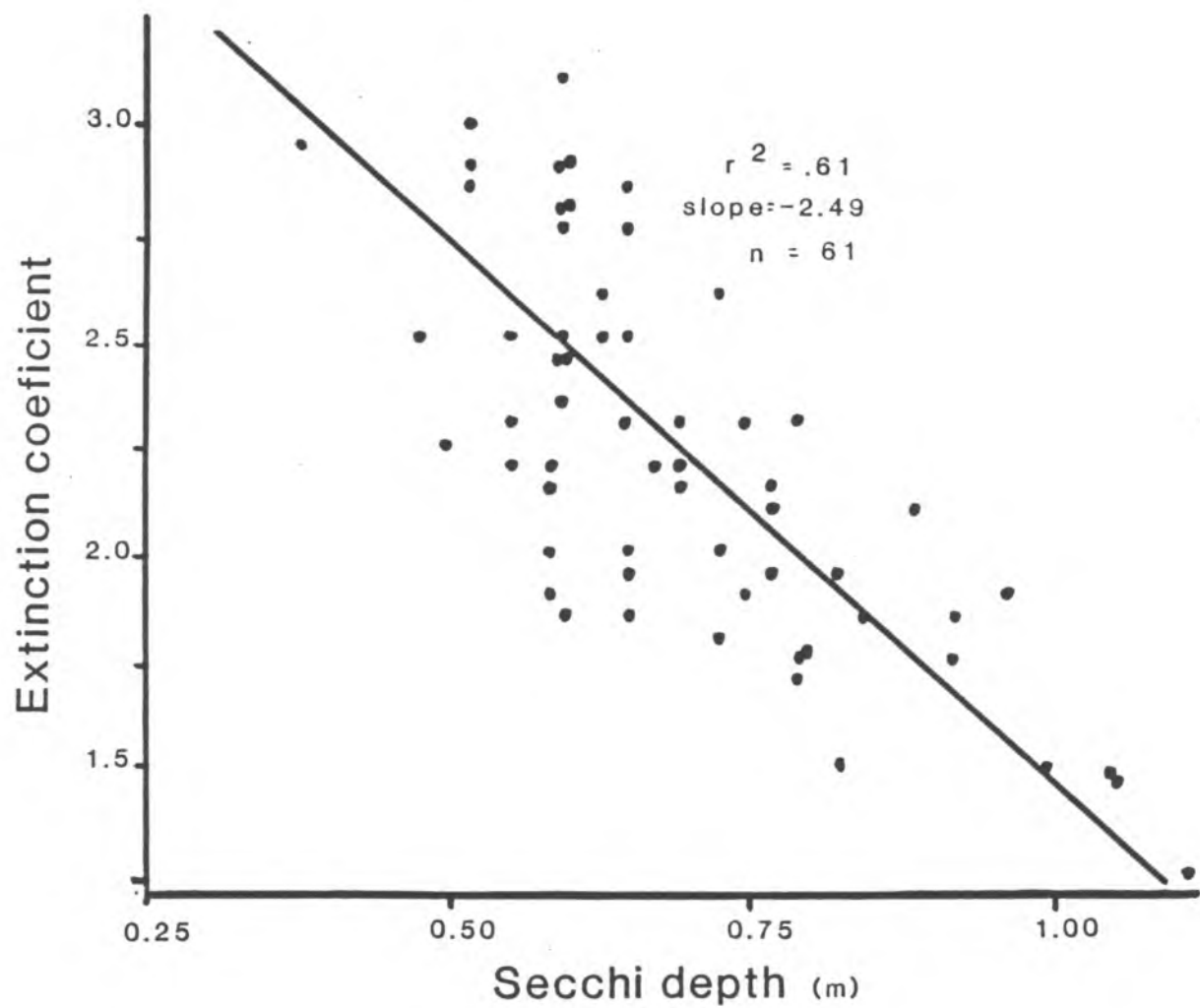


Figure 4. Relationship between extinction coefficient and Secchi depth on Lake Chapala.

or storage were acid-washed polyethylene bottles unless otherwise stated. The first set was stored in 125 ml bottles and preserved with 1.5 ml 0.1N H_2SO_4 to a pH of about 6.0. The second set was collected into four-liter bottles. After collection, each sample was immediately placed into a darkened ice chest and kept at the environmental temperature by filling the chest with lake water. Total sampling time was less than three hours.

The water samples were returned to an onshore work station (Figure 1) for further processing. The four-liter samples were gently shaken to ensure homogeneity and two one-liter aliquots were then taken from each. The first was immediately placed on ice. Later, it was filtered through a Gelman type A/E glass fiber filter. The filter was frozen for subsequent chlorophyll determination, and the filtrate was refrigerated for determination of soluble reactive phosphorus (SRP). The second aliquot was preserved with 2.0 ml concentrated sulfuric acid and placed on ice. This sample was used for determinations of total phosphorus (TP) and total nitrogen (TN). In addition, four aliquots were taken from each of the four discrete-depth samples. These were poured into 125 ml glass-stoppered bottles and used to measure phytoplankton productivity. Finally, three 125 ml aliquots were taken from the composite sample. The first was used for determination of pH and alkalinity. The second was preserved with 1.0 ml of formalin and returned to Baylor

University for determination of turbidity. The third sample was preserved with Lugol's solution for phytoplankton identification.

Phytoplankton Productivity

Field Methods The ^{14}C isotope dilution method of Steeman Nielson (1952), as modified by Lind (1979), was used to measure net phytoplankton production. This is a radioactive tracer technique based on the assumption that the uptake of carbon as ^{14}C or ^{12}C in phytoplankton photosynthesis is proportional to their concentrations in the water.

Water samples were collected from each sampling station (see above) and returned to the onshore work station. There, replicate light and dark bottles were filled with water from each collection depth. The bottles were Pyrex or Kimax 125 ml glass-stoppered bottles.

After the bottles were filled, they were inoculated with 1.00 ml $\text{Na}_2^{14}\text{CO}_3$ solution at a known specific activity between 0.30 and 1.00 uci ml^{-1} (Appendix A). The inoculum was injected into the bottom of each sample using a 4-inch, 14-gauge laboratory cannula and a Hamilton² gas-tight syringe with Chaney adaptor. Each bottle was quickly stoppered and gently shaken to ensure dispersal of

² The Hamilton Company, Reno, Nevada.

the ^{14}C solution. They were then strapped into an incubation rack which was painted black to inhibit any backscattering of light. All work was done in the shade to avoid light shock to the algae. The samples were then taken to the incubation station (Figure 1) and suspended at the surface, 0.5 m, 1.0 m, and 2.0 m. The 2.0 m incubation was always near the limit of the euphotic zone. The light intensity at that depth averaged $1.5 \pm 1.7\%$ of the surface light. This corresponds well to the widely accepted value of 1.0% surface light for the depth of the euphotic zone (Lind 1979). Maximum elapsed time from collection of the first sample to initiation of incubation in the lake was 4.5 h. Maximum elapsed time following inoculation with the isotope until incubation was 15 min.

The samples were incubated for two hours between 11:00 A.M. to 2:00 P.M., normally from 11:30 A.M. to 1:30 P.M. After incubation, the samples were retrieved and placed in darkened ice chests to prevent further carbon fixation. They were promptly covered with crushed ice and returned to the laboratory for filtration.

Filtration and Storage of ^{14}C An aliquot from each sample was filtered upon return to the laboratory. Filtration was made through a 47mm 0.45u pore Gelman membrane filter at about 0.33 atmospheres of vacuum. After filtration, the filter was rinsed with 3-4 ml of 2% HCL

solution (v/v), to prevent carbonate precipitation on the filters. This was followed by a 3-4 ml distilled water rinse (Lind 1979). A 50 ml aliquot of each sample was filtered from stations 03, 11, 15, and 28. The volume filtered from station 26 depended upon the amount of suspended sediments in the sample. Usually, a 25 ml aliquot was filtered, but as little as 5 ml and as much as 50 ml was filtered on occasion. The light bottles were filtered first. All filtrations were complete within six hours of removal from the lake. Lind (1966) has shown that short delays in filtration do not seriously affect sample activity if the samples are kept on ice and in the dark.

The filter, with its coating of phytoplankton cells, was then placed into a liquid scintillation vial. Placement was such that the filter lined the inner wall with the coating of phytoplankton towards the inside of the vial. The filters were dried in a dessicator over silica gel for 48-72 h. After complete drying, the vials were capped and sealed in airtight plastic bags. Each sample was returned to Baylor University within six months and counted using liquid scintillation techniques.

Liquid Scintillation Counting Filters were dried and transported to Baylor University in either large (20 ml) or small (7.5 ml) polyethylene liquid scintillation vials. Upon arrival, the samples were opened and left for one day

in a dessicator to assure that the filters were still completely dry. The vials were then filled with fluor. This fluor consisted of 4.0 g of 1,5 biphenyloxazole (PPO) and 0.1 g of 1,4-bis-2-[4-methyl-5 phenyl-oxazoly] (dimethyl POPOP) dissolved in 1.0 liter of toluene (Lind 1979).

Activity in the phytoplankton of each sample was determined by single counts in an automatic Beckman LS-1800 liquid scintillation counter. Samples were counted to a 5% confidence level ($2 \text{ sigma} = 5.0$). The sample count was shown to be independent of the position of the filter relative to the detectors (Appendix C). Quench in each sample was determined by an external standard technique utilizing ^{137}Cs and reported as an H number. This H number corresponds to the relative shift in the Compton edge in the quenched sample relative to an unquenched standard. Counting channel windows were set at 0 and 700. This allowed for effective counting of the ^{14}C activity regardless of how quench might shift the distribution of activity (Beckman 1982). However, because quench not only shifts the distribution of activity but also lowers the counting efficiency (Wang and Willis 1965, Beckman 1982), a quench curve was necessary. This quench curve was made by first filtering progressively greater volumes of Lake Chapala water through membrane filters. Then, these filters were dried, filled with fluor, and spiked with an internal standard. The internal spike was 5 μl ^{14}C labeled toluene at a specific activity of $737.7 \text{ DPM } \mu\text{l}^{-1}$ at 5 C. Separate

quench curves were made for the large and the small vials. Because the small vials had to be counted while inside of larger ones, their quench was somewhat higher. Both quench curves are presented in Table 3. The efficiency of the liquid scintillation counter, determined by counting a nitrogen purged, unquenched standard was 97.4%. Therefore, the average loss of efficiency at normal quench levels for the samples was only 3-4% in the large vials and 7-10% in the small ones.

Calculation of Daily Photosynthesis and Photosynthetic Efficiency Following determination of radioactive activity (counts per minute) within each sample, photosynthesis was calculated using the formulas given by Lind (1979):

$$P = P_1 - P_d$$

and

$$P_1 \text{ or } P_d = (r/R) (C) (f)$$

where

P = phytoplankton photosynthesis in mg C per m^3

P_1 or P_d = carbon uptake per m^3 in the light and dark bottle, respectively

r = uptake of ^{14}C in counts per minute (CPM) =
(CPM volume filtered) (bottle volume/volume filtered)

R = ^{14}C inoculated in CPM =
(CPM ^{14}C added) (efficiency of counter)

Table 3. Quenching effect of progressively greater quantities of Lake Chapala water filtered onto a 47mm, 0.45u membrane filter.

Vial size	H no.	Counts Min ⁻¹	% Counting Efficiency
Large	31.4	3463.	93.9
	55.6	3430.	93.0
	73.6	3441.	93.3
	89.8	3428.	92.9
	94.6	3415.	92.6
Small	66.7	3331.	90.3
	76.1	3303.	89.6
	88.4	3216.	87.2
	86.4	3171.	86.4
	111.6	3136.	85.1
	123.0	3074.	83.4

C = inorganic carbon (^{12}C) available in mg per m^3
 (inorganic carbon calculated from pH and total
 alkalinity data (Lind 1979))

f = correction for slower uptake of ^{14}C as
 compared with $^{12}\text{C} = 1.06$

This gives volumetric production rates for the phytoplankton community at the incubation light intensity. However, because the light penetration across the lake was not uniform, the light intensity at which a sample was incubated did not necessarily correspond to the light intensity at 0.5 m, 1.0 m, and 2.0 m at the collection station. Therefore, estimation of areal phytoplankton productivity at the collection station required a correction for differences in light extinction between the collection and incubation stations. This was done by calculating the depths at each collection station corresponding to the incubation light intensities and integrating the volumetric production data over these depths.

The integration above yields net areal phytoplankton productivity for the two hour incubation period. This represents about 31% of NPP (Appendix B). $\text{NPP}(\text{eu})$ was calculated by dividing NPP by the euphotic depth at the collection station. $\text{NPP}(\text{mix})$ was calculated by dividing NPP by the lake's depth at that station. $\text{NPP}(\text{max})$ was usually the productivity at 0.5 m.

Photosynthetic efficiency of light utilization was calculated as follows:

$$\text{Efficiency (\%)} = \frac{(\text{mg C m}^{-2} \text{ incubation}^{-1}) (0.67) * 100}{(\text{Irradiance}) (0.70) (0.46)}$$

Where: 0.67 = Einsteins required to photosynthesize 1.0 g Carbon assuming 8 photons are necessary to photosynthesize one molecule of CO₂

Irradiance = Einsteins incubation period⁻¹

0.70 = percent of solar radiation not reflected from the air-water interface

0.46 = converts total solar radiation to photosynthetically active radiation

Algal Bioassays

Algal bioassay techniques for measuring nutrient limitation are varied. Currently used methods range from laboratory experiments using small samples of sterile lake water inoculated with standard test organism (Environ. Protec. Agency 1978), to very large in situ plastic enclosures of natural populations (e.g., Schelske and Stormer 1972), to open cylinders isolating a column of water (Goldman 1962, Lund 1972). Some argue for the use of standard laboratory algal species grown under specific environmental conditions as the best way of understanding

nutrient control over the phytoplankton population (Environ. Protec. Agency 1978). Others argue that in situ assays using natural phytoplankton populations are more applicable to answering questions about a specific system because it more closely approximates what is going on in the lake (Komarkova 1979).

In this study, two natural population bioassays were conducted in an effort to determine the nutrient mostly likely limiting phytoplankton growth. A sixty-liter water sample was collected from 0.5 m at either station 15 (October 08) or station 11 (November 02). The sample was returned to the lab and, after careful mixing, siphoned into 3.75-liter polyethylene bottles. Each bottle was spiked with nitrate nitrogen, ammonia nitrogen, phosphorus, a micronutrient solution, or kept as a control (Table 4). Initial nutrient concentrations and phytoplankton biomass were determined from the remaining water. For this experiment, biomass was measured as chlorophyll fluorescence. The containers were incubated at approximate lake temperature at about 60% surface light. Samples were gently shaken and rearranged daily. The experiment was terminated after six days, and final nutrient concentrations and phytoplankton biomass were determined.

Table 4. Nutrient solutions used in the natural population bioassay for limiting nutrients in Lake Chapala.

Nutrient Solution	Reagent	Increase in elemental concentration (ug l ⁻¹)	Environmental concentration (ug l ⁻¹)
Nitrogen	KNO ₃	400	150 - 400
Phosphorus	NaH ₂ PO ₄	400	300 - 600
Micronutrient*			
B	H ₃ BO ₃	32.5	?
Mn	MnCl ₂ ·4H ₂ O	115.4	?
Zn	ZnCl ₂	1.57	?
Co	CoCl ₂ ·6H ₂ O	0.35	?
Cu	CuCl ₂ ·2H ₂ O	0.004	?
Mo	Na ₂ MoO ₄ ·2H ₂ O	2.88	?
Fe	FeCl ₃ ·6H ₂ O	33.05	?

* = micronutrient solution after Environ. Prot. Agency 1978.

Phytoplankton Biomass

Chlorophyll a concentration was normally used as a measure of phytoplankton biomass. For series 1 - 12, chlorophyll a was measured for each water sample collected. However, because chlorophyll a was vertically invariant (see below), analyses were made only of the composite and 0.5 m samples during series 13 - 23. A deep sample also was taken during these series to see if the homogeneity of phytoplankton biomass in the euphotic zone extended to the lake bottom.

Chlorophyll a concentrations were determined from one liter water samples using the trichromatic equations of Strickland and Parsons (1972). Techniques used were those described by Lind (1979) for glass fiber filters. Filters were stored by freezing them inside individually sealed plastic pouches. Storage never exceeded 30 da. Absorbance of each extract was read on a Shimadzu model UV-240 narrow band pass spectrophotometer.

For the bioassay experiments, biomass was estimated as chlorophyll fluorescence using a Turner Designs Fluorometer³ Model 10.

³ Turner Designs, Mountain View, California 94043.

Chemical Analyses

For series 1 - 12, each water sample was analyzed for TP, SRP, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and TKN. However, because these chemical parameters were found to be vertically invariant through the upper 2.0 m of the water column (see below), analyses were made only of the composite and 0.5 m samples during series 13 - 23. A deep sample also was taken during these series to determine if the chemical homogeneity in the euphotic zone extended to the lake bottom.

pH was determined upon returning to the onshore work station by a Corning Model 5 portable pH meter. Total alkalinity as $\text{mg CaCO}_3 \text{ l}^{-1}$ was determined in the field or immediately upon return to the lab by titrating with 0.02 N sulfuric acid to a pH endpoint of 4.5. pH and alkalinity did not vary with depth so measurements were made only on the composite samples.

Since Lake Chapala was suspected of being chemically limited by nitrogen, priority was given to the analysis of inorganic nitrogen as ammonia or nitrate. Ammonia nitrogen ($\text{NH}_4\text{-N}$) was routinely analyzed within 12 h of sampling, and always within 24 h. Nitrate nitrogen ($\text{NO}_3\text{-N}$) was analyzed within 36 h of sampling. All analyses were normally complete within 4 da of sampling.

Each chemical determination was made in duplicate. Internal spikes covering the entire range of observed concentrations were routinely used to establish the accuracy and recovery of each technique and determine if correction factors were necessary. All colorimetric determinations were on a Bausch & Lomb Spectronic 20.

Samples for TP, SRP, and $\text{NH}_4\text{-N}$ were analyzed by the colorimetric methods in Lind (1979) with the following modifications. Ammonia nitrogen analyses were done on 25.0 ml water samples instead of 50.0 ml samples. Total Phosphorus and SRP analyses were done on 10.0 ml samples instead of 50.0 ml samples. Nitrate nitrogen concentration was determined by the batch cadmium reduction technique of Davidson and Woof (1978) using cadmium fillings. Approximately 7.5 g of of cadmium filings were used on 10.0 ml water samples. Shaking time was two hr. Total nitrogen concentration was determined by the Kjeldahl method using an ion selective electrode (Environ. Protec. Agency 1979).

Turbidity

Because a reliable nephelometer was unavailable in Mexico, 125 ml samples from series 1-12 were preserved with 1.0 ml of formalin and returned to Baylor. Because of delays of up to six months, the samples were shaken on a mechanical shaker for 24 h to resuspend the sediments before

measurement on a Hach model 2100A turbidometer. No turbidity measurements were made for series 13-23.

Phytoplankton Identification and Enumeration

Phytoplankton were identified using Smith (1933), Edmondson (1963), and Prescott (1951). Enumeration was made using the drop count method developed by W. T. Edmondson (Vollenweider 1969).

Data Analyses

All statistical data analyses were performed using the statistical programs of SPSS^X (SPSS, Inc. 1983).

Analysis of Variance (ANOVA) An ANOVA tests for differences in means among three or more populations (or experimental groups). This analysis tests the null hypothesis that the means of all populations are equal. It assumes that the data from each population is normally distributed, that all populations have equal variances, and that all sample sizes are equal (Zar 1974). Three distinct applications of the ANOVA were used.

First, a one-way analysis of variance was used to test for differences in phytoplankton biomass among the experimental treatment groups in the natural population bioassays. That is, did the addition of phosphorus,

nitrogen, or micronutrient solution increase phytoplankton biomass? For this analysis, there were five experimental treatments (nutrient additions), each replicated three times.

Second, a complete randomized block design analysis was used to test for differences in nutrient concentration and phytoplankton biomass among sampling depths for series 1-12. In other words, were nutrient concentrations or phytoplankton biomass higher at any particular depth? For this test, each sampling station on each sampling date was treated as a block. Since each sampling series consisted of two sampling dates on each of which three stations were sampled (see above), there were 72 blocks. Each block was tested at four levels (depths).

Third, two-way analysis of variance was used to detect differences in the physical, chemical, and biological parameters among the five stations and among the 23 sampling series. The station factor (ST) is considered a fixed-effect variable because the stations were specifically selected to represent different areas of the lake. The series factor (SR) was considered a random-effect variable. Even though the sampling was done at roughly equal intervals, environmental conditions present on the lake were not under experimental control. Since one factor was fixed and one was random, this was a Model III ANOVA. There are five levels of the ST factor, and 23 levels of the SR

factor, making this a 5 X 23 factorial.

Two-way analysis of variance with replicate observations of the variable under consideration is desirable because the interaction between the two factors can be assessed. Such is the case for the analyses of NPP, NPP(max), NPP(eu), NPP(mix), phytoplankton biomass, TP, SRP, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and TN. For each of these variables, two replicate observations for the 115 combinations of the two factors were made, making a total of 230 data in each experiment.

The equation tested was:

$$Y_{ijk} = ST_i + SR_j + ST*SR_{ij} + \text{error}_{ijk}$$

For Secchi depth, extinction coefficient, photic depth, and Z(mix):Z(eu) ratios there was only one observation per cell. Thus, the interaction between ST and SR could not be evaluated and was assumed to be insignificant. The equation tested was:

$$Y_{ijk} = ST_i + SR_j + \text{residual}_{ijk}$$

The test of the random factor SR must be interpreted with caution. Because no test of the interaction between ST and SR is possible, this interaction must be assumed to be insignificant. If a significant interaction exists, one stands a chance of failing to reject H_0 when H_0 is, in fact, false (Type II error). However, if a significant difference is concluded, that conclusion may be accepted (Zar 1974).

• Multiple Range Tests When an ANOVA rejects the null hypothesis that all population means are equal, a multiple range test is called for to determine between which population means differences exist. This analysis considers the null hypothesis $H_0: \mu_a = \mu_b$, where a and b denote any possible pair of groups. The significance level stated for this analysis is the probability of encountering at least one Type I error during the course of comparing all the pairs of means. It is not the probability of committing a Type I error for a single comparison (Zar 1974).

In this study, the Student Newman-Keuls (SNK) multiple range test was used to uncover specific differences among stations (in physical, chemical, or biological parameters), or among experimental groups (natural population bioassays).

Scheffe's multiple contrast test was used to test for differences in nutrient concentration, phytoplankton productivity, or Secchi depth between the wet and dry seasons. For this test, series 1-10 and 22-23 were considered as part of the wet season, while series 11-22 were considered part of the dry season. The null hypothesis tested was $\mu_{\text{wet}} - \mu_{\text{dry}} = 0$.

Differences between coefficients of variation (C.V.)

The variance ratio proposed by Lewontin (1960, cited by Zar 1974), was used to test the null hypothesis that two samples came from populations with identical C.V.'s. This test was

used to compare the NPP at Station 26 with every other station, and to compare the NPP at a given station between the wet and dry seasons.

Regression Analysis Regression analysis examines the relationship between a dependent variable and one or more independent variables. The magnitude of the dependent variable is assumed to be determined by the magnitude of the independent variable(s).

In this study, multiple regression analysis was used to test the effects of various environmental physical and chemical parameters upon NPP and phytoplankton biomass. Multiple regression equations were built utilizing the stepwise procedure. Independent variables were entered into the equation in order of the probability of the F statistic. The variable with the smallest probability of F was entered into the equation if this value was smaller than the entry criterion (PIN). Once a variable was entered, all variables in the equation were again examined. If the F value of any variable then exceeded the removal criteria (POUT), that variable was removed. This process continued until no more variables in the equation needed to be removed, and no variables not in the equation were eligible for entry (SPSS, Inc. 1983). The probability of F to enter (PIN) and to remove (POUT) a variable from the equation was 0.05 and 0.10, respectively.

Correlation Analysis Correlation analysis examines the relationship between two random variables. That is, the magnitude of one variable may change as the magnitude of the other changes, but it is not reasonable to consider there to be one dependent and one independent variable (Zar 1974).

In this study, correlation analysis was used to examine the relationship between extinction coefficient and Secchi depth (both of which are presumably dependent upon the amount of suspended solids in the water).

Correlation analysis was also used to examine the relationship between lake depth and various chemical parameters, and between phytoplankton productivity or biomass and various physical and chemical parameters.

RESULTS

Vertical Variations

Lake Chapala was always near isothermal during early morning sampling (Table 5). While re-sampling later in the day was rarely possible, the data available indicate that by noon, on days with little wind action, the top one-half meter was usually thermally isolated from the rest of the water column. Data from four dates illustrate this point (Figure 5). This same pattern of surface warming on calm days was seen in thermal profiles measured at noon at the incubation station (Table 6). On days with considerable wind action, the water column remained near isothermal throughout the day. On calmer days, stratification began to develop around 10:00 A.M. and was well established by noon (Figure 6). Isothermy was always re-established by evening.

At sampling time, Lake Chapala was also vertically homogeneous with respect to phytoplankton biomass, TP, SRP, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and TN (Table 7). A complete randomized block analysis show no difference among depths for these variables (Table 8).

Table 5. Vertical temperature (C) profiles (Surface, 0.5 m, 1.0 m, 2.0 m) at each collection station on each sampling date. Measurements were made between 6:30 and 9:30 A.M.

Date	Station 03	Station 11	Station 15	Station 28	Station 26
11/08/83	23.1, 23.2, 23.2, 23.2	23.8, 23.9, 24.0, 24.0	23.8, 23.8, 23.8, 23.8	24.2, 24.2, 24.2, 24.2	23.4, 23.8, 23.9, 24.0
12/08/83	23.0, 23.0, 23.1, 23.5	23.6, 23.6, 23.9, 23.9	24.0, 24.0, 24.0, 24.0		
15/08/83			22.0, 22.6, 22.8, 22.9		
16/08/83			23.2, 23.2, 23.2, 23.1	23.4, 23.5, 23.6, 23.6	22.8, 22.9, 23.0, 23.1
31/08/83	24.3, 24.4, 24.5, 24.5	24.4, 24.6, 24.7, 24.8	23.5, 23.4, 23.6, 23.6		
02/09/83			23.0, 23.1, 23.3, 23.4	23.8, 24.4, 24.4, 24.4	23.8, 23.9, 24.0, 24.0
13/09/83	22.6, 22.7, 22.8, 22.8	23.5, 23.5, 23.6, 23.6	22.8, 22.8, 22.9, 23.0		
15/09/83			22.6, 22.6, 22.6, 22.6	22.9, 22.9, 22.9, 22.9	22.8, 22.8, 22.8, 22.8
26/09/83	22.2, 22.1, 22.1, 22.1	23.1, 23.1, 23.1, 23.1	22.4, 22.5, 22.5, 22.5		
27/09/83			22.3, 22.3, 22.3, 22.3	22.4, 22.4, 22.4, 22.4	22.4, 22.4, 22.4, 22.4
11/10/83			22.5, 22.5, 22.5, 22.5	22.9, 22.9, 22.9, 22.9	22.8, 22.8, 22.8, 22.8
12/10/83	23.5, 23.5, 23.5, 23.5	23.9, 23.9, 23.9, 23.8	24.9, 24.6, 24.0, 23.9		
24/10/83			21.7, 21.7, 21.7, 21.7	22.6, 22.6, 22.5, 22.5	21.6, 21.6, 21.6, 21.6
25/10/83	22.6, 22.6, 22.6, 22.5	22.4, 22.5, 22.5, 22.5	22.0, 22.0, 22.0, 22.0		
07/11/83	20.4, 20.4, 20.4, 20.4	20.8, 20.7, 20.6, 20.6	20.6, 20.6, 20.4, 20.4	21.2, 21.2, 21.2, 21.2	20.2, 20.2, 20.3, 20.3
08/11/83			21.0, 21.0, 21.0, 20.8		
17/11/83			20.0, 20.0, 20.0, 20.0	20.3, 20.2, 20.3, 20.3	20.2, 20.3, 20.3, 20.3
18/11/83	19.7, 19.7, 19.7, 19.7	20.5, 20.5, 20.5, 20.5	20.2, 20.2, 20.2, 20.1		
01/12/83	18.4, 18.4, 18.4, 18.4	18.2, 18.6, 18.6, 18.6	18.0, 18.0, 18.0, 18.0		
02/12/83			18.9, 18.9, 18.9, 18.9	18.2, 18.7, 18.7, 18.8	18.5, 18.2, 18.2, 18.4
20/12/83	16.6, 16.6, 16.8, 16.8	17.2, 17.2, 17.4, 17.4	17.0, 17.0, 17.0, 17.0		
21/12/83			15.4, 15.6, 15.6, 15.6	15.2, 15.6, 15.7, 15.7	15.0, 15.2, 15.2, 15.2
09/01/84			16.2, 16.6, 16.7, 16.7	17.2, 17.2, 17.3, 17.4	17.4, 17.6, 17.6, 17.8
10/01/84	16.8, 17.0, 17.0, 17.1	17.0, 17.0, 17.0, 17.0	16.8, 16.8, 16.8, 16.8		
31/01/84			16.9, 16.9, 16.9, 16.9	17.6, 17.7, 17.7, 17.7	17.2, 17.4, 17.4, 17.4
01/02/84	16.8, 17.0, 17.0, 17.0	17.4, 17.4, 17.4, 17.4	17.8, 17.8, 17.8, 17.8	18.2, 18.2, 18.2, 18.2	18.7, 18.7, 18.7, 18.7
20/02/84			17.8, 17.8, 17.7, 17.7		
21/02/84	18.2, 18.2, 18.2, 18.3	19.1, 19.1, 19.1, 19.1	19.4, 19.4, 19.4, 19.4		
14/03/84	19.4, 19.4, 19.4, 19.4	20.0, 20.0, 21.0, 21.0	21.3, 21.3, 21.3, 21.3	19.4, 19.4, 19.4, 19.4	21.6, 21.6, 21.7, 21.7
15/03/84			20.2, 20.2, 20.2, 20.2	20.4, 20.4, 20.4, 20.3	20.2, 20.4, 20.4, 20.4
09/04/84	19.7, 19.8, 19.8, 19.8	19.9, 20.0, 20.0, 20.0	20.2, 20.2, 20.2, 20.2	20.4, 20.6, 20.6, 20.6	20.6, 20.8, 21.0, 21.0
10/04/84			20.2, 20.2, 20.2, 20.2		
23/04/84	19.3, 19.3, 19.5, 19.5	19.8, 20.2, 20.2, 20.2	19.6, 19.8, 19.8, 19.6		
16/05/84	19.4, 19.4, 19.4, 19.4	20.0, 20.0, 20.0, 20.0	20.8, 20.5, 20.3, 20.2	18.1, 18.2, 18.2, 18.2	18.3, 18.2, 18.2, 18.2
17/05/84	20.2, 20.4, 20.4, 20.6	20.6, 20.6, 20.8, 20.8	20.2, 20.2, 20.2, 20.2		
04/06/84			20.6, 20.4, 20.3, 20.1	21.0, 20.8, 20.6, 20.6	20.7, 21.0, 21.0, 21.0
06/06/84	23.2, 23.4, 23.4, 23.4	22.6, 23.2, 23.4, 23.4	23.8, 23.8, 23.8, 23.8		
27/06/84			23.4, 23.4, 23.3, 23.2	23.4, 23.5, 23.5, 23.5	23.4, 23.3, 23.3, 23.3
28/06/84					

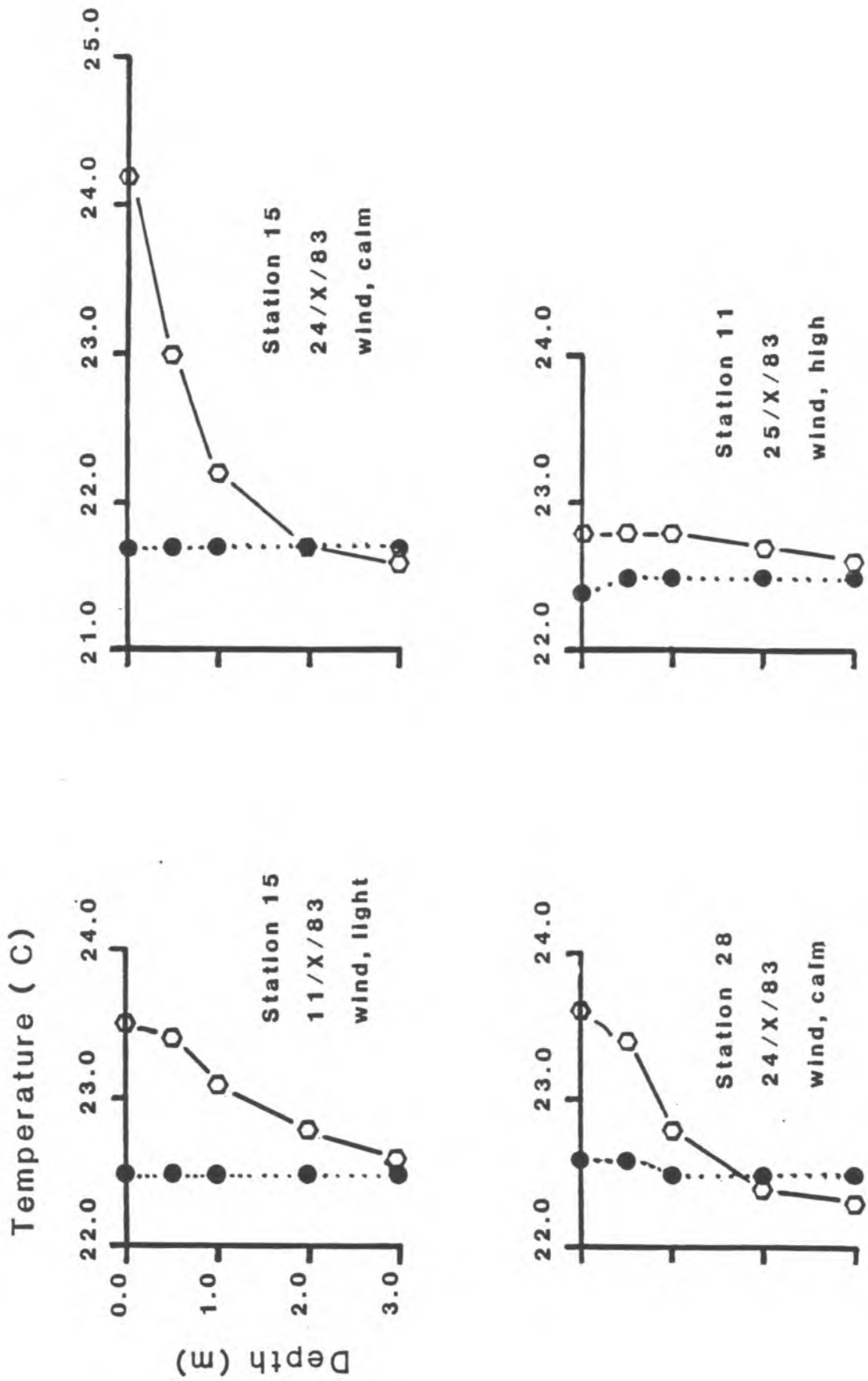


Figure 5. Vertical profiles showing early morning (●—●) and noontime (○—○) temperatures through the upper 3.0 m of the water column.

Table 6. Noontime temperature (C) profile (surface, 0.5 m, 1.0 m, 2.0 m, and 3.0 m) at the incubation station. Wind codes: 0 = no wind, 1 = light wind, 2 = strong wind.

Date	Wind	Temperature Profile	-	Date	Wind	Temperature Profile
14/06/83	1	25.2, 25.2, 24.9, 24.3, 24.0	-	01/12/83	2	19.8, 19.8, 19.8, 19.8, 19.0
27/06/83	1	25.4, 24.6, 24.6, 23.9, 23.7	-	02/12/83	1	21.0, 20.6, 20.1, 20.1, 20.0
28/06/83	1	26.0, 26.0, 25.0, 24.5, 24.3	-	20/12/83	3	20.0, 20.0, 20.0, 19.8
11/08/83	3	24.7, 25.1, 25.2, 25.1, 24.8	-	21/12/83	3	23.2, 22.8, 23.0, 23.0, 23.0
12/08/83	3	25.1, 25.1, 25.1, 24.8, 24.8	-	09/01/84	1	19.4, 19.0, 18.6, 18.0
15/08/83	3	24.2, 24.2, 24.2, 24.2, 24.0	-	10/01/84	3	17.9, 17.8, 17.7, 17.4, 17.3
16/08/83	1	25.8, 25.5, 24.8, 24.6, 24.5	-	31/01/84	2	19.2, 18.4, 18.2, 18.0, 17.9
31/08/83	3	24.8, 24.9, 25.0, 25.0	-	01/02/84	2	19.2, 19.2, 18.4, 18.2, 18.2
02/09/83	3	24.5, 24.5, 24.5, 24.6	-	20/02/84	3	20.6, 20.7, 20.6, 20.5
13/09/83	3	24.7, 24.8, 24.8, 24.6	-	21/02/84	1	20.4, 20.4, 20.4, 19.6, 19.6
15/09/83	3	24.4, 24.2, 24.2, 23.9	-	14/03/84	3	22.0, 21.4, 21.3, 21.3, 21.3
26/09/83	3	24.1, 24.0, 23.9, 23.6, 23.5	-	15/03/84	3	21.0, 21.1, 21.1, 21.0, 20.9
27/09/83	3	23.4, 23.4, 23.4, 23.3	-	09/04/84	2	22.6, 21.4, 21.4, 20.8
11/10/83	3	23.8, 23.6, 23.5, 23.5	-	10/04/84	2	22.0, 21.0, 20.7, 20.3, 20.2
12/10/83	1	24.8, 24.2, 23.8, 23.5, 23.5	-	23/04/84	3	21.8, 21.8, 21.6, 21.4
24/10/83	1	25.3, 24.2, 23.4, 22.9, 22.7	-	24/04/84	2	22.3, 21.7, 21.6, 21.3, 21.2
25/10/83	3	23.4, 23.4, 23.4, 23.4	-	16/05/84	1	23.6, 23.0, 22.8, 22.5
07/11/83	2	23.4, 23.2, 22.2, 21.2, 21.0	-	17/05/84	3	22.7, 22.7, 22.6, 22.6
08/11/83	1	22.3, 22.2, 21.7, 21.5, 21.6	-	04/06/84	1	22.4, 22.2, 22.0, 21.6, 21.2
17/11/83	3	22.0, 21.9, 21.9, 21.7, 21.4	-	06/06/84	2	21.9, 21.7, 21.4, 21.0
18/11/83	2	22.9, 22.0, 21.5, 21.3, 21.0	-	27/06/84	1	26.0, 25.0, 24.8, 24.8
			-	28/06/84	2	27.0, 26.8, 25.7, 25.0, 24.7

Temperature (C)

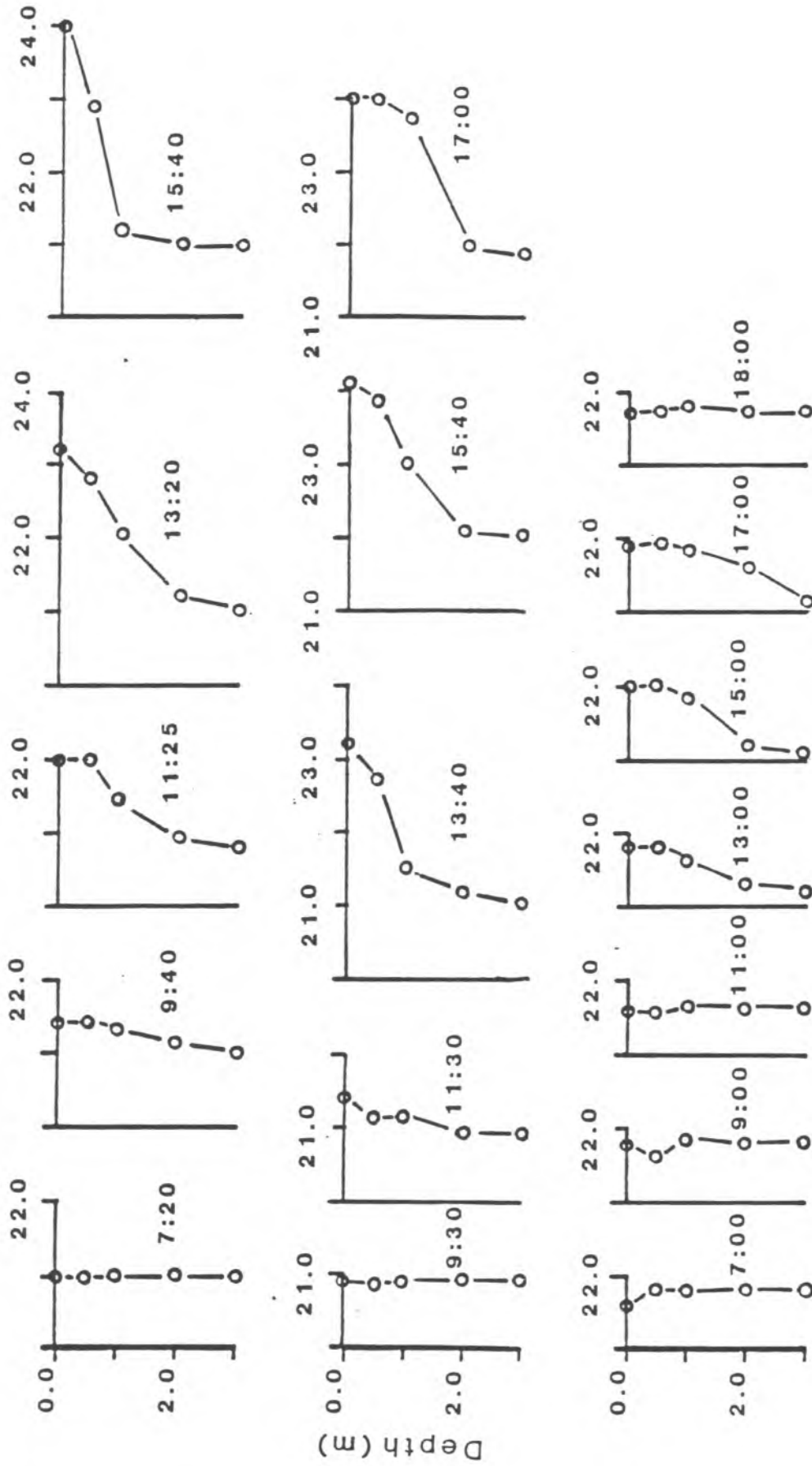


Figure 6. Diel pattern of thermal stratification at the Incubation Station on 01 November, 1983, 14 November, 1983, and 16 April, 1984, respectively. The wind on the first two dates was very calm, while on the last it was quite strong.

Table 7. Vertical distribution of phytoplankton biomass and nutrients through the upper two meters of the water column.

STATION 03

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
13/06/83	0.0	3.28	594.	470.	25.	124.	.52
	.5	2.36	581.	477.	26.	140.	.48
	1.0	1.75	584.	481.	25.	122.	.30
	2.0	2.52	597.	480.	26.	117.	.16
	Com	2.52	542.	488.	24.	114.	.14
28/06/83	0.0	2.05	504.	486.	101.	36.	.36
	.5	2.05	488.	484.	109.	32.	.33
	1.0	2.54	547.	486.	90.	31.	.35
	2.0	2.27	488.	488.	109.	31.	.30
	Com	2.81	487.	489.	97.	31.	.34
19/07/83	0.0	1.81	454.	438.	54.	35.	.26
	.5	1.69	461.	443.	50.	34.	.39
	1.0	1.69	467.	443.	52.	39.	.43
	2.0	1.30	469.	442.	54.	37.	.11
	Com	1.63	446.	442.	55.	35.	.06
2/08/83	0.0	3.31	440.	427.	18.	157.	1.41
	.5	2.80	439.	420.	15.	264.	1.60
	1.0	3.39	430.	423.	15.	281.	2.51
	2.0	3.38	433.	432.	19.	238.	2.01
	Com	2.77	407.	426.	15.	211.	1.83
15/08/83	0.0	1.74	477.	407.	52.	60.	.40
	.5	2.09	480.	403.	62.	65.	.30
	1.0	1.51	502.	391.	71.	75.	.24
	2.0	1.97	477.	379.	70.	70.	.43
	Com	2.09	454.	381.	72.	95.	.44
31/08/83	0.0	2.80	496.	418.	0.	48.	.79
	.5	2.72	504.	416.	0.	57.	.31
	1.0	2.31	508.	412.	0.	106.	.61
	2.0	2.77	507.	412.	9.	86.	.53
	Com	2.67	487.	416.	0.	44.	.20
13/09/83	0.0	4.88	436.	393.	44.	125.	.64
	.5	4.69	434.	397.	12.	33.	.84
	1.0	4.95	436.	395.	11.	32.	.43
	2.0	4.69	441.	385.	17.	52.	.49
	Com	4.75	412.	393.	20.	31.	.31
26/09/83	0.0	6.56	451.	395.	32.	12.	1.97
	.5	6.10	446.	388.	32.	22.	1.66
	1.0	5.59	451.	392.	34.	18.	1.55
	2.0	5.56	448.	403.	37.	20.	1.15
	Com	5.74	431.	398.	37.	21.	1.30
12/10/83	0.0	5.90	441.	379.	274.	29.	.41
	.5	5.92	457.	380.	277.	23.	.40
	1.0	5.79	436.	371.	272.	20.	.39
	2.0	6.41	447.	367.	274.	22.	.41
	Com	6.39	421.	375.	275.	32.	.31
25/10/83	0.0	7.80	399.	372.	142.	30.	.88
	.5	7.88	398.	380.	119.	27.	1.08
	1.0	7.19	396.	355.	124.	29.	.81
	2.0	7.63	395.	360.	138.	31.	1.34
	Com	7.39	383.	370.	66.	34.	.94
8/11/83	0.0	11.30	391.	372.	66.	27.	.48
	.5	11.04	402.	372.	65.	33.	.60
	1.0	10.78	386.	364.	60.	26.	.46
	2.0	11.27	391.	373.	75.	23.	.29
	Com	11.64	368.	371.	72.	21.	.45
18/11/83	0.0	10.33	395.	367.	68.	23.	.91
	.5	10.69	403.	364.	70.	17.	.91
	1.0	10.70	395.	365.	68.	10.	.89
	2.0	10.81	393.	372.	69.	14.	1.24
	Com	10.52	373.	372.	69.	21.	1.08
1/12/83	.5	6.37	400.	361.	41.	36.	.05
	Com	5.64	384.	315.	40.	50.	.04
	Prf	6.05	383.	343.	42.	36.	.05
20/12/83	.5	5.72	375.	352.	22.	23.	.25
	Com	5.27	373.	358.	25.	19.	.20
	Prf	5.18	379.	354.	24.	17.	.20
10/01/84	.5	5.66	364.	389.	31.	24.	.72
	Com	6.04	375.	394.	26.	31.	.53
	Prf	5.27	362.	401.	30.	27.	.65
1/02/84	.5	5.95	366.	372.	40.	29.	.53
	Com	5.21	384.	359.	44.	38.	.48
	Prf	6.09	369.	376.	37.	27.	.62
21/02/84	.5	3.40	384.	363.	10.	28.	.39
	Com	3.97	368.	361.	9.	46.	.59
	Prf	3.79	367.	361.	5.	29.	.47
14/03/84	.5	4.09	394.	326.	21.	6.	.80
	Com	4.51	371.	322.	25.	5.	.75
	Prf	4.50	392.	328.	20.	7.	.73
10/04/84	.5	3.34	393.	393.	15.	15.	.78
	Com	3.83	406.	396.	19.	17.	.42
	Prf	3.24	412.	391.	15.	19.	.65
24/04/84	.5	3.41	373.	357.	39.	55.	.39
	Com	2.97	369.	341.	47.	54.	.52
	Prf	2.95	365.	351.	47.	54.	.56
16/05/84	.5	4.87	406.	379.	44.	28.	.46
	Com	4.63	397.	367.	45.	43.	.31
	Prf	5.07	404.	362.	45.	25.	.44
4/06/84	.5	6.66	449.	421.	55.	28.	.24
	Com	6.56	456.	420.	66.	27.	.36
	Prf	6.82	457.	413.	59.	31.	.32
27/06/84	.5	5.18	399.	407.	23.	22.	.35
	Com	5.18	400.	408.	30.	22.	.24
	Prf	4.18	413.	416.	22.	20.	.31

Table 7 (continued)

STATION 11

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
13/06/83	0.0	2.85	571.	490.	26.	112.	.09
	.5	2.61	581.	487.	27.	88.	.09
	1.0		597.	488.	31.	107.	.06
	2.0	2.41	552.	482.	25.	122.	.08
	Com	2.68	559.	488.	25.	233.	.08
28/06/83	0.0	1.55	525.	485.	86.	41.	.44
	.5	2.45	494.	476.	106.	27.	.35
	1.0	2.69	498.	489.	104.	39.	.35
	2.0	2.66	494.	496.	90.	22.	.26
	Com	2.22	465.	492.	86.	39.	.31
19/07/83	0.0	.78	462.	441.	58.	48.	.01
	.5	1.04	466.	451.	55.	32.	.08
	1.0	.52	480.	442.	57.	32.	.09
	2.0	1.66	473.	441.	50.	25.	.05
	Com	0.88	469.	440.	53.	33.	.21
2/08/83	0.0	2.14	434.	418.	22.	88.	1.91
	.5	2.55	426.	423.	22.	80.	2.28
	1.0	2.35	425.	418.	18.	80.	2.16
	2.0	2.75	433.	428.	27.	79.	1.55
	Com	2.44	405.	430.	24.	109.	2.06
15/08/83	0.0	1.62	495.	416.	57.	72.	.50
	.5	1.74	496.	423.	52.	66.	.46
	1.0	1.86	484.	405.	55.	76.	.34
	2.0	1.62	482.	409.	53.	57.	.23
	Com	1.76	468.	409.	63.	67.	.54
31/08/83	0.0	4.65	500.	398.	18.	48.	1.14
	.5	4.45	495.	398.	20.	49.	2.99
	1.0	4.74	495.	404.	20.	57.	1.33
	2.0	4.54	495.	404.	19.	56.	.99
	Com	4.64	473.	406.	23.	74.	.88
13/09/83	0.0	4.56	427.	387.	48.	50.	1.14
	.5	4.29.	389.	46.	47.	89.	.89
	1.0	4.83	425.	372.	46.	59.	.95
	2.0	4.88	427.	378.	40.	50.	.78
	Com	5.19	412.	377.	55.	61.	.74
26/09/83	0.0	4.08	439.	398.	39.	9.	1.17
	.5	4.23	436.	396.	30.	6.	1.62
	1.0	4.34	432.	406.	37.	13.	1.75
	2.0	3.85	434.	398.	40.	11.	1.43
	Com	4.19	417.	398.	46.	23.	1.15
12/10/83	0.0	5.90	457.	367.	194.	18.	.25
	.5	5.65	475.	375.	192.	16.	.24
	1.0	6.03	477.	369.	200.	23.	.21
	2.0	5.73	453.	373.	185.	11.	.21
	Com	5.89	443.	373.	189.	16.	.11
Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
25/10/83	0.0	6.60	384.	358.	138.	38.	.60
	.5	6.77	387.	368.	130.	35.	.70
	1.0	6.85	389.	364.	115.	42.	.96
	2.0	7.44	393.	376.	110.	38.	.85
	Com	6.92	373.	373.		40.	.90
8/11/83	0.0	9.65	379.	362.	129.	24.	.43
	.5	10.27	382.	373.	125.	27.	.38
	1.0	9.48	385.	367.	139.	25.	.38
	2.0	10.14	390.	371.	124.	26.	.50
	Com	9.77	357.	374.	124.	23.	.45
18/11/83	0.0	8.62	378.	354.	94.	21.	1.03
	.5	8.56	379.	351.	98.	17.	.99
	1.0	8.55	383.	351.	99.	24.	1.08
	2.0	8.71	388.	357.	105.	18.	.94
	Com	8.59	366.	369.	104.	21.	1.59
1/12/83	.5	5.25	399.	322.	94.	48.	.08
	Com	5.40	399.	335.	88.	41.	.09
20/12/83	.5	5.62	377.	359.	95.	36.	.09
	Com	4.86	379.	362.	46.	24.	.28
	.5	5.48	361.	361.	44.	28.	.25
10/01/84	.5	4.26	380.	401.	69.	22.	.49
	Com	5.64	395.	394.	71.	26.	.45
	.5	4.56	376.	405.	70.	25.	.45
1/02/84	.5	5.46	361.	380.	94.	28.	.46
	Com	4.18	377.	387.	90.	38.	.53
21/02/84	.5	6.25	368.	376.	89.	27.	.55
	Com	4.77	386.	365.	11.	45.	.36
	.5	4.89	361.	363.	13.	30.	.49
14/03/84	.5	5.56	375.	372.	14.	30.	.40
	Com	3.84	368.	341.	25.	13.	.67
	.5	3.09	381.	339.	21.	24.	.59
10/04/84	.5	3.81	371.	346.	21.	22.	.54
	Com	3.94	402.	397.	22.	22.	.30
24/04/84	.5	3.66	375.	352.	25.	25.	.27
	Com	3.79	408.	400.	23.	25.	.23
16/05/84	.5	3.28	375.	358.	43.	64.	.44
	Com	3.98	369.	358.	38.	39.	.46
	.5	4.17	391.	353.	45.	18.	.28
	Com	2.89	393.	357.	51.	31.	.25
4/06/84	.5	4.27	395.	359.	47.	20.	.31
	Com	5.72	433.	399.	39.	31.	.36
27/06/84	.5	5.70	432.	420.	38.	19.	.52
	Com	6.34	438.	404.	35.	17.	.24
	.5	4.20	384.	411.	24.	12.	.24
	Com	4.34	386.	411.	35.	23.	.56
	.5	5.09	387.	409.	47.	42.	.26

Table 7 (continued)

STATION 15

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
13/06/83	0.0	1.93	565.	509.	30.	123.	.08
	.5	1.44	573.	509.	23.	135.	.08
	1.0	1.65	597.	508.	34.	123.	.06
	2.0	1.35	578.	516.	25.	123.	.05
	Com	2.16	453.	504.	25.	110.	.04
14/06/83	0.0	2.98	498.	498.	14.	109.	.03
	.5	2.89	571.	507.	21.	109.	.05
	1.0	2.84	587.	501.	17.	109.	.06
	2.0	3.29	557.	507.	25.	109.	.08
	Com	2.66	533.	507.	27.	153.	.06
27/06/83	0.0	1.51	522.	527.	82.	26.	.68
	.5	1.43	531.	533.	78.	33.	.40
	1.0	1.56	515.	535.	108.	34.	.34
	2.0	1.79	526.	521.	98.	16.	.34
	Com	1.56	491.	535.	82.	51.	.34
28/06/83	0.0	2.20	522.	526.	69.	17.	.65
	.5	1.94	522.	535.	66.	22.	.58
	1.0	2.09	533.	528.	86.	33.	.46
	2.0	2.40	531.	535.	78.	28.	.38
	Com	1.81	495.	512.	92.	8.	.36
19/07/83	0.0	1.16	472.	446.	68.	40.	.13
	.5	1.29	475.	453.	69.	46.	.13
	1.0	1.89	491.	443.	79.	40.	.13
	2.0	1.04	490.	444.	76.	54.	.08
	Com	1.91	465.	445.	79.	53.	.10
23/07/83	0.0	1.78	487.	452.	66.	113.	.35
	.5	1.96	478.	467.	68.	100.	.35
	1.0	2.64	497.	458.	51.	89.	.05
	2.0	2.07	482.	462.	63.	100.	.03
	Com	2.09	467.	460.	71.	126.	.03
17/08/83	0.0	4.03	433.	437.	255.	77.	2.98
	.5	3.91	442.	434.	239.	73.	2.90
	1.0	4.16	440.	442.	246.	109.	3.29
	2.0	3.28	442.	444.	248.	93.	3.36
	Com	3.89	420.	475.	243.	127.	1.19
27/08/83	0.0	4.25	448.	437.	174.	115.	2.01
	.5	4.61	452.	437.	197.	97.	2.28
	1.0	4.90	446.	436.	195.	91.	2.21
	2.0	4.79	456.	441.	194.	106.	2.01
	Com	4.42	427.	434.	201.	148.	1.86
15/08/83	0.0	.93	497.	435.	566.	63.	.43
	.5	.70	480.	415.	553.	69.	.28
	1.0	1.39	483.	423.	566.	81.	.58
	2.0	.70	484.	425.	579.	73.	.58
	Com	0.78	458.	425.	510.	80.	.35
16/08/83	0.0		452.	421.	420.	71.	.95
	.5	1.04	452.	415.	444.	72.	.86
	1.0	.81	454.	417.	457.	76.	.70
	2.0		472.	411.	480.	61.	.78
	Com		438.	437.	447.	56.	.73
31/08/83	0.0	2.69	500.	408.	197.	73.	.55
	.5	2.72	495.	418.	168.	72.	.75
	1.0	2.05	498.	428.	187.	83.	
	2.0	2.41	498.	418.	167.	83.	
	Com	2.39	475.	418.	165.	74.	
27/09/83	0.0	3.00	503.	418.	431.	52.	2.19
	.5	2.95	505.	422.	422.	57.	2.19
	1.0	3.15	507.	432.	405.	101.	2.43
	2.0	2.97	503.	426.	454.	71.	.91
	Com	2.96	482.	420.	330.	58.	.49
13/09/83	0.0	3.59	451.	380.	410.	49.	.36
	.5	3.10	439.	387.	407.	47.	.78
	1.0	3.58	421.	391.	401.	57.	1.08
	2.0	3.49	421.	391.	401.	50.	.56
	Com	3.04	406.	387.	404.	51.	.43
15/09/83	0.0	3.58	415.	397.	750.	38.	.45
	.5	3.38	441.	397.	743.	38.	.43
	1.0	3.82	421.	399.	699.	39.	.45
	2.0	3.58	441.	399.	749.	42.	.43
	Com	3.85	419.	383.	762.	40.	.31
26/09/83	0.0	4.76	443.	398.	335.	21.	1.33
	.5	4.29	425.	396.	330.	23.	1.75
	1.0	4.12	429.	391.	340.	22.	.70
	2.0	4.09	437.	388.	336.	34.	.43
	Com	4.09	422.	389.	340.	30.	.57
27/09/83	0.0	4.74	423.	400.	254.	41.	1.83
	.5	4.07	429.	400.	247.	40.	1.62
	1.0	4.87	446.	405.	245.	40.	1.30
	2.0	3.72	432.	403.	249.	41.	1.30
	Com	4.17	417.	401.	256.	42.	2.45
11/10/83	0.0	5.58	459.	371.	518.	33.	.43
	.5	5.74	451.	366.	504.	27.	.41
	1.0	5.56	453.	381.	485.	28.	.38
	2.0	4.87	451.	369.	495.	26.	.35
	Com	5.45	423.	381.	450.	40.	.40
12/10/83	0.0	5.55	465.	377.	328.	26.	.19
	.5	5.23	453.	373.	364.	27.	.18
	1.0	5.24	459.	377.	336.	25.	.14
	2.0	5.57	467.	373.	354.	36.	.35
	Com	5.56	436.	373.	344.	31.	.38

Table 7 (continued)

STATION 15

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
24/10/83	0.0	5.43	403.	376.	380.	44.	.73
	.5	5.51	398.	374.	395.	53.	.73
	1.0	5.52	404.	374.	399.	47.	.64
	2.0	5.03	403.	366.	374.	49.	.74
	Com	5.11	382.	358.	393.	49.	.76
25/10/83	0.0	5.74	388.	361.	374.	43.	.85
	.5	5.78	387.	359.	307.	32.	.73
	1.0	5.82	387.	363.	309.	43.	.90
	2.0	5.92	395.	362.	309.	34.	.93
	Com	5.43	373.	376.	376.	31.	.79
7/11/83	0.0	3.95	390.	403.	578.	37.	.38
	.5	4.42	388.	392.	577.	34.	.41
	1.0	4.31	391.	399.	586.	29.	.55
	2.0	4.20	389.	398.	615.	33.	.41
	Com	4.44	362.	396.	528.	39.	.39
8/11/83	0.0	5.40	386.	381.	479.	30.	.38
	.5	5.55	387.	385.	483.	31.	.46
	1.0	5.07	385.	386.	473.	29.	.34
	2.0	5.08	387.	381.	477.	37.	.33
	Com	4.82	364.	387.	521.	29.	.33
17/11/83	0.0	5.22	397.	373.	223.	25.	1.03
	.5	6.66	393.	374.	244.	22.	1.08
	1.0	6.45	398.	380.	242.	20.	1.05
	2.0	6.86	404.	373.	243.	30.	.99
	Com	6.57	376.	371.	263.	22.	.98
18/11/83	0.0	8.46	382.	375.	182.	25.	1.14
	.5	7.87	395.	376.	187.	22.	1.03
	1.0	8.00	386.	376.	187.	21.	1.13
	2.0	8.02	397.	378.	194.	29.	1.04
	Com	8.20	374.	374.	197.	20.	
1/12/83	.5	4.15	374.	321.	195.	39.	
	Com	3.54	389.	341.	225.	56.	
	Prf	4.32	381.	318.	212.	54.	
2/12/83	.5	3.45	393.	331.	232.	44.	.23
	Com	3.70	391.	326.	219.	43.	.20
	Prf	3.83	379.	328.	198.	43.	.18
20/12/83	.5	4.45	392.	354.	74.	25.	.20
	Com	3.40	390.	379.	75.	29.	.28
	Prf	3.84	378.	367.	70.	23.	.15
21/12/83	.5	4.02	399.	360.	69.	25.	.25
	Com	3.89	379.	358.	64.	23.	.18
	Prf	2.87	389.	360.	67.	26.	.20
9/01/84	.5	3.89	376.	394.	116.	22.	.49
	Com	3.96	378.	409.	118.	25.	.54
	Prf	3.08	375.	406.	126.	29.	.42
10/01/84	.5	4.87	396.	397.	66.	18.	.39
	Com	5.30	396.	395.	67.	20.	.42
	Prf	5.03	395.	401.	65.	18.	.42
31/01/84	.5	4.35	395.	397.	117.	38.	.46
	Com	3.64	370.	364.	124.	35.	.53
	Prf	4.49	366.	365.	116.	36.	.50
1/02/84	.5	5.73	371.	372.	92.	24.	.48
	Com	4.34	384.	364.	96.	22.	.50
	Prf	4.98	382.	373.	96.	20.	.44
20/02/84	.5	5.18	387.	380.	30.	50.	.33
	Com	4.98	371.	381.	23.	43.	.51
	Prf	5.02	387.	379.	17.	51.	.44
21/02/84	.5	3.86	378.	382.	48.	38.	.35
	Com	4.69	378.	388.	45.	41.	.56
	Prf	3.49	402.	394.	47.	47.	.48
14/03/84	.5	5.03	384.	339.	31.	25.	.75
	Com	4.20	388.	341.	40.	24.	.69
	Prf	4.09	387.	325.	36.	25.	.73
15/03/84	.5	4.12	388.	353.	39.	16.	.82
	Com	4.32	386.	343.	34.	15.	.84
	Prf	4.52	386.	342.	40.	17.	.92
9/04/84	.5	4.22	397.	402.	16.	23.	1.02
	Com	4.22	402.	402.	20.	24.	.71
	Prf	3.52	412.	403.	16.	22.	.71
10/04/84	.5	2.87	398.	399.	23.	24.	.56
	Com	3.47	391.	400.	18.	22.	.25
	Prf	3.74	397.	405.	22.	25.	.42
23/04/84	.5	3.51	371.	367.	52.	56.	.38
	Com	3.44	370.	370.	55.	52.	.48
	Prf	2.90	370.	365.	54.	60.	.41
24/04/84	.5	3.28	376.	362.	43.	58.	.43
	Com	3.66	371.	364.	41.	53.	.41
	Prf	2.91	382.	367.	44.	67.	.44
16/05/84	.5	6.19	445.	413.	72.	24.	.28
	Com	5.17	444.	404.	72.	32.	.29
	Prf	4.98	450.	401.	72.	28.	.25
17/05/84	.5	4.54	456.	417.	72.	23.	.34
	Com	5.92	438.	413.	74.	29.	.32
	Prf	5.10	449.	420.	76.	24.	.31
4/06/84	.5	6.23	438.	405.	53.	22.	.21
	Com	6.89	442.	410.	48.	21.	.19
	Prf	5.65	440.	413.	51.	24.	.24
6/06/84	.5	7.80	446.	419.	44.	22.	.32
	Com	6.05	445.	422.	44.	20.	.41
	Prf	5.06	447.	425.	46.	29.	.46
27/06/84	.5	4.13	392.	410.	26.	22.	.24
	Com	4.26	393.	410.	25.	26.	.22
	Prf	4.83	397.	411.	20.	21.	.22
28/06/84	.5	5.40	393.	411.	29.	21.	.24
	Com	5.10	391.	413.	32.	22.	.26
	Prf	5.82	400.	407.	34.	27.	.31

Table 7 (continued)

STATION 26

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
14/06/83	0.0	10.33	598.	587.	26.	156.	.11
	.5	8.99	687.	597.	26.	156.	.13
	1.0	8.22	617.	592.	32.	156.	.13
	2.0	8.31	711.	592.	30.	156.	.14
	Com	8.06	507.	581.	25.	156.	.14
27/06/83	0.0	7.91	525.	499.	153.	97.	.84
	.5	574.	510.	510.	139.	96.	.53
	1.0	6.69	545.	516.	60.	115.	.45
	2.0	7.12	556.	507.	127.	231.	.48
	Com	7.12	526.	510.	141.	1581.	1.59
23/07/83	0.0		828.	763.	852.	1754.	1.59
	.5		786.	695.	1605.	1598.	2.09
	1.0		799.	704.	1554.	1627.	1.50
	2.0		801.	666.	1374.	1715.	1.74
	Com		747.	743.	1533.	129.	1.13
1/08/83	0.0	6.34	401.	409.	690.	150.	1.13
	.5	6.08	492.	410.	673.	180.	.94
	1.0	6.59	535.	416.	736.	204.	1.06
	2.0	4.83	517.	427.	650.	151.	2.45
	Com	6.08	418.	421.	676.	163.	.95
16/08/83	0.0	2.44	482.	508.	640.	164.	.86
	.5	2.78	474.	496.	542.	176.	.70
	1.0	2.09	449.	506.	627.	163.	.73
	2.0	2.09	471.	494.	640.	85.	1.36
	Com	2.22	440.	488.	580.	96.	2.60
2/09/83	0.0	6.79	500.	416.	554.	82.	.45
	.5	6.03	476.	410.	619.	83.	.45
	1.0	6.54	505.	408.	625.	109.	.45
	2.0	6.66	522.	400.	635.	119.	.53
	Com	7.05	500.	404.	670.	108.	.56
15/09/83	0.0	4.47	417.	356.	718.	8.	.38
	.5	4.99	415.	356.	755.	11.	.63
	1.0	5.16	433.	374.	781.	9.	.58
	2.0	4.93	432.	348.	762.	14.	.58
	Com	5.00	408.	338.	831.	52.	.61
27/09/83	0.0	5.85	402.	380.	444.	59.	.34
	.5	4.92	409.	378.	470.	48.	.63
	1.0	4.96	414.	379.	448.	58.	.80
	2.0	5.20	418.	377.	453.	71.	.55
	Com	5.99	399.	376.	466.		
11/10/83	0.0	12.40	572.	363.	41.		
	.5	11.06	482.	367.	40.		
	1.0	12.60	466.	373.	48.		
	2.0	12.21	476.	365.	47.		
	Com	12.22	489.	373.	53.		

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
24/10/83	0.0	12.31	404.	371.	149.	22.	1.61
	.5	11.93	398.	375.	168.	36.	1.84
	1.0	10.89	396.	367.	171.	21.	1.36
	2.0	10.79	392.	371.	159.	18.	.90
	Com	11.22	367.	383.	167.	40.	1.23
7/11/83	0.0	14.40	401.	390.	214.	49.	.74
	.5	15.36	402.	393.	215.	49.	.74
	1.0	13.63	389.	389.	210.	45.	.51
	2.0	14.09	395.	390.	212.	44.	.63
	Com	14.12	374.	395.	196.	43.	.63
17/11/83	0.0	14.25	375.	371.	139.	27.	1.28
	.5	14.11	382.	370.	163.	32.	1.15
	1.0	13.35	393.	372.	173.	36.	.91
	2.0	13.51	384.	372.	158.	24.	1.09
	Com	13.62	381.	367.	163.	26.	1.35
2/12/83	.5	8.26	401.	369.	42.	88.	.26
	Com	4.84	389.	388.	35.	102.	.34
	Prf	4.75	449.	370.	42.	93.	.34
21/12/83	.5	7.71	418.	416.	34.	64.	.51
	Com	7.26	409.	425.	34.	66.	.66
	Prf	6.84	412.	424.	35.	67.	.61
9/01/84	.5	13.90	425.	409.	30.	58.	1.19
	Com	13.85	414.	420.	35.	51.	.91
	Prf	16.27	411.	417.	34.	40.	1.04
31/01/84	.5	14.44	531.	525.	96.	81.	.83
	Com	12.54	525.	541.	98.	132.	.73
	Prf	13.64	547.	555.	104.	87.	.68
20/02/84	.5	10.51	450.	441.	20.	91.	.57
	Com	9.90	451.	424.	21.	130.	.48
	Prf	8.13	449.	423.	17.	108.	.49
15/03/84	.5	5.98	430.	406.	39.	44.	.82
	Com	6.24	448.	427.	50.	49.	.89
	Prf	6.18	442.	416.	42.	47.	1.06
9/04/84	.5	7.78	507.	473.	29.	67.	.75
	Com	9.26	497.	477.	25.	78.	1.86
	Prf	7.81	500.	482.	24.	70.	1.38
23/04/84	.5	11.91	494.	487.	41.	110.	1.07
	Com	10.59	499.	485.	31.	105.	1.51
	Prf	11.22	487.	488.	31.	116.	.58
17/05/84	.5	12.00	545.	472.	47.	75.	.73
	Com	13.28	543.	484.	50.	80.	.72
	Prf	12.72	545.	481.	47.	82.	.64
6/06/84	.5	9.65	506.	447.	39.	28.	.66
	Com	11.03	526.	452.	43.	160.	.58
	Prf	11.00	548.	475.	61.	217.	.95
28/06/84	.5	12.46	452.	418.	77.	85.	.34
	Com	9.50	468.	450.	76.	93.	.41
	Prf	10.13	474.	449.	81.	93.	.50

Table 7 (continued)

STATION 28

Date	Z	Biomass	TP	SRP	NO ₃ -N	NH ₄ -N	TN
14/06/83	0.0	4.37	584.	530.	15.	118.	.03
	.5	4.21	588.	530.	18.	118.	.06
	1.0	3.71	567.	530.	21.	118.	.09
	2.0	3.63	577.	530.	17.	118.	.08
	Com	3.67	549.	530.	21.	118.	.08
27/06/83	0.0	3.36	509.	503.	82.	33.	.43
	.5	3.02	530.	511.	78.	55.	.39
	1.0	5.79	515.	513.	109.	57.	.64
	2.0	2.62	517.	505.	78.	43.	.40
	Com	2.51	511.	512.	92.	53.	.56
23/07/83	0.0	2.28	469.	436.	54.	94.	.04
	.5	2.17	468.	443.	55.	100.	
	1.0	2.09	482.	445.	69.	100.	
	2.0	1.96	472.	443.	58.	137.	.03
	Com	2.09	459.	443.	58.	223.	.05
1/08/83	0.0	1.79	453.	438.	10.	75.	2.58
	.5	1.92	448.	435.	10.	89.	2.33
	1.0	1.78	444.	451.	0.	85.	2.11
	2.0	2.38	444.	444.	0.	81.	
	Com	1.63	429.	494.	6.		2.51
16/08/83	0.0	2.55	462.	377.	195.	92.	1.34
	.5	2.55	459.	385.	199.	90.	.93
	1.0	2.55	455.	405.	209.	86.	.96
	2.0	2.44	456.	377.	210.	81.	1.03
	Com	2.61	432.	387.	193.	81.	.75
2/09/83	0.0	4.13	505.	404.	509.	43.	
	.5	3.58	499.	410.	499.	56.	.85
	1.0	3.78	500.	402.	528.	67.	1.84
	2.0	3.88	502.	408.	506.	62.	
	Com	3.25	470.	404.	483.	52.	
15/09/83	0.0	3.82	425.	373.	693.	69.	.53
	.5	3.62	439.	381.	649.	62.	.64
	1.0	3.36	443.	364.	649.	66.	.69
	2.0	3.79	432.	370.	624.	67.	.95
	Com	3.65	421.	372.	649.	66.	.49
27/09/83	0.0	3.35	433.	331.	466.	18.	.52
	.5	2.81	423.	385.	449.	11.	.51
	1.0	3.29	415.	387.	462.	17.	.61
	2.0	2.95	404.	388.	370.	18.	.83
	Com	3.03	393.	389.	504.	34.	1.11
11/10/83	0.0	6.38	472.	364.	386.	22.	.46
	.5	4.16	459.	370.	415.	32.	.34
	1.0	4.57	468.	371.	415.	27.	.41
	2.0	4.54	459.	370.	379.	27.	.41
	Com	4.59	438.	373.	399.	30.	.39
24/10/83	0.0	6.30	391.	356.	394.	42.	1.01
	.5	6.11	399.	354.	394.	34.	.79
	1.0	6.41	404.	365.	389.	22.	1.04
	2.0	6.60	397.	365.	399.	42.	.90
	Com	6.06	381.	368.	355.	47.	.67
7/11/83	0.0	8.55	392.	393.	272.	31.	.43
	.5	7.82	387.	393.	274.	38.	.69
	1.0	8.25	387.	392.	261.	33.	.50
	2.0	7.76	387.	397.	265.	29.	.41
	Com	7.72	363.	385.	274.	32.	.50
17/11/83	0.0	5.08	399.	376.	339.	17.	.99
	.5	5.13	388.	376.	361.	21.	.94
	1.0	4.82	396.	365.	355.	20.	1.23
	2.0	4.97	402.	371.	367.	22.	1.08
	Com	4.82	379.	383.	399.	19.	.96
2/12/83	.5	4.62	392.	351.	260.	42.	.13
	Com	3.07	386.	348.	244.	48.	.15
	Prf	3.27	398.	349.	208.	58.	.18
21/12/83	.5	2.81	395.	378.	133.	29.	.15
	Com	2.13	398.	376.	142.	30.	.18
	Prf	3.07	390.	377.	140.	31.	.20
9/01/84	.5	5.82	380.	397.	69.	23.	.70
	Com	5.97	381.	401.	72.	23.	.42
	Prf	3.98	384.	399.	74.	23.	.53
31/01/84	.5	6.41	392.	404.	129.	18.	.40
	Com	6.91	407.	408.	119.	33.	.37
	Prf	7.02	371.	412.	115.	21.	.25
20/02/84	.5	4.55	382.	379.	42.	81.	.44
	Com	3.20	387.	385.	40.	71.	.38
	Prf	4.42	387.	375.	40.	45.	.33
15/03/84	.5	4.39	388.	345.	63.	35.	.82
	Com	3.70	392.	345.	75.	23.	.75
	Prf	4.18	393.	351.	72.	32.	.95
9/04/84	.5	6.00	435.	446.	17.	40.	2.81
	Com	5.08	435.	444.	16.	36.	1.02
	Prf	4.55	438.	443.	19.	35.	3.17
23/04/84	.5	5.51	407.	425.	29.	73.	.66
	Com	4.80	422.	422.	36.	73.	.50
	Prf	4.12	410.	430.	40.	71.	.58
17/05/84	.5	4.88	409.	378.	57.	33.	.31
	Com	4.91	410.	394.	58.	32.	.32
	Prf	4.90	429.	373.	56.	33.	.31
6/06/84	.5	5.68	454.	407.	38.	40.	.46
	Com	5.84	453.	416.	38.	47.	.36
	Prf	5.55	446.	407.	40.	54.	.41
28/06/84	.5	4.46	409.	407.	31.	18.	.16
	Com	3.94	412.	408.	32.	19.	.24
	Prf	4.82	416.	407.	31.	19.	.29

Table 8. Statistical test for differences in phytoplankton biomass and nutrient concentration among sampling depths.

Variable	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Significance
Biomass	Block	2368.83	58	41.15	213.80	.000
	Depth	1.20	3	0.40	2.10	.11
	Residual	32.91	171	0.19		
Total Phosphorus	Block	1305455.48	59	22126.36	94.48	.000
	Depth	204.81	3	68.27	0.29	.83
	Residual	41453.68	177	234.20		
Soluble Reactive Phosphorus	Block	1004012.23	59	17017.16	279.00	.000
	Depth	84.57	3	28.19	0.46	.71
	Residual	10795.93	177	60.99		
Nitrate Nitrogen	Block	17752352.43	59	266989.02	122.79	.000
	Depth	8744.90	3	2914.97	1.34	.26
	Residual	384859.60	177	2174.35		
Ammonia Nitrogen	Block	10296992.83	59	174525.30	657.06	.000
	Depth	784.77	3	261.59	0.98	.40
	Residual	47013.73	177	265.61		
Total Nitrogen	Block	82.79	59	1.40	20.73	.000
	Depth	0.29	3	0.10	1.45	.23
	Residual	11.51	170	0.07		

Horizontal Variations

Lake Chapala was warm, shallow and turbid (Table 9). Significant differences existed among stations in the measured physical parameters (Table 10). The difference in average Secchi depth among stations is more clearly seen in Figure 7. Of the five stations sampled, Station 26 was the shallowest and subject to the most light attenuation, while Station 11 was relatively deep and clear. Although Station 26 was by far the most turbid station it was also the most shallow and consequently the ratio of $Z(\text{mix})$ to $Z(\text{eu})$ was no greater there than at most other stations (Table 11, Figure 8). In fact, ignoring data from the peak of the rainy season (July 23 - September 15), Station 26 actually has a relatively favorable light climate (Table 9).

Means and standard deviations of the chemical parameters are presented in Table 12. Significant differences existed in nutrient concentrations among stations (Table 13, Table 14).

The overall TN:TP ratio by weight on Lake Chapala was only 1.48. Of this phosphorus, 93% was SRP and therefore presumably directly available to the phytoplankton community. The annual mean concentration of the two forms of inorganic nitrogen were fairly high. However, annual median values, especially at Stations 03 and 11, were much lower (Table 12). This is due to a large nitrogen pulse

Table 9. Physical characteristics of each station on Lake Chapala. Values are presented as follows:

mean + one standard deviation
(observed range)
n = number of observations

Station	Surface Temp (C)	Secchi Depth (m)	Extinction Coefficient (n^{-1})	Photic Depth (m)	Lake Depth (m)	Z(mix):Z(eu) Ratio
03	20.5 +2.4 (16.6, 24.3) n = 23	0.62 +0.15 (0.36, 0.94) n = 22	2.500 +0.43 (1.637, 3.826) n = 23	1.89 +0.35 (1.02, 2.39) n = 23	4.42 +0.47 (3.45, 4.95) n = 23	2.43 +0.65 (2.27)* (1.80, 4.85) n = 23
11	20.9 +2.4 (17.0, 24.4) n = 23	0.71 +0.18 (0.45, 1.12) n = 22	2.290 +0.490 (1.225, 2.985) n = 23	2.11 +0.43 (1.40, 3.45) n = 23	6.93 +0.47 (5.95, 7.45) n = 23	3.40 +0.67 (3.49) (1.84, 5.32) n = 23
15	20.5 +2.4 (15.4, 24.9) n = 46	0.58 +0.11 (0.38, 0.94) n = 45	2.570 +0.310 (1.797, 3.135) n = 46	1.80 +0.30 (1.05, 2.75) n = 46	6.93 +0.47 (5.95, 7.45) n = 46	3.96 +0.79 (3.88) (2.31, 6.71) n = 46
28	20.6 +2.4 (15.2, 24.2) n = 23	0.54 +0.17 (0.23, 0.99) n = 23	2.900 +0.820 (1.891, 6.222) n = 23	1.77 +0.41 (1.05, 2.44) n = 23	5.18 +0.47 (4.20, 5.70) n = 23	3.25 +0.89 (2.96) (2.23, 5.24) n = 23
26	20.5 +2.4 (15.0, 23.4) n = 23	0.18 +0.13 (0.03, 0.66) n = 23	9.730 +3.180 (2.818, 16.790) n = 23	0.62 +0.30 (0.24, 1.64) n = 23	1.93 +0.47 (0.95, 2.45) n = 23	3.71 +2.00 (3.03)** (1.49, 9.38) n = 23

* median value of Z(mix):Z(eu) ratio given in parenthesis

** without data from July 23 to September 15 1983, Station 26 mean ratio = 2.91 + 0.87

Table 10. Two-way analysis of variance testing for differences in the physical factors relating to the underwater light climate among stations and among sampling series.

Variable	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Significance
Secchi Depth	Station	3.752	4	0.938	63.62	p<.001
	Series	1.096	22	0.050	3.38	p<.001
	Residual	1.253	85	0.015		
Extinction Coefficient	Station	952.740	4	238.185	110.32	p<.001
	Series	57.924	22	2.633	1.22	p=.253
	Residual	190.001	88	2.159		
Photic Depth	Station	30.954	4	7.739	76.934	p<.001
	Series	4.581	22	0.208	2.070	p=.009
	Residual	8.852	88	0.101		
Z(mix): Z(eu)	Station	30.828	4	7.707	8.774	p<.001
	Series	55.939	22	2.543	2.895	p<.001
	Residual	77.294	88	0.878		

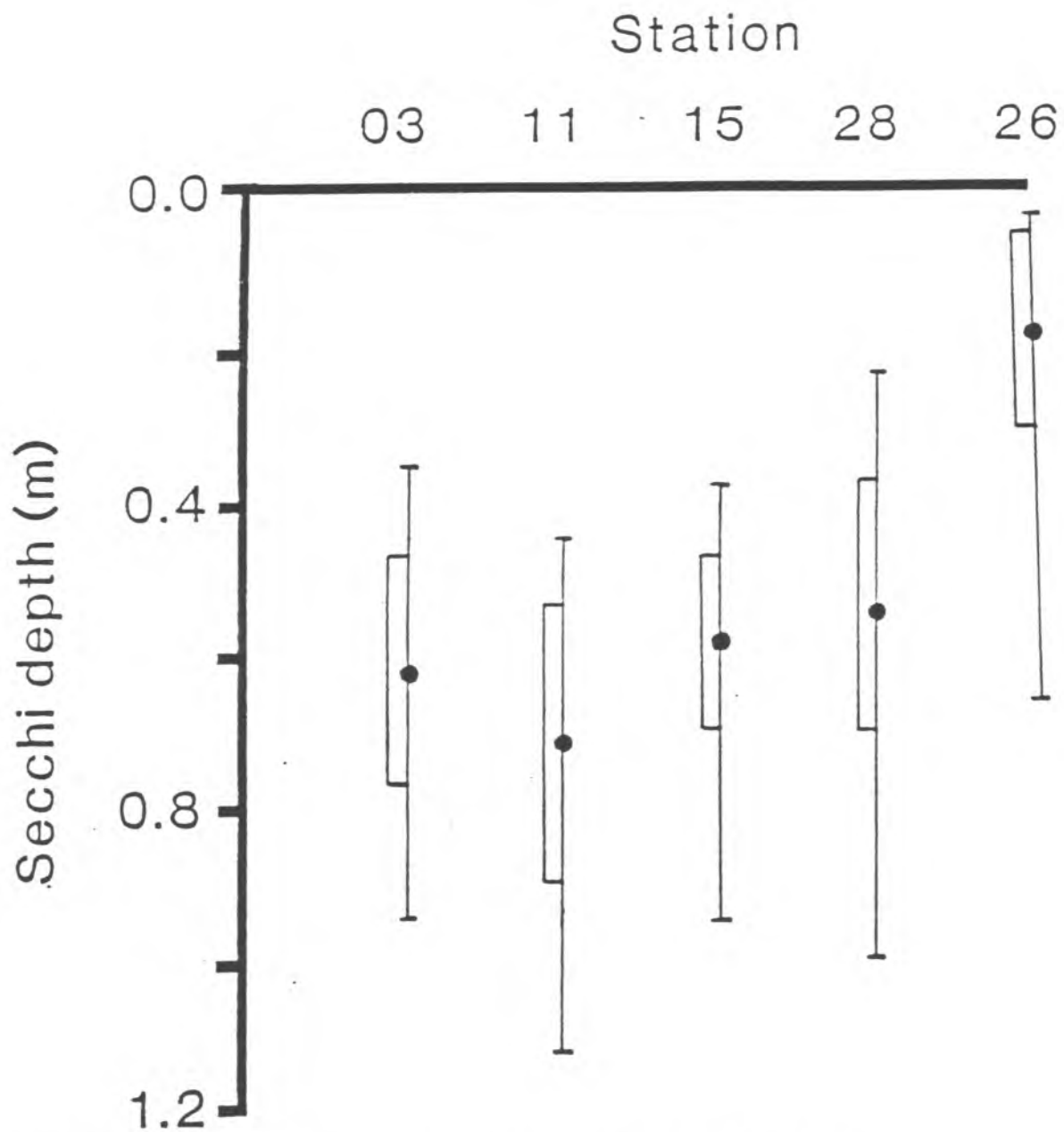


Figure 7. Range, mean, and one standard deviation about the mean of Secchi depth for each station on Lake Chapala.

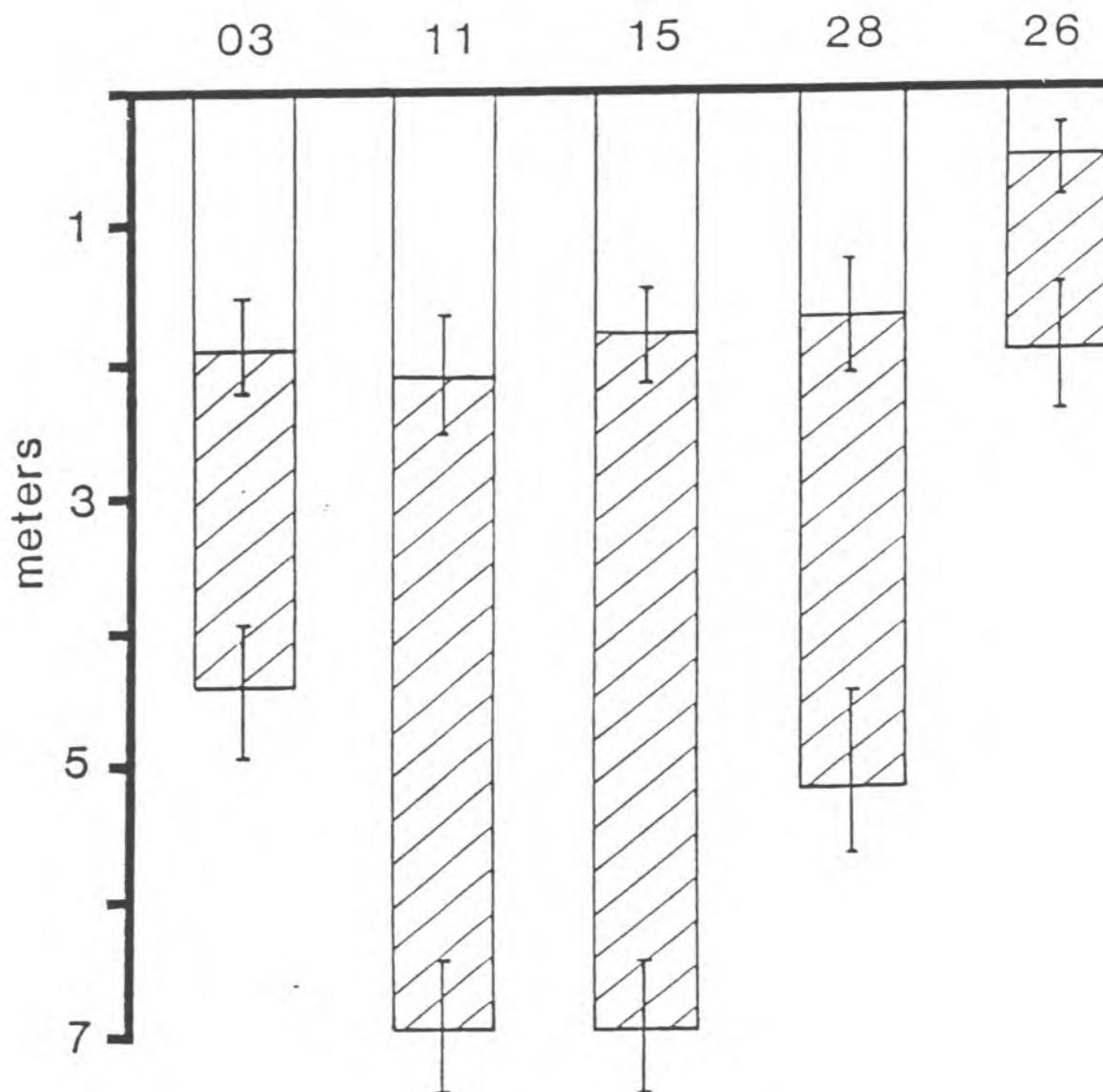


Figure 8. Mean euphotic depth (clear) in relation to the entire mixing depth (hatched) at each station. Bars are one standard deviation about the mean.

Table 12. Chemical characteristics of each station on Lake Chapala. Values are presented as follows:

mean + one standard deviation
(observed range)

median

n = number of observations

Station	pH	Total Alkalinity mg l ⁻¹	Total Phosphorus ug l ⁻¹	Soluble Phosphorus ug l ⁻¹	Nitrate Nitrogen ug l ⁻¹	Ammonia Nitrogen ug l ⁻¹	Total Nitrogen mg l ⁻¹
03	(8.3, 8.7) 8.5 n = 23	257 +27 (180, 324) 252 n = 23	426 +57 (368, 587) 400 n = 23	388 +43 (315, 468) 392 n = 23	53 +56 (*, 273) 40 n = 23	48 +52 (*, 273) 32 n = 23	0.58 +0.46 (0.04, 2.12) .45 n = 23
11	(8.3, 8.9) 8.5 n = 23	272 +68 (197, 777) 255 n = 23	424 +55 (361, 582) 399 n = 23	392 +41 (335, 488) 387 n = 23	62 +45 (13, 195) 46 n = 23	38 +23 (11, 107) 31 n = 23	0.60 +0.51 (0.05, 2.05) .46 n = 23
15	(8.2, 8.9) 8.5 n = 46	252 +25 (196, 324) 247 n = 46	428 +55 (370, 585) 405 n = 46	403 +46 (326, 531) 398 n = 46	190 +185 (18, 729) 97 n = 46	44 +27 (15, 125) 32 n = 46	0.61 +0.59 (*, 3.20) .48 n = 46
28	(8.2, 8.7) 8.5 n = 23	250 +29 (199, 324) 240 n = 23	433 +49 (381, 574) 416 n = 23	405 +46 (345, 530) 394 n = 23	186 +187 (*, 649) 94 n = 23	49 +29 (16, 118) 37 n = 23	0.62 +0.51 (0.04, 2.29) .45 n = 23
26	(7.4-8.6) 8.4 n = 23	231 +61 (63, 332) 234 n = 23	487 +93 (387, 800) 469 n = 23	452 +81 (365, 702) 427 n = 23	255 +356 (20, 1443) 75 n = 23	159 +324 (*, 1628) 88 n = 23	0.86 +0.48 (0.13, 1.86) .74 n = 23

* = below detection limits

Table 13. Two-way analysis of variance testing for significant differences in nutrient concentration among stations and among sampling series.

Variable	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Significance
Total P	Series	670011.95	22	30455.09	169.79	p<.001
	Station	115884.71	4	28971.17	11.03	p<.001
	Series*Station	231126.49	88	2626.44	14.64	p<.001
	Error	20628.00	115	179.37		
Soluble P	Series	460546.12	22	20933.91	307.97	p<.001
	Station	100436.65	4	25109.16	11.43	p<.001
	Series*Station	193422.75	88	2197.99	32.34	p<.001
	Error	7817.00	115	67.97		
Nitrate N	Series	3062390.8	22	139199.6	53.81	p<.001
	Station	1311510.7	4	327877.7	5.81	p<.001
	Series*Station	4967587.3	88	56449.9	21.83	p<.001
	Error	297455.5	115	2586.6		
Ammonia N	Series	1276547.4	22	58024.9	167.92	p<.001
	Station	444748.1	4	111187.0	2.60	p<.050
	Series*Station	3769390.5	88	42834.0	123.96	p<.001
	Error	39737.5	115	345.5		
Total N	Series	38.21	22	1.74	22.99	p<.001
	Station	2.47	4	0.62	2.67	p<.050
	Series*Station	20.16	87	0.23	3.07	p<.001
	Error	8.54	113	0.08		

Table 14. Student Newman-Keuls test for specific differences in nutrient concentration among stations. $H_0: a - b = 0.0$ where a and b are the mean values of the variable under consideration at two stations. Stations on the same line have means which are not significantly different from each other.

Variable	Comparison a vs. b	Difference a - b =	q	P	q (.01, 115, p)	Conclusion
Total	26 vs. 11	60.2	30.40	5	4.709	reject H_0
Phosphorus	26 vs. 03	57.6	29.09	4	4.497	reject H_0
(SE=1.98)	26 vs. 15	53.9	27.22	3	4.200	reject H_0
	26 vs. 28	50.0	25.25	2	3.702	reject H_0
	28 vs. 11	10.2	5.15	4	4.497	reject H_0
	28 vs. 03	7.6	3.84	3	4.200	accept H_0
	28 vs. 15 (do not test)					accept H_0
	15 vs. 11	6.3	3.18	3	4.200	accept H_0
	15 vs. 03 (do not test)					accept H_0
	03 vs. 11 (do not test)					accept H_0
Overall conclusion: <u>11</u> <u>03</u> <u>15</u> <u>28</u> <u>26</u> *						
Soluble	26 vs. 11	56.8	46.56	5	4.709	reject H_0
Reactive	26 vs. 03	56.4	46.23	4	4.497	reject H_0
Phosphorus	26 vs. 15	44.3	36.31	3	4.200	reject H_0
(SE=1.22)	26 vs. 28	44.0	36.07	2	3.702	reject H_0
	28 vs. 11	12.8	10.49	4	4.497	reject H_0
	28 vs. 03	12.4	10.16	3	4.200	reject H_0
	28 vs. 15	0.3	0.25	2	3.702	accept H_0
	15 vs. 11	12.1	9.92	3	4.200	reject H_0
	15 vs. 03	12.5	10.25	2	3.702	reject H_0
	03 vs. 11	0.5	0.41	2	3.702	accept H_0
Overall conclusion: <u>11</u> <u>03</u> <u>15</u> <u>28</u> <u>26</u>						
Nitrate	26 vs. 03	186.9	24.92	5	4.709	reject H_0
Nitrogen	26 vs. 11	178.0	23.73	4	4.497	reject H_0
(SE=7.50)	26 vs. 28	53.7	7.16	3	4.200	reject H_0
	26 vs. 15	45.3	6.04	2	3.702	reject H_0
	15 vs. 03	141.6	18.88	4	4.497	reject H_0
	15 vs. 11	132.7	17.69	3	4.200	reject H_0
	15 vs. 28	8.4	1.12	2	3.702	accept H_0
	28 vs. 03	133.2	17.76	3	4.200	reject H_0
	28 vs. 11	124.3	16.57	2	3.702	reject H_0
	11 vs. 03	8.9	1.19	2	3.702	accept H_0
Overall conclusion: <u>03</u> <u>11</u> <u>28</u> <u>15</u> <u>26</u>						
Ammonia	26 vs. 11	116.0	42.34	5	4.709	reject H_0
Nitrogen	26 vs. 15	109.9	40.11	4	4.497	reject H_0
(SE=2.74)	26 vs. 03	107.5	39.23	3	4.200	reject H_0
	26 vs. 28	104.7	38.21	2	3.702	reject H_0
	28 vs. 11	11.3	4.12	4	4.497	accept H_0
	28 vs. 15 (do not test)					accept H_0
	28 vs. 03 (do not test)					accept H_0
	03 vs. 11 (do not test)					accept H_0
	03 vs. 15 (do not test)					accept H_0
	15 vs. 11 (do not test)					accept H_0
Overall conclusion: <u>11</u> <u>15</u> <u>03</u> <u>28</u> <u>26</u>						
Total	26 vs. 11	.277	6.76	5	4.709	reject H_0
Nitrogen	26 vs. 03	.274	6.68	4	4.497	reject H_0
(SE=.041)	26 vs. 15	.248	6.05	3	4.200	reject H_0
	26 vs. 28	.224	5.46	2	3.702	reject H_0
	28 vs. 11	.054	1.32	4	4.497	accept H_0
	28 vs. 03 (do not test)					accept H_0
	28 vs. 15 (do not test)					accept H_0
	15 vs. 11 (do not test)					accept H_0
	15 vs. 03 (do not test)					accept H_0
	03 vs. 11 (do not test)					accept H_0
Overall conclusion: <u>11</u> <u>03</u> <u>15</u> <u>28</u> <u>26</u>						

* Type II error. More data needed to determine if stations 03 and 15 belong with station 11 or station 28.

that entered the lake at the onset of the rainy period (see below).

The annual means and standard deviations of phytoplankton productivity and biomass at each station are given in Table 15. Phytoplankton productivity was significantly different among stations (Table 16). NPP was highest at Station 11 and lowest at Station 26. However, on a volumetric basis, NPP(max), NPP(mix), and NPP(eu) were all highest at Station 26 and lowest at Station 15 (Table 17).

The daily photosynthetic profiles (Table 18) illustrate three basic differences in phytoplankton productivity among stations. First, in relation to the other stations, the photic zone at Station 26 was very small while at Station 11 it was relatively large. Second, the productivity per unit volume was about twice as high at Station 26 than at any other station. Third, productivity at Station 26 was subject to large variability. Testing for differences in coefficients of variation in NPP shows that Station 26 was significantly more variable than the other stations.

Intensive taxonomic investigation of the phytoplankton community was not attempted. However, based on examination of water samples from each series at each station, four conclusions about this community are possible. First, the heterocystic blue-green algae are notable by their absence. In fact, they were apparently primarily represented by two

Table 15. Phytoplankton productivity and biomass at each station on Lake Chapala. Values are presented as follows:
 mean + one standard deviation
 (observed range)
 n = number of observations

STATION	Biomass (mg Chlorophyll m ⁻³)	NPP (mg Carbon m ⁻² day ⁻¹)	NPP (eu) (mg Carbon m ⁻³ day ⁻¹)	NPP (mix) (mg Carbon m ⁻³ day ⁻¹)	NPP (max) (mg Carbon m ⁻³ day ⁻¹)
03	4.96 +2.51 (1.63, 10.98) n = 23	249.1 +80.9 (67.7, 422.6) n = 23	135.8 +52.2 (39.4, 277.9) n = 23	56.4 +18.3 (17.6, 101.8) n = 23	281.6 +120.0 (88.4, 685.8) n = 23
11	4.51 +2.07 (0.88, 9.77) n = 23	281.3 +140.2 (129.0, 783.9) n = 23	137.1 +73.1 (62.6, 408.3) n = 23	40.8 +22.4 (21.7, 129.6) n = 23	276.5 +107.1 (85.8, 657.7) n = 23
15	3.99 +1.55 (0.59, 8.04) n = 46	208.8 +79.8 (74.2, 454.8) n = 46	119.7 +51.2 (34.0, 255.5) n = 46	30.3 +12.0 (10.2, 66.4) n = 46	231.3 + 65.8 (124.3, 396.1) n = 46
28	4.30 +1.56 (1.93, 8.11) n = 23	212.6 +74.8 (100.0, 374.2) n = 23	133.1 +63.9 (55.0, 331.1) n = 23	41.6 +16.3 (18.2, 87.0) n = 23	271.6 +129.0 (118.4, 793.5) n = 23
26	9.28 +3.44 (2.25, 14.12) n = 23	150.6 +92.9 (6.5, 348.4) n = 23	244.9 +122.8 (14.0, 585.0) n = 23	85.9 +73.2 (4.2, 328.7) n = 23	528.4 +361.3 (18.4, 1987.7) n = 23

Table 16. Two-way analysis of variance testing for significant differences in phytoplankton productivity and biomass among stations and among sampling series.

Variable	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Significance
NPP	Series	1120941.	22	50952.	65.42	p<.001
	Station	405131.	4	101283.	7.39	p<.001
	Series*Station	1206572.	88	13711.	17.60	p<.001
	Error	89568.	115	799.		
NPP (eu)	Series	1079146.	22	49052.	135.59	p<.001
	Station	652277.	4	163069.	13.11	p<.001
	Series*Station	1094526.	88	12438.	34.38	p<.001
	Error	41604.	115	362.		
NPP (mix)	Series	214737.	22	9761.	268.49	p<.001
	Station	122589.	4	30647.	7.35	p<.001
	Series*Station	367085.	88	4171.	114.74	p<.001
	Error	4181.	115	36.		
NPP (max)	Series	2949871.	22	134085.	36.34	p<.001
	Station	2624245.	4	656061.	12.53	p<.001
	Series*Station	4608764.	88	52372.	14.19	p<.001
	Error	424303.	115	3690.		
Biomass	Series	865.27	22	39.33	129.78	p<.001
	Station	808.62	4	202.15	50.10	p<.001
	Series*Station	351.04	87	4.04	13.31	p<.001
	Error	34.55	114	0.30		

Table 18. Daily phytosynthetic production ($\text{mg C m}^{-3} \text{ day}^{-1}$) at each station on Lake Chapala

STATION 03			STATION 03			STATION 03		
DATE	Z	mg C m^{-3}	DATE	Z	mg C m^{-3}	DATE	Z	mg C m^{-3}
130683	0.00	172.9	121083	0.00	146.1	210284	0.00	131.9
	0.48	245.8		0.56	336.5		0.45	208.4
	0.95	141.0		1.13	177.4		0.90	61.3
	1.90	20.6		2.25	33.9		1.80	16.5
280683	0.00	314.5	251083	0.00	176.5	140384	0.00	265.8
	0.33	631.0		0.54	313.9		0.55	254.5
	0.65	254.2		1.09	60.3		1.10	61.3
	1.30	72.3		2.17	13.2		2.21	9.7
190783	0.00	70.6	81183	0.00	377.7	100484	0.00	138.1
	0.43	94.5		0.48	433.2		0.58	218.4
	0.86	30.6		0.96	186.5		1.17	71.9
	1.72	3.5		1.92	35.2		2.35	7.4
20883	0.00	105.2	181183	0.00	332.9	240484	0.00	152.6
	0.45	217.4		0.60	227.1		0.48	186.5
	0.89	176.1		1.20	64.8		0.95	53.9
	1.78	42.3		2.39	24.8		1.91	11.6
150883	0.00	53.2	11283	0.00	228.4	160584	0.00	151.0
	0.39	262.9		0.58	270.0		0.49	207.4
	0.78	207.4		1.16	104.5		0.98	71.0
	1.55	118.7		2.34	19.7		1.96	13.2
310883	0.00	88.1	201283	0.00	197.7	40684	0.00	263.9
	0.35	191.9		0.50	499.0		0.50	287.1
	0.70	156.8		1.00	114.2		1.00	48.4
	1.40	64.5		2.00	34.5		2.00	16.1
130983	0.00	146.8	100184	0.00	173.5	270684	0.00	215.5
	0.52	212.6		0.50	307.1		0.45	221.6
	1.04	167.1		1.00	79.0		0.89	83.2
	2.08	42.3		2.00	43.5		1.79	16.8
260983	0.00	170.3	10284	0.00	197.4			
	0.26	397.1		0.41	348.7			
	0.51	229.7		0.82	134.8			
	1.02	55.2		1.64	22.3			

Table 18 (continued).

STATION 11 DATE	Z	mg C m ⁻³	STATION 11 DATE	Z	mg C m ⁻³	STATION 11 DATE	Z	mg C m ⁻³
130683	0.00	135.2	121083	0.00	210.3	210284	0.00	190.3
	0.48	161.0		0.55	287.7		0.47	267.1
	0.95	176.1		1.10	142.3		0.95	71.6
	1.90	18.7		2.19	35.5		1.90	18.4
280683	0.00	341.3	251083	0.00	175.5	140384	0.00	168.7
	0.48	681.0		0.62	299.7		0.58	196.5
	0.96	490.0		1.24	97.4		1.16	57.4
	1.92	100.0		2.48	14.5		2.33	8.1
190783	0.00	101.6	81183	0.00	193.5	100484	0.00	272.9
	0.86	103.9		0.52	324.5		0.57	295.2
	1.73	66.8		1.04	162.9		1.13	78.1
	3.45	7.4		2.08	38.1		2.27	7.1
20883	0.00	103.2	181183	0.00	341.0	240484	0.00	136.8
	0.45	228.4		0.63	199.4		0.45	205.8
	0.90	154.2		1.26	41.0		0.90	53.9
	1.79	41.6		2.52	20.3		1.79	11.6
150883	0.00	73.5	11283	0.00	207.4	160584	0.00	139.4
	0.47	248.4		0.50	317.4		0.55	200.0
	0.94	208.1		1.01	99.0		1.10	54.8
	1.89	78.7		2.02	17.4		2.20	12.6
310883	0.00	115.5	201283	0.00	158.4	40684	0.00	242.3
	0.50	379.7		0.48	287.7		0.54	313.5
	1.01	290.0		0.96	103.9		1.08	46.8
	2.02	95.8		1.91	13.9		2.16	14.5
130983	0.00	138.1	100184	0.00	168.7	270684	0.00	205.5
	0.71	274.2		0.48	246.5		0.46	236.8
	1.43	184.5		0.95	63.2		0.93	79.7
	2.85	27.1		1.91	28.4		1.85	12.9
260983	0.00	177.7	10284	0.00	141.0			
	0.35	401.0		0.41	298.7			
	0.70	240.3		0.82	84.8			
	1.40	57.4		1.64	18.1			

Table 18 (continued).

STATION 15 DATE	Z	mg C m ⁻³	STATION 15 DATE	Z	mg C m ⁻³	STATION 15 DATE	Z	mg C m ⁻³
130683	0.00	160.6	150883	0.00	72.6	111083	0.00	167.4
	0.48	171.9		0.37	157.4		0.50	311.6
	0.95	111.0		0.75	121.0		1.00	184.3
	1.90	21.9		1.49	49.4		2.01	26.5
140683	0.00	431.9	160883	0.00	144.5	121083	0.00	197.4
	0.38	565.8		0.26	245.5		0.42	254.2
	0.77	322.9		0.52	171.0		0.84	127.1
	1.54	75.8		1.04	75.5		1.68	30.3
270683	0.00	193.5	310883	0.00	91.6	241083	0.00	126.1
	0.33	372.9		0.39	173.2		0.34	271.6
	0.66	287.1		0.79	143.2		0.68	184.5
	1.33	68.7		1.58	53.5		1.36	38.7
280683	0.00	296.1	20983	0.00	157.1	251083	0.00	239.0
	0.35	366.1		0.30	121.3		0.46	179.4
	0.70	215.2		0.58	44.2		0.93	83.5
	1.41	61.9		1.17	12.9		1.86	11.3
190783	0.00	85.5	130983	0.00	154.2	71183	0.00	86.1
	0.69	83.9		0.49	362.9		0.49	165.8
	1.38	19.4		0.97	257.7		0.98	56.1
	2.75	3.9		1.94	59.4		1.96	10.6
230783	0.00	147.4	150983	0.00	123.9	81183	0.00	160.0
	0.52	254.8		0.39	215.2		0.47	204.2
	1.03	112.3		0.79	188.4		0.94	87.1
	2.07	21.0		1.58	44.5		1.89	14.8
10883	0.00	154.2	260983	0.00	113.5	171183	0.00	255.2
	0.40	359.4		0.39	348.1		0.52	243.5
	0.80	326.1		0.78	194.5		1.04	80.0
	1.61	75.2		1.56	49.4		2.07	15.2
20883	0.00	277.4	270983	0.00	172.3	181183	0.00	269.7
	0.45	420.3		0.37	326.5		0.55	142.6
	0.89	293.9		0.74	135.5		1.10	37.1
	1.78	61.6		1.47	29.0		2.21	15.8

Table 18 (continued).

STATION DATE	Z	mg C m ⁻³	STATION DATE	Z	mg C m ⁻³	STATION DATE	Z	mg C m ⁻³
11283	0.00	126.1	200284	0.00	191.0	160584	0.00	195.2
	0.46	218.1		0.50	229.4		0.55	241.3
	0.91	79.7		1.00	58.7		1.10	68.1
	1.82	18.4		2.00	15.5		2.20	14.5
21283	0.00	150.3	210284	0.00	135.2	170584	0.00	155.2
	0.49	222.9		0.43	214.8		0.41	268.7
	0.98	71.3		0.85	58.7		0.82	122.6
	1.96	21.6		1.70	14.2		1.64	34.5
201283	0.00	113.9	140384	0.00	169.0	40684	0.00	177.7
	0.46	193.9		0.48	286.8		0.49	242.6
	0.92	77.7		0.96	77.7		0.89	39.0
	1.84	10.6		1.91	15.5		1.96	10.0
211283	0.00	109.0	150384	0.00	132.9	60684	0.00	163.9
	0.54	191.9		0.46	364.2		0.51	239.7
	1.08	73.5		0.91	92.9		1.03	69.4
	2.16	20.6		1.82	27.7		2.06	14.2
90184	0.00	117.4	90484	0.00	184.2	270684	0.00	178.7
	0.46	153.2		0.43	171.9		0.45	212.6
	0.91	60.6		0.87	82.6		0.89	79.7
	1.82	25.2		1.73	17.1		1.79	14.2
100184	0.00	141.3	100484	0.00	268.1	280684	0.00	242.9
	0.46	202.6		0.50	292.6		0.48	297.1
	0.91	64.2		1.00	86.8		0.95	117.4
	1.82	29.4		2.00	13.5		1.91	17.4
310184	0.00	121.6	230484	0.00	94.2			
	0.45	173.5		0.50	112.9			
	0.90	38.7		1.00	52.6			
	1.80	10.6		2.00	12.3			
10284	0.00	172.3	240484	0.00	170.6			
	0.42	204.8		0.48	200.6			
	0.84	59.0		0.95	48.1			
	1.67	11.6		1.91	13.5			

Table 18 (continued).

STATION 26 DATE	Z	mg C m ⁻³	STATION 26 DATE	Z	mg C m ⁻³	STATION 26 DATE	Z	mg C m ⁻³
140683	0.00	623.9	111083	0.00	537.1	200284	0.00	162.3
	0.13	1807.7		0.16	752.9		0.15	390.0
	0.27	897.7		0.32	405.5		0.30	44.8
	0.52	185.2		0.63	60.0		0.60	19.0
270683	0.00	637.1	241083	0.00	543.2	150384	0.00	336.1
	0.15	1291.3		0.09	653.2		0.18	493.2
	0.30	527.4		0.19	383.5		0.63	168.1
	0.58	116.1		0.37	90.0		0.73	32.3
230783	0.00	51.9	71183	0.00	595.2	90484	0.00	481.0
	0.11	19.4		0.24	566.1		0.14	467.1
	0.23	10.3		0.48	215.2		0.29	142.9
	0.46	4.5		0.95	49.4		0.57	39.4
10883	0.00	361.9	171183	0.00	349.0	230484	0.00	232.3
	0.09	411.6		0.26	506.5		0.17	225.8
	0.19	275.5		0.52	152.3		0.33	165.2
	0.37	84.2		1.04	44.5		0.67	30.6
160883	0.00	334.2	21283	0.00	520.6	170584	0.00	435.5
	0.07	342.6		0.19	599.0		0.12	589.4
	0.14	269.4		0.38	169.7		0.25	250.6
	0.28	96.1		0.77	33.2		0.49	85.8
20983	0.00	380.6	211283	0.00	238.1	60684	0.00	257.4
	0.06	290.3		0.19	392.9		0.14	291.3
	0.12	131.3		0.39	145.5		0.28	114.8
	0.24	55.2		0.78	42.9		0.57	11.6
150983	0.00	223.5	90184	0.00	456.1	280684	0.00	412.9
	0.08	316.1		0.15	560.6		0.13	441.9
	0.17	238.4		0.30	172.3		0.26	189.0
	0.34	66.8		0.60	78.1		0.52	25.2
270983	0.00	285.2	310184	0.00	422.3			
	0.41	470.0		0.13	382.9			
	0.82	189.7		0.25	54.5			
	1.64	34.8		0.51	41.0			

Table 18 (continued).

STATION DATE	Z	mg C m ⁻³	STATION DATE	Z	mg C m ⁻³	STATION DATE	Z	mg C m ⁻³
140683	0.00	771.0	111083	0.00	171.6	200284	0.00	159.0
	0.32	603.2		0.56	323.2		0.45	233.9
	0.65	385.2		1.12	134.2		0.89	61.0
	1.29	118.1		2.24	23.9		1.79	4.8
270683	0.00	291.3	241083	0.00	112.3	150384	0.00	174.2
	0.28	572.6		0.33	340.6		0.44	271.6
	0.57	370.0		0.65	226.1		0.88	79.4
	1.13	106.5		1.31	52.9		1.77	20.6
230783	0.00	101.6	71183	0.00	163.9	90484	0.00	295.8
	0.54	333.5		0.50	295.5		0.19	248.4
	1.08	135.8		1.00	122.3		0.38	87.1
	2.15	20.6		2.00	26.5		0.77	16.8
10883	0.00	92.9	171183	0.00	163.5	230484	0.00	109.7
	0.44	224.5		0.52	229.0		0.22	136.5
	0.87	212.3		1.04	76.1		0.45	73.2
	1.75	64.8		2.07	14.5		0.89	13.2
160883	0.00	183.2	21283	0.00	189.0	170584	0.00	167.7
	0.27	377.4		0.48	239.4		0.40	226.8
	0.55	329.4		0.95	68.1		0.80	85.2
	1.09	100.6		1.91	12.6		1.59	25.2
20983	0.00	192.9	211283	0.00	78.7	60684	0.00	211.9
	0.26	188.7		0.52	125.5		0.46	219.7
	0.52	79.0		1.05	41.6		0.92	50.0
	1.05	24.8		2.10	13.5		1.84	7.1
150983	0.00	98.4	90184	0.00	162.9	280684	0.00	143.9
	0.26	244.5		0.46	255.5		0.50	205.5
	0.52	164.2		0.91	69.0		0.99	73.2
	1.04	56.1		1.82	31.9		1.98	8.7
270983	0.00	117.4	310184	0.00	202.3			
	0.61	251.9		0.37	209.7			
	1.22	111.3		0.74	48.7			
	2.44	22.9		1.48	10.3			

genera within the family Chroococcaceae (Agmenellum and probably Anacystis). Second, diatoms were also very sparse. Third, the net phytoplankton community was dominated by the genera Clostridium, Ceratium, and Staurostrum in that order. Finally, the nanoplankton community was primarily composed of unicellular and colonial green algae and flagellates such as Sphaeocystis, Oocystis, Coccomyxa, Crucigenia, Scenedesmus, Euglena, and possibly Platydorina.

Seasonal Variations

The physical and chemical parameters showed significant seasonal changes during the course of this study (Table 10, Table 13, Table 19). Lake surface temperature varied as expected of a lake at this latitude. The annual range was from 15 to 25 C, with the annual maxima occurring in August and the minima in December-January (Table 5).

Rainfall was almost exclusively limited to the five months between June and October, with about 70% of the annual total falling during July and August. These rains increased the lake's depth and Secchi depth (Figure 9, Table 21). They also affected the lake's chemical environment. The concentrations of TP, SRP and Alkalinity were negatively correlated with lake depth (Figures 10-14, Table 20). The seasonal patterns of $\text{NH}_4\text{-N}$ at each station showed a major peak in concentration during the rainy season.

Table 19. Physical, Chemical and Biological characteristics of each station on Lake Chapal between June, 1983 and June, 1984.

Station 03																
Physical					Chemical					Biological						
DATE	SERIES	SECCHI	EXT	IRRAD PHOTIC-2	DEPTH	PH	ALK	TP	SRP	NO ₃ -N	NH ₄ -N	TN	NPP	NPP(max)	BIOMASS	
130683	1	.61	2.494	17.13	1.90	8.5	324	587	479	25	125	.33	261.3	245.8	2.19	
280683	2	.53	2.594	17.13	1.30	8.5	292	519	486	98	32	.34	361.3	631.0	2.35	
190783	3	.71	2.972	12.02	1.72	8.3	288	465	442	52	38	.34	67.7	94.5	1.63	
20883	4	.51	2.186	17.03	1.78	8.3	275	434	425	16	255	2.12	251.6	217.4	3.28	
150883	5	.91	2.234	16.71	1.55	8.7	253	490	392	67	70	.31	271.0	262.9	1.73	
310883	6	.94	2.086	17.22	1.40	8.4	250	506	414	3	86	.56	183.9	191.9	2.53	
130983	7	.36	1.637	17.14	2.09	8.5	180	436	393	16	47	.54	296.8	212.6	4.85	
260983	8	.86	3.826	18.20	1.02	8.5	240	449	394	34	19	1.54	212.9	336.5	5.95	
121083	9	.74	1.872	16.75	2.25	8.3	234	443	372	273	22	.40	383.9	336.5	5.95	
251083	10	.58	2.171	12.49	2.17	8.3	252	396	363	128	29	.98	238.7	313.9	7.47	
81183	11	.74	2.569	16.66	1.92	8.4	248	391	368	65	27	.45	422.6	653.2	10.98	
181183	12	.64	2.420	9.66	2.39	8.4	254	396	366	69	13	.97	271.0	227.1	10.67	
11283	13	.75	2.146	15.70	2.35	8.4	245	384	315	40	50	.04	303.2	270.0	5.64	
201283	14	.50	2.768	16.32	2.00	8.6	254	373	358	25	19	.20	348.4	499.0	5.27	
100184	15	.60	2.519	12.86	2.00	8.5	243	375	394	26	31	.53	245.2	307.1	6.04	
10284	16	.50	2.768	15.54	1.64	8.5	243	375	394	44	38	.48	258.1	348.7	5.21	
210284	17	.60	2.519	14.12	1.80	8.5	252	368	361	9	46	.59	154.8	208.4	3.97	
140384	18	.65	2.395	9.89	2.21	8.6	252	371	322	25	5	.75	238.7	254.5	4.51	
100484	19	.60	2.519	15.30	2.36	8.5	268	406	396	19	17	.42	216.1	218.4	3.83	
240484	20	.55	2.644	14.73	1.91	8.5	282	369	341	47	54	.52	151.6	186.5	2.97	
160584	21	.58	2.569	14.40	1.96	8.7	269	397	367	45	43	.31	180.6	207.4	4.63	
40684	22	.50	2.768	13.96	2.00	8.4	270	456	420	66	27	.36	216.1	287.1	6.56	
270684	23	.48	2.818	14.09	1.79	8.5	251	400	408	30	22	.24	193.5	221.6	5.18	

Station 11																
Physical					Chemical					Biological						
DATE	SERIES	SECCHI	EXT	IRRAD PHOTIC-2	DEPTH	PH	ALK	TP	SRP	NO ₃ -N	NH ₄ -N	TN	NPP	NPP(max)	BIOMASS	
130683	1	.61	2.494	17.13	1.90	8.5	317	582	487	28	107	.05	129.0	161.0	2.53	
280683	2	.94	1.755	17.13	1.92	8.5	292	499	488	99	33	.34	783.9	681.0	2.51	
190783	3	.84	1.458	12.02	1.45	8.4	296	474	443	55	32	.06	216.1	103.9	.88	
20883	4	.79	2.169	17.03	1.79	8.3	286	428	421	21	80	2.05	235.5	228.4	2.44	
150883	5	.86	1.833	16.71	1.89	8.7	263	487	410	54	70	.35	312.9	248.4	1.76	
310883	6	1.07	1.451	17.22	2.02	8.5	248	496	402	19	54	1.41	474.2	379.7	4.64	
130983	7	1.12	1.525	17.14	2.85	8.4	197	427	378	45	54	.93	461.3	274.2	4.79	
260983	8	.66	2.800	18.20	1.40	8.6	255	434	401	36	11	1.59	300.0	401.0	4.19	
121083	9	.84	1.922	16.75	2.19	8.5	249	469	370	195	19	.22	332.3	287.7	5.89	
251083	10	.76	2.121	12.49	2.48	8.3	252	389	367	119	40	.85	306.5	299.7	6.92	
81183	11	.66	2.370	16.66	2.08	8.5	255	385	368	133	25	.41	351.6	324.5	9.77	
181183	12	.69	2.295	9.66	2.52	8.4	245	383	352	100	21	1.03	241.9	199.4	8.59	
11283	13	.61	2.494	15.70	2.02	8.6	245	399	335	88	41	.09	267.7	317.4	5.40	
201283	14	.45	2.893	16.32	1.91	8.6	244	379	362	46	24	.28	235.5	287.7	4.86	
100184	15	.55	2.644	12.86	1.91	8.4	242	395	394	71	26	.45	190.3	246.5	5.64	
10284	16	.50	2.768	15.54	1.64	8.6	240	377	387	90	38	.53	187.1	298.7	4.18	
210284	17	.65	2.395	14.12	1.90	8.6	248	361	363	13	30	.49	206.5	267.1	4.89	
140384	18	.70	2.270	9.89	2.33	8.7	248	381	339	21	24	.59	196.8	196.5	3.09	
240484	20	.56	2.619	15.30	2.27	8.6	263	416	398	25	25	.27	280.6	295.2	3.94	
160584	21	.69	2.295	14.73	1.79	8.6	270	369	358	38	39	.46	148.4	205.8	3.28	
40684	22	.58	2.569	13.96	2.20	8.9	267	393	357	51	31	.25	177.4	200.0	2.89	
270684	23	.52	2.985	13.96	2.16	8.3	274	432	420	30	19	.52	235.5	313.5	5.70	
				14.09	1.85	8.6	262	306	411	35	23	.56	200.0	236.8	4.34	

Table 19. (continued)

Station 15			Physical			Chemical					Biological					
DATE	SERIES	SECCHI	EXT	IRRAD	PHOTIC-Z	DEPTH	PH	ALK	TP	SRP	NO ₃ -N	NH ₄ -N	TN	NPP	NPP (max)	BIO MASS
130683	1	-61	2,494	13.13	1.90	5.95	8.5	324	585	510	30	125	.06	103.2	171.9	1.58
140683	1	-.56	2,619	17.78	1.54	5.95	8.4	312	576	503	19	109	.06	251.6	565.8	2.95
270683	2	-.69	2,295	17.78	1.33	6.05	8.9	304	521	531	98	29	.39	372.9	521.9	1.58
280683	3	-.61	2,395	17.13	1.41	6.05	8.4	296	530	530	79	28	.48	293.5	366.1	2.13
130783	2	-.61	1,828	12.02	2.75	6.35	8.3	282	486	445	76	44	.08	93.5	83.9	1.52
210783	1	-.53	2,895	16.15	2.07	6.55	8.3	277	489	459	58	96	.14	241.9	254.8	2.30
10883	4	-.69	2,197	17.91	1.61	6.85	8.2	251	440	440	246	96	.30	403.2	359.4	3.92
20883	4	-.56	2,186	17.03	1.78	6.85	8.3	262	449	438	193	98	.20	454.8	420.3	4.75
150883	5	-.71	2,324	16.71	1.49	7.05	8.6	231	485	423	566	75	.51	154.8	157.4	1.07
160883	5	-.61	1,855	16.25	1.05	7.05	8.5	219	457	416	455	71	.78	161.3	245.5	.59
310883	6	-.94	1,825	17.22	1.58	7.25	8.3	242	497	420	176	80	.65	187.1	173.2	2.32
20983	6	-.79	2,046	6.32	1.18	7.25	8.4	228	505	427	421	81	1.99	74.2	121.3	3.06
130983	7	-.89	1,797	17.14	1.94	7.25	8.3	250	427	389	403	53	.84	419.4	362.9	3.48
150983	7	-.66	2,370	17.02	1.58	7.25	8.3	196	428	399	729	39	.44	218.7	215.2	3.66
260983	8	-.56	2,512	18.20	1.56	7.45	8.5	258	431	392	337	24	.90	274.2	348.1	4.22
270983	8	-.61	3,135	17.39	1.47	7.45	8.5	242	437	403	247	41	1.42	216.1	326.5	4.48
111083	9	-.67	2,935	16.81	2.01	7.45	8.4	219	453	375	494	28	.38	312.9	311.6	5.45
211083	9	-.64	2,494	16.75	1.68	7.45	8.5	235	461	376	343	27	.20	229.0	254.2	5.35
121083	10	-.66	2,514	16.15	1.36	7.45	8.5	227	402	373	391	48	.68	219.4	271.6	5.40
251083	10	-.66	2,370	12.49	1.86	7.45	8.3	243	389	362	316	39	.87	193.5	179.4	5.82
71183	11	-.56	2,619	18.26	1.96	7.35	8.4	223	390	398	589	32	.47	135.5	165.8	4.26
81183	11	-.56	2,619	16.66	1.89	7.35	8.4	252	386	385	477	32	.37	190.3	204.2	5.16
171183	12	-.53	2,693	15.36	2.07	7.35	8.5	237	398	376	241	23	1.04	232.3	243.5	6.43
181183	12	-.56	2,619	9.66	2.21	7.35	8.4	241	390	376	188	24	1.10	177.7	142.6	8.04
11283	13	-.50	2,768	15.70	1.82	7.35	8.7	234	389	341	225	56	.20	177.4	218.1	3.54
21283	13	-.58	2,569	13.86	1.96	7.35	8.6	240	391	326	219	43	.20	190.3	222.9	3.70
220283	14	-.40	3,017	16.32	1.84	7.25	8.6	240	390	379	75	29	.28	161.3	193.9	3.40
211283	14	-.58	2,569	15.12	2.16	7.25	8.6	238	379	358	64	23	.18	190.3	191.9	3.89
90184	15	-.50	2,768	16.69	1.82	7.25	8.6	222	378	409	118	25	.54	138.7	153.2	3.96
100184	15	-.50	2,768	12.86	1.82	7.25	8.4	239	396	395	67	20	.42	164.5	202.6	5.30
310184	16	-.60	2,519	11.84	1.80	7.05	8.5	240	370	364	124	35	.53	119.4	173.5	3.64
10284	16	-.52	2,718	15.54	1.67	7.05	8.6	236	384	364	96	22	.50	148.4	204.8	4.34
200284	17	-.50	2,519	11.77	2.00	7.05	8.6	240	371	381	23	43	.51	190.3	229.4	4.98
210284	17	-.54	2,669	14.12	1.70	7.05	8.5	242	378	388	45	41	.56	145.2	214.8	4.69
140384	18	-.50	2,768	9.99	1.91	6.85	8.7	252	386	341	40	24	.69	216.1	286.8	4.20
150384	18	-.61	2,494	14.06	1.82	6.85	8.6	255	386	343	34	15	.84	238.7	364.2	4.32
90484	19	-.50	2,768	14.28	1.73	6.75	8.7	255	407	402	20	24	.71	167.7	171.9	4.22
100484	19	-.42	2,967	15.30	2.00	6.75	8.7	264	391	400	18	22	.25	258.1	342.2	3.47
230484	20	-.53	2,693	15.11	2.00	6.65	8.5	273	371	370	55	52	.48	119.4	112.9	3.44
240484	20	-.55	2,644	14.73	1.91	6.65	8.5	273	371	364	41	53	.41	154.8	200.6	3.66
160584	21	-.69	2,295	14.40	2.20	6.45	8.6	269	444	404	74	22	.29	225.8	241.3	5.17
170584	21	-.38	3,067	14.21	1.64	6.45	8.6	242	438	413	74	29	.32	219.4	268.7	5.92
40684	22	-.48	2,818	13.96	1.96	6.35	8.4	268	442	410	48	21	.19	164.5	242.6	6.89
60684	22	-.53	2,693	14.31	2.06	6.35	8.4	273	445	422	44	20	.41	203.2	239.7	6.05
270684	23	-.48	2,818	14.09	1.79	6.45	8.7	258	393	410	25	26	.22	180.6	212.6	4.26
280684	23	-.55	2,644	14.86	1.91	6.45	8.5	256	391	413	32	22	.26	171.0	297.1	5.10

Table 19 (continued)

Station 28										Station 26									
Physical					Chemical					Physical					Chemical				
DATE	SERIES	SECCHI	EXT	IRRAD	PHOTIC-Z	DEPTH	PH	ALK	TP	SRP	NO ₃ -N	NH ₄ -N	TN	NPP	NPP(max)	BIOHASS			
140683	1	.36	3.117	13.13	1.29	4.20	8.7	324	574	530	19	118	.08	264.5	603.2	3.85			
270683	2	.53	2.693	17.78	1.13	4.30	8.6	300	518	510	94	51	.52	374.2	572.6	4.37			
230783	3	.61	2.778	16.15	2.15	4.80	8.2	279	476	443	62	107	.04	296.8	333.5	2.09			
100883	4	.74	2.016	17.91	1.75	5.10	8.2	271	446	446	2	83	2.29	287.1	224.5	1.93			
160883	5	.53	3.040	16.25	1.09	5.30	8.5	226	457	393	206	86	1.02	287.1	377.4	2.53			
20983	6	.76	2.293	6.32	1.06	5.50	8.4	221	501	405	516	61	1.35	100.0	188.7	3.80			
150983	7	.41	3.550	17.02	1.05	5.50	8.3	199	438	370	649	66	.71	148.4	244.5	3.54			
270983	8	.99	1.891	17.39	2.44	5.70	8.4	230	416	388	441	16	.63	277.4	251.9	3.14			
111083	9	.74	2.645	16.81	2.24	5.70	8.3	226	465	370	404	28	.41	329.0	323.2	4.71			
241083	10	.64	2.612	16.15	1.31	5.70	8.5	226	400	362	392	31	.96	254.8	340.6	6.38			
71183	11	.58	2.569	18.26	2.00	5.60	8.5	244	388	394	266	33	.51	277.4	295.5	8.12			
171183	12	.53	2.693	15.36	2.07	5.60	8.4	233	396	370	357	20	1.12	203.2	229.0	4.94			
21283	13	.55	2.644	13.86	1.91	5.60	8.4	234	398	376	142	30	.15	190.3	239.4	3.07			
211283	14	.56	2.619	15.12	2.11	5.50	8.6	234	398	376	142	30	.18	116.1	125.5	2.13			
90184	15	.50	2.768	16.69	1.82	5.50	8.6	228	381	401	72	23	.42	190.3	255.5	5.97			
310184	16	.38	3.067	11.84	1.48	5.30	8.5	236	407	408	119	33	.37	129.0	209.7	6.91			
200284	17	.48	2.818	11.77	1.79	5.30	8.5	240	387	385	40	71	.38	161.3	233.9	3.20			
150384	18	.58	2.569	14.06	1.77	5.10	8.6	231	392	345	75	23	.75	196.8	271.6	3.70			
90484	19	.23	6.222	14.28	1.39	5.00	8.7	265	435	444	16	37	1.03	167.7	248.4	5.08			
230484	20	.28	3.316	15.11	1.62	4.90	8.6	278	422	422	36	73	.45	122.6	136.5	4.80			
170584	21	.34	3.166	14.21	1.59	4.70	8.6	272	410	394	58	32	.32	171.0	226.8	4.91			
60684	22	.40	3.017	14.31	1.84	4.60	8.4	270	453	416	38	47	.36	164.5	219.7	5.84			
280684	23	.59	2.544	14.86	1.98	4.70	8.4	258	412	408	32	19	.24	180.6	205.5	3.94			

Station 26										Station 26									
Physical					Chemical					Physical					Chemical				
DATE	SERIES	SECCHI	EXT	IRRAD	PHOTIC-Z	DEPTH	PH	ALK	TP	SRP	NO ₃ -N	NH ₄ -N	TN	NPP	NPP(max)	BIOHASS			
140683	1	.15	7.556	13.13	.53	.95	8.6	312	645	592	30	157	.13	238.7	1807.7	8.62			
270683	2	.30	5.124	17.78	.59	1.05	8.6	286	551	510	144	81	.54	345.2	1291.3	7.00			
230783	3	.03	13.100	16.15	.46	1.55	7.4	63	800	702	1443	1628	1.83	6.5	19.4				
100883	4	.15	9.450	17.91	.37	1.85	7.7	156	508	416	703	173	1.03	96.8	411.6	6.11			
160883	5	.10	10.597	16.25	.28	2.05	8.0	124	461	504	618	171	.79	67.7	342.6	2.25			
20983	6	.25	10.232	6.32	.24	2.25	8.3	204	504	408	617	88	1.67	38.7	290.3	6.50			
150983	7	.13	11.043	17.02	.34	2.25	8.4	218	395	389	212	45	.60	274.2	566.1	14.12			
270583	8	.66	2.818	17.39	1.64	2.45	8.2	225	413	379	452	10	.60	348.4	470.0	5.10			
111083	9	.25	9.384	16.81	.63	2.45	8.4	212	498	368	46	60	.60	261.3	752.9	12.22			
241083	10	.25	9.210	16.15	.37	2.45	8.4	218	397	370	165	24	1.38	145.2	653.2	11.22			
71183	11	.28	5.811	18.26	.95	2.35	8.4	233	387	372	163	32	1.03	216.1	506.5	13.62			
171183	12	.28	5.199	15.36	1.04	2.35	8.4	233	387	372	163	32	1.03	216.1	506.5	13.62			
21283	13	.20	11.737	13.86	.77	2.35	8.3	240	388	308	35	103	.35	193.5	599.0	4.83			
211283	14	.17	11.539	15.12	.78	2.25	8.5	234	445	464	36	73	.73	141.9	392.9	7.91			
90184	15	.12	10.466	16.69	.60	2.25	8.4	230	525	541	98	131	.92	151.6	560.6	13.85			
310184	16	.10	12.027	11.84	.51	2.05	8.6	246	450	423	20	130	.47	74.2	382.9	12.55			
200284	17	.12	16.790	11.77	.60	2.05	8.6	246	450	423	20	130	.47	67.7	390.0	9.90			
150384	18	.22	6.561	14.06	.73	1.85	8.5	298	448	427	51	49	.89	154.8	493.2	6.25			
90484	19	.12	13.497	14.28	.57	1.75	8.6	270	496	477	26	77	1.86	125.8	467.1	9.25			
230484	20	.13	8.505	15.11	.67	1.65	8.5	295	507	485	31	104	1.51	103.2	225.8	10.58			
170584	21	.07	12.531	14.21	.49	1.45	8.4	294	541	486	51	180	.71	148.4	509.4	13.27			
60684	22	.00	9.529	14.31	.57	1.35	8.2	279	525	451	44	160	.50	77.4	291.3	11.04			
280684	23	.08	11.149	14.86	.52	1.45	8.2	227	469	452	75	94	.40	116.1	441.9	9.52			

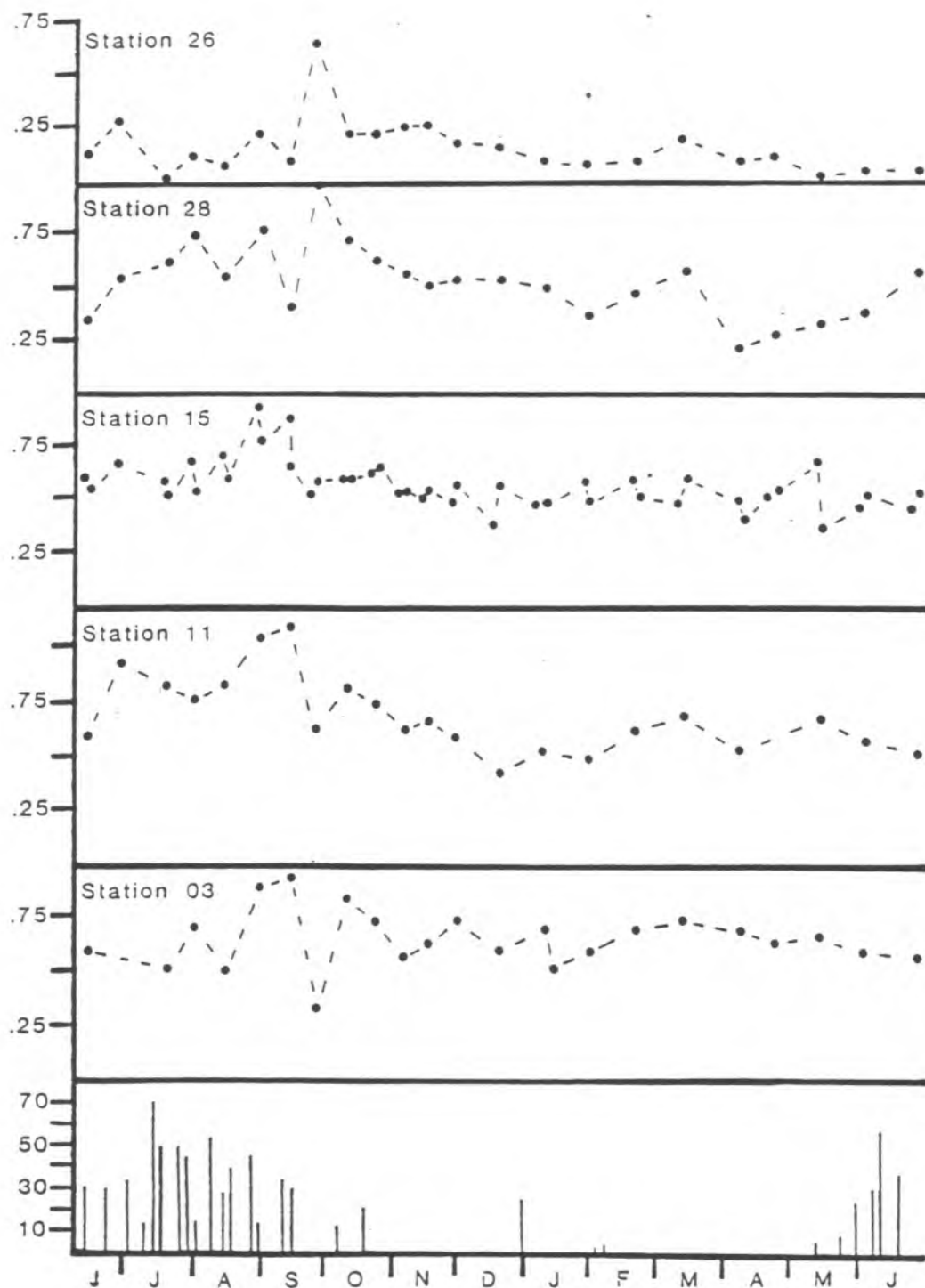


Figure 9. Seasonal pattern of Secchi Depth (m) at each station in relation to rainfall (mm) (bottom panel).

Table 20. Pearson Correlation analysis of the relationship between lake depth and selected chemical parameters. Values are presented as follows:
 Pearson correlation coefficient (associated p value)
 n = number of observations

Station	Total Phosphorus	Soluble Phosphorus	Total Alkalinity	Nitrate Nitrogen	Ammonia Nitrogen
03	-.48 (.012) n = 23	-.63 (.001) n = 23	-.74 (.000) n = 23	.19 (.200) n = 23	-.19 (.199) n = 23
11	-.43 (.027) n = 23	-.68 (.000) n = 23	-.77 (.000) n = 22	.38 (.039) n = 23	-.30 (.086) n = 23
15	-.53 (.000) n = 46	-.70 (.000) n = 46	-.86 (.000) n = 46	.60 (.000) n = 46	-.23 (.062) n = 46
28	-.59 (.002) n = 23	-.78 (.000) n = 23	-.89 (.000) n = 23	.67 (.000) n = 23	-.45 (.017) n = 23
26	-.67 (.000) n = 23	-.68 (.000) n = 23	-.33 (.061) n = 23	.05 (.406) n = 23	-.25 (.131) n = 23
ALL	-.56 (.000) n = 138	-.68 (.000) n = 138	-.41 (.000) n = 138	.26 (.001) n = 138	-.20 (.010) n = 138

Table 21. Sheffe's Multiple Contrast analysis comparing selected physical, chemical and biological parameters between wet and dry seasons.
(Ho: mean of rainy season - mean of dry season = 0.0)

Variable	Units	Mean Wet Season	Mean Dry Season	Wet-Dry	Error Mean square	Confidence Interval *
TP	(ug l ⁻¹)	471.9	402.0	69.9	179.4	[64.1 , 75.7]
SRP	(ug l ⁻¹)	427.8	385.5	42.3	68.0	[38.7 , 45.9]
NO ₃ -N	(ug l ⁻¹)	203.3	85.5	117.8	2586.6	[95.6 , 140.0]
NH ₄ -N	(ug l ⁻¹)	88.3	40.6	47.7	345.5	[39.6 , 55.8]
TN	(ug l ⁻¹)	0.742	0.588	0.158	0.076	[0.034 , 0.270]
Biomass	(mg Chloro m ⁻³)	4.55	6.28	-1.74	0.303	[-1.98 , -1.49]
NPP	(mg C m ⁻² day ⁻¹)	255.2	195.2	60.0	778.9	[47.4 , 72.6]
NPP(eu)	(mg C m ⁻³ day ⁻¹)	190.6	26.5	64.1	361.8	[55.8 , 72.6]
NPP(mix)	(mg C m ⁻³ day ⁻¹)	63.2	43.5	19.7	36.4	[17.1 , 22.3]
NPP(max)	(mg C m ⁻³ day ⁻¹)	342.9	290.6	52.3	3689.6	[25.8 , 78.7]
Secchi	(m)	0.57	0.47	0.10	0.015	[0.02 , 0.18]

* If confidence interval does not contain the point 0.0, Ho can be rejected at the .001 level.

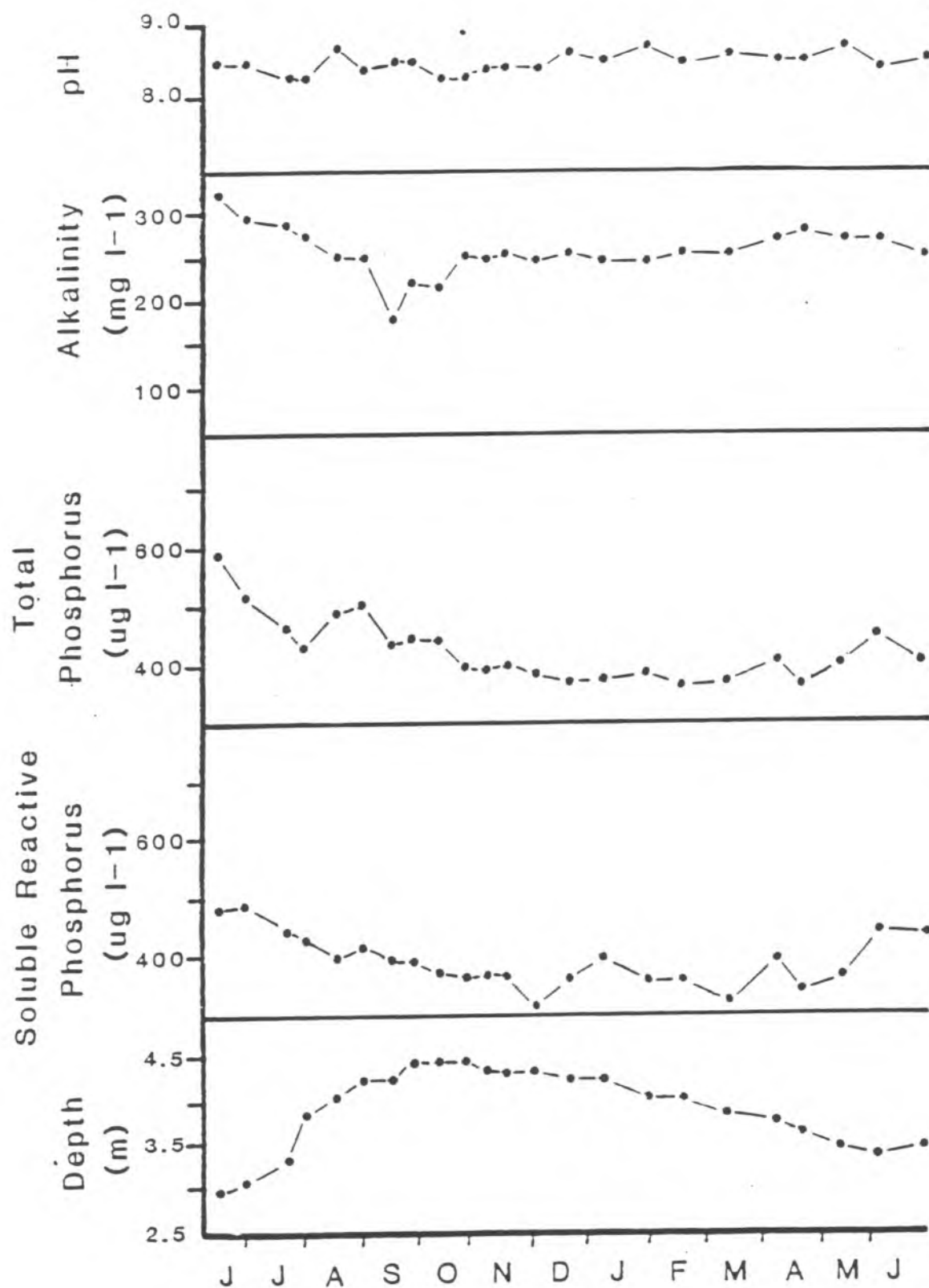


Figure 10. Seasonal pattern of various chemical parameters in relation to lake depth at station 03.

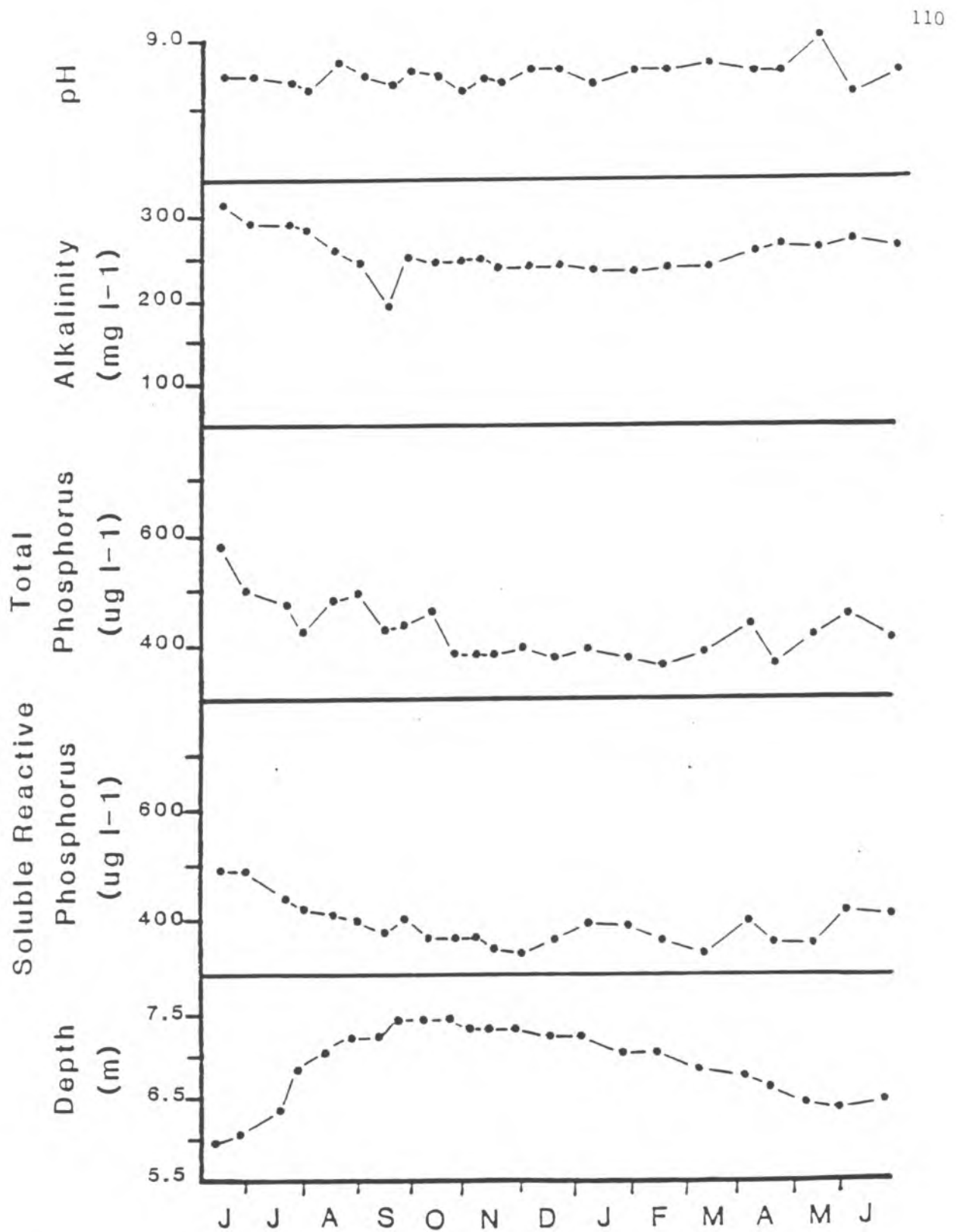


Figure 11. Seasonal pattern of various chemical parameters in relation to lake depth at station 11.

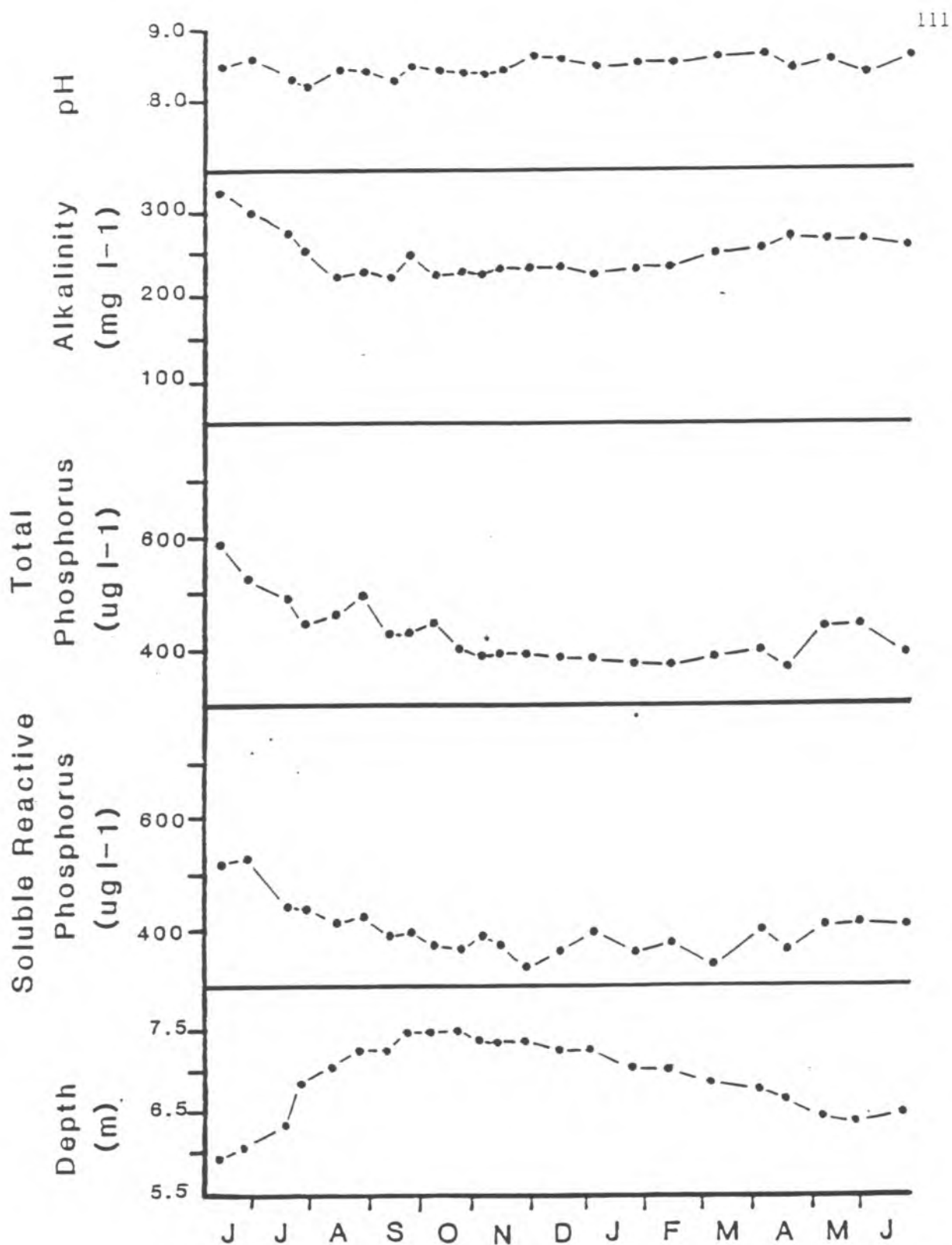


Figure 12. Seasonal pattern of various chemical parameters in relation to lake depth at station 15.

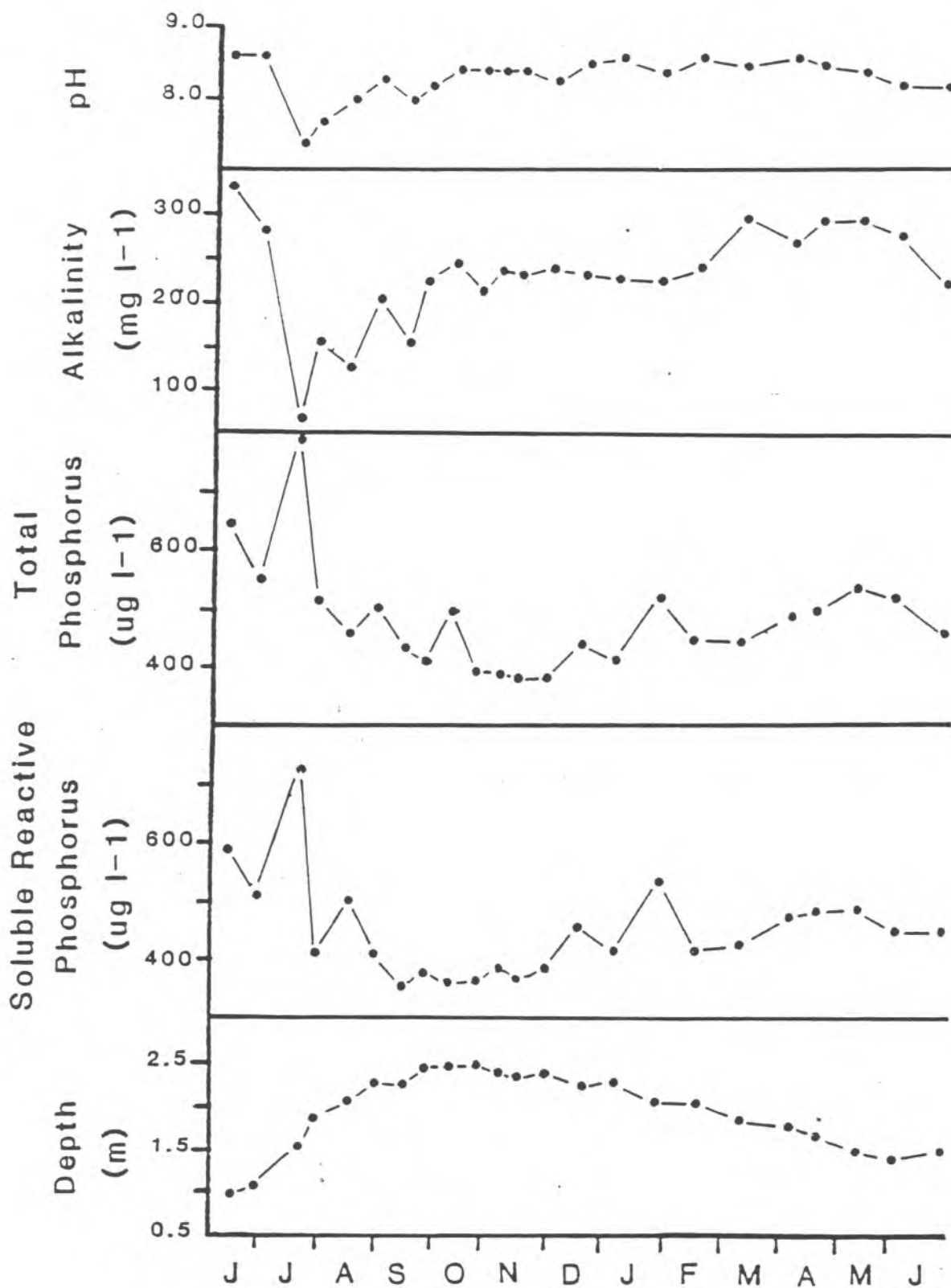


Figure 13. Seasonal pattern of various chemical parameters in relation to lake depth at station 26.

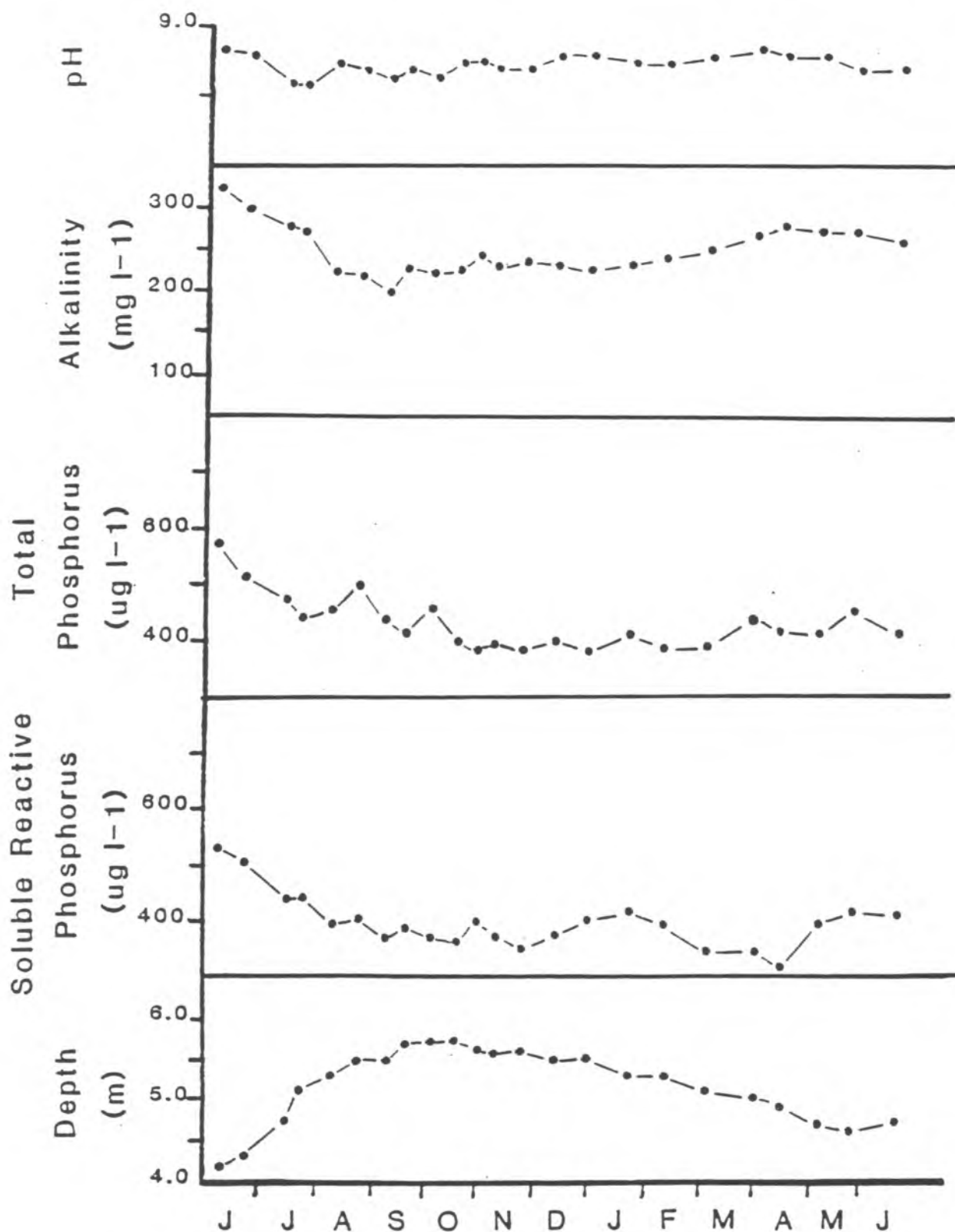


Figure 14. Seasonal pattern of various chemical parameters in relation to lake depth at station 28.

Concentrations of $\text{NH}_4\text{-N}$ during the dry season were low. Nitrate nitrogen concentrations increased sharply with the onset of the rainy season at Stations 26, 28 and 15. However, increases in $\text{NO}_3\text{-N}$ concentrations at Stations 03 and 11 were not seen until the end of the rainy season. Nitrate nitrogen concentrations also were low during most of the dry season (Figures 15-19, Table 21).

Net areal phytoplankton productivity was relatively low at all stations on Lake Chapala (Table 15). Across all stations, NPP varied from 6.5 to 783.9 $\text{mg C m}^{-2} \text{ day}^{-1}$, while phytoplankton biomass ranged between 0.6 and 14.1 $\text{mg chlorophyll a m}^{-3}$ (Table 19). Carbon uptake by phytoplankton in the dark was not important averaging only $3.0 \pm 2.0\%$ of fixation at the depth of optimal light intensity. Photosynthetic efficiency averaged $0.95 \pm 0.38\%$.

Phytoplankton productivity showed important seasonal differences (Table 19). The annual coefficients of variation in NPP for Stations 03, 11, 15, 28 and 26 were 33%, 50%, 38%, 35%, and 62% respectively. The coefficient of variation for the entire lake was 46%. At Station 15, where productivity was routinely measured on consecutive days, the mean daily coefficient of variation was only 21.5%, about half of the annual coefficient of variation at that station.

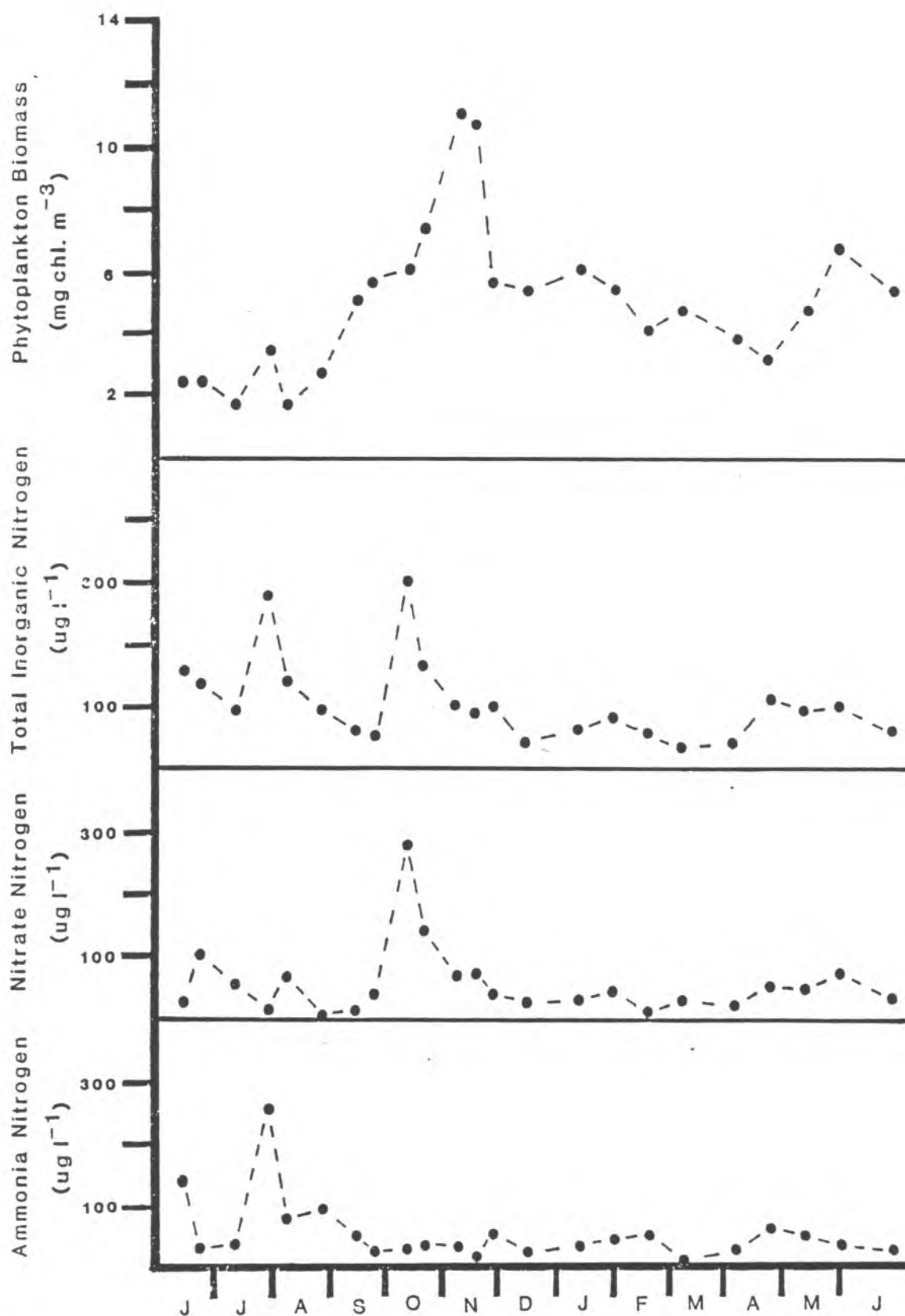


Figure 15. Seasonal pattern of inorganic nitrogen and phytoplankton biomass at station 03.

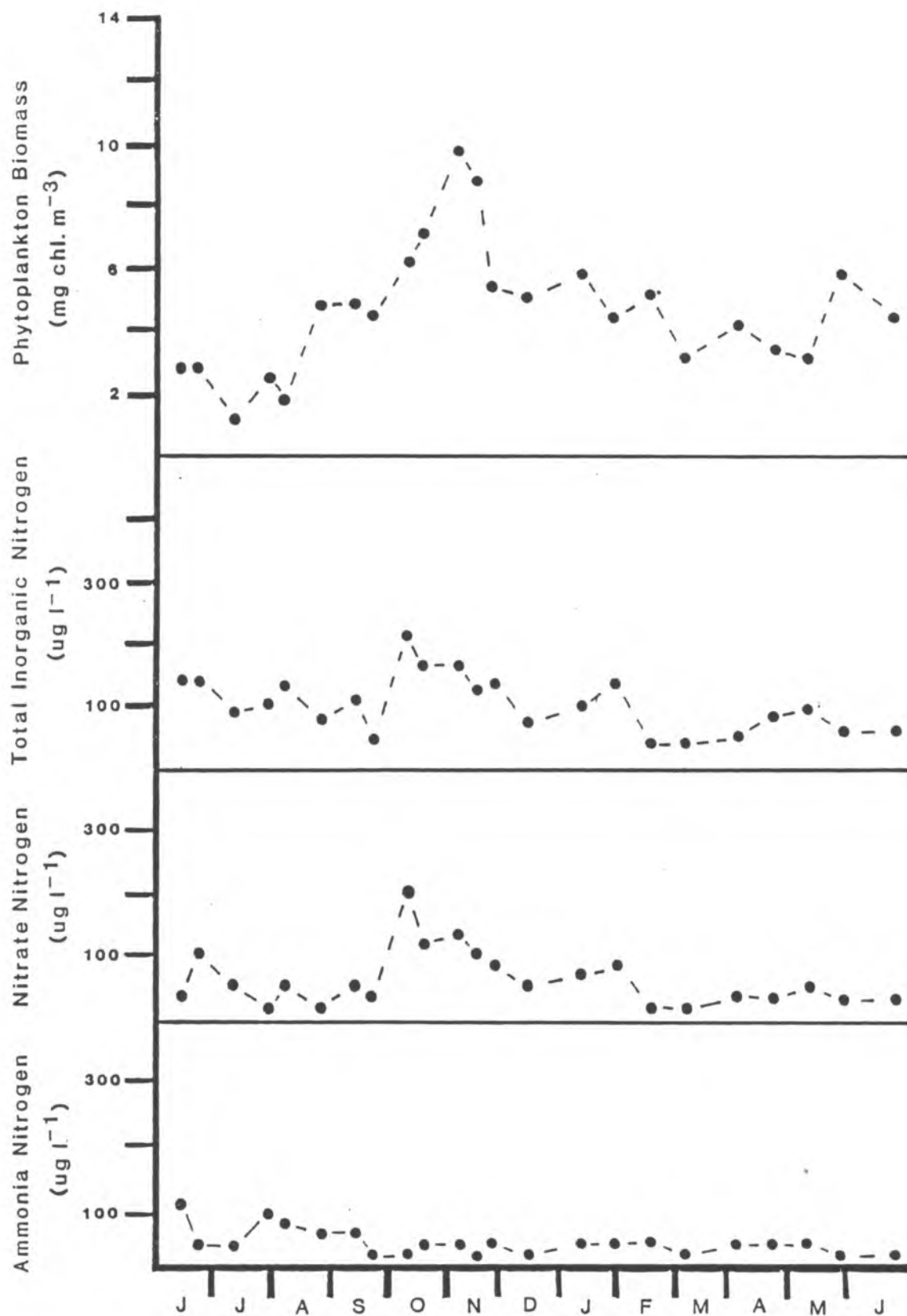


Figure 16. Seasonal pattern of inorganic nitrogen and phytoplankton biomass at station 11.

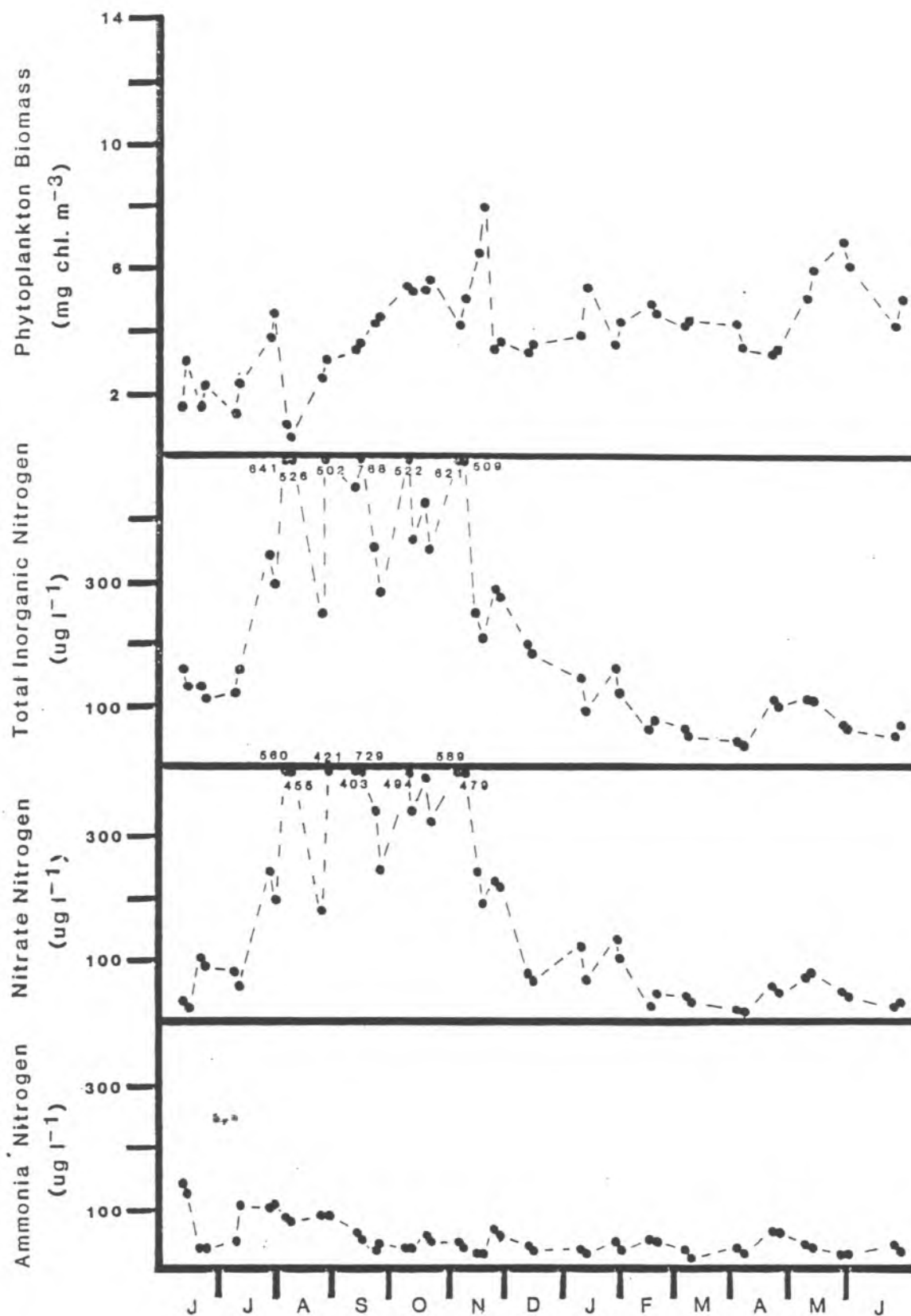


Figure 17. Seasonal pattern of inorganic nitrogen and phytoplankton biomass at station 15.

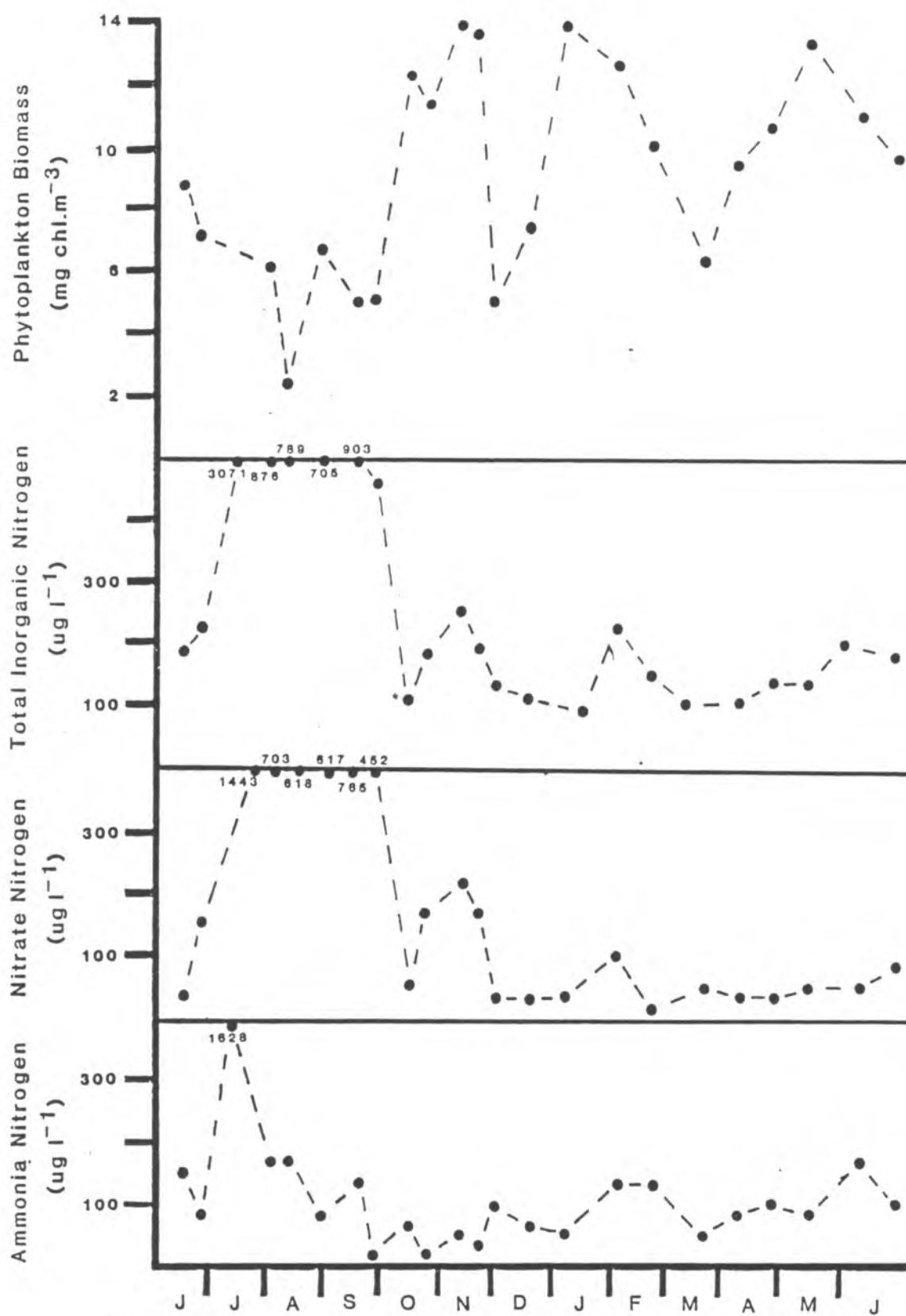


Figure 18. Seasonal pattern of inorganic nitrogen and phytoplankton biomass at station 26.

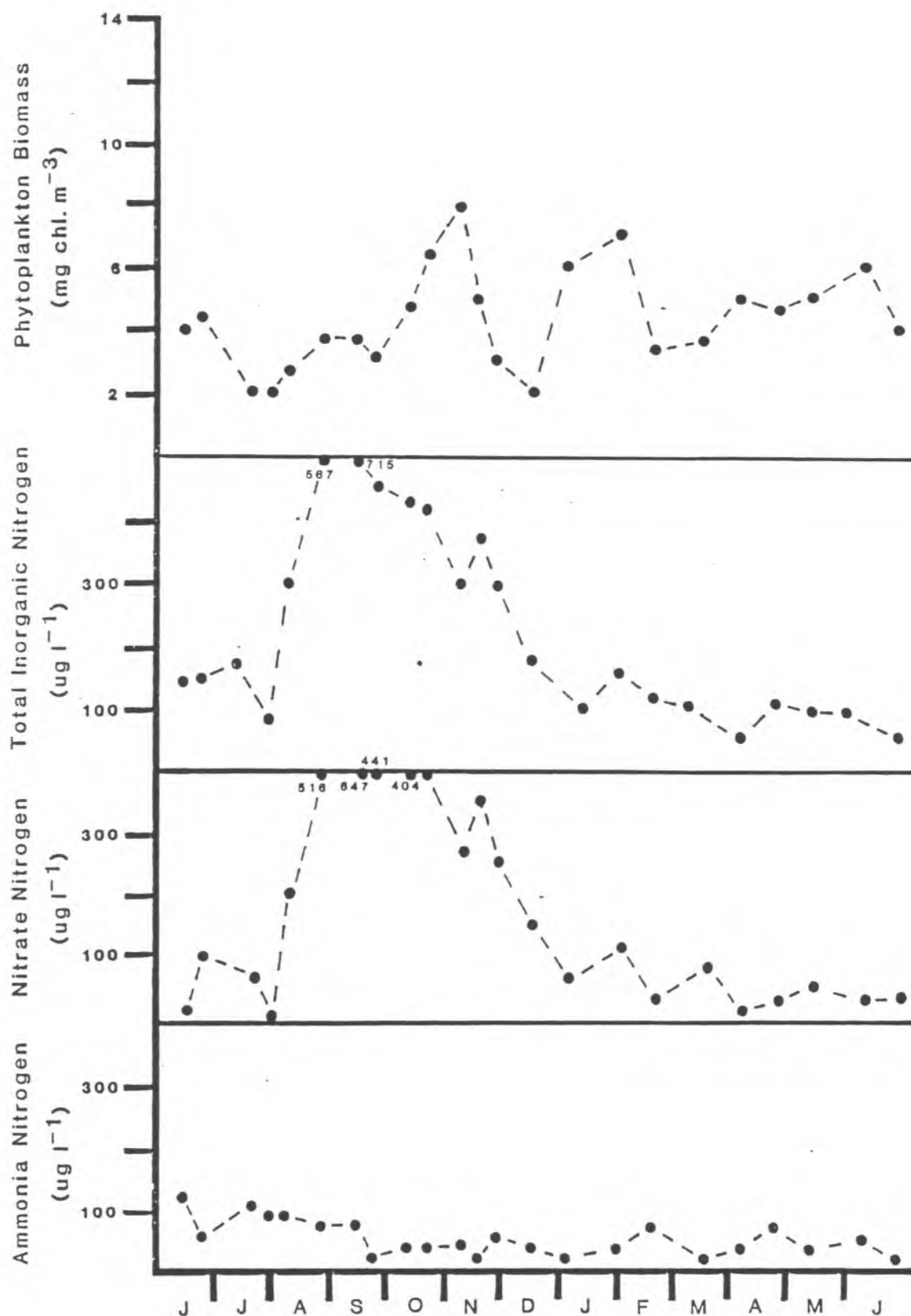


Figure 19. Seasonal pattern of inorganic nitrogen and phytoplankton biomass at station 28.

Across the lake, NPP was both significantly higher (Table 21, Figures 20-24) and significantly more variable during the rainy season (Table 22). At Station 26 the very low NPP during July and August 1983 were due to the very turbid waters flowing in from the Rio Lerma.

Phytoplankton biomass at Stations 03, 11 and 15 showed a steady increase during the rainy period, but did not reach a maximum until November. This major peak was followed by a steady decline throughout the dry period. Stations 28 and 26 showed multiple peaks in biomass through the course of the study (Figures 15-19). Phytoplankton biomass was poorly correlated with the environmental physical and chemical factors (Table 23). However, increases in biomass generally followed peaks in inorganic nitrogen concentrations (Figures 15-19). Unlike phytoplankton productivity, phytoplankton biomass was significantly greater during the dry season (Table 21).

Factors Affecting Phytoplankton Productivity and Biomass

NPP was most highly correlated with Secchi depth, irradiance, or (Secchi X irradiance) at all stations (Table 23). Regression equations with NPP as the dependent variable and relevant physical, chemical, and biological parameters as independent variables explain more than 50% of the variability at each station except 15 (Table 24).

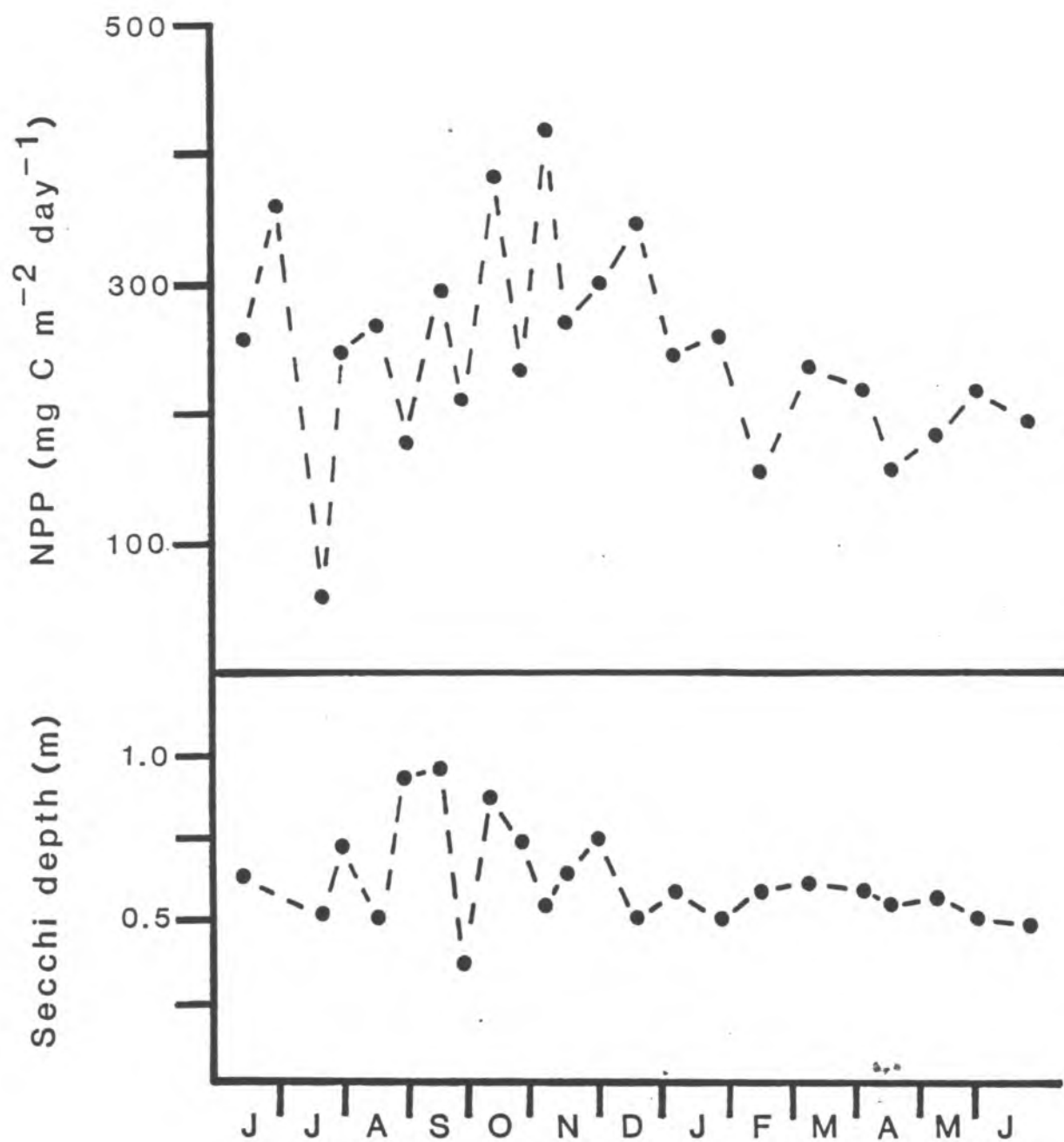


Figure 20. Seasonal pattern of net daily phytoplankton productivity (NPP) and Secchi depth at station 03.

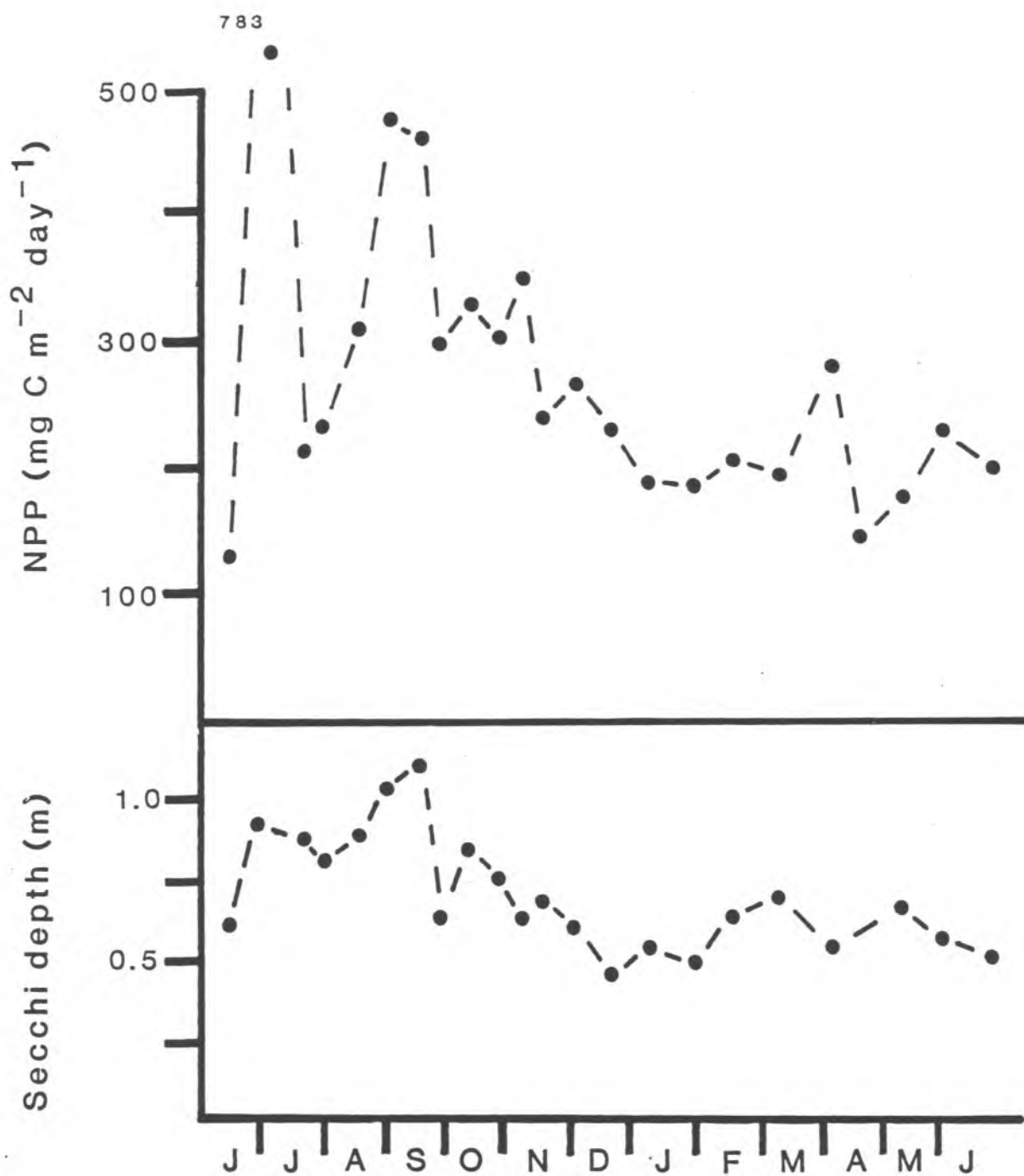


Figure 21. Seasonal pattern of net daily phytoplankton productivity (NPP) and Secchi depth at station 11.

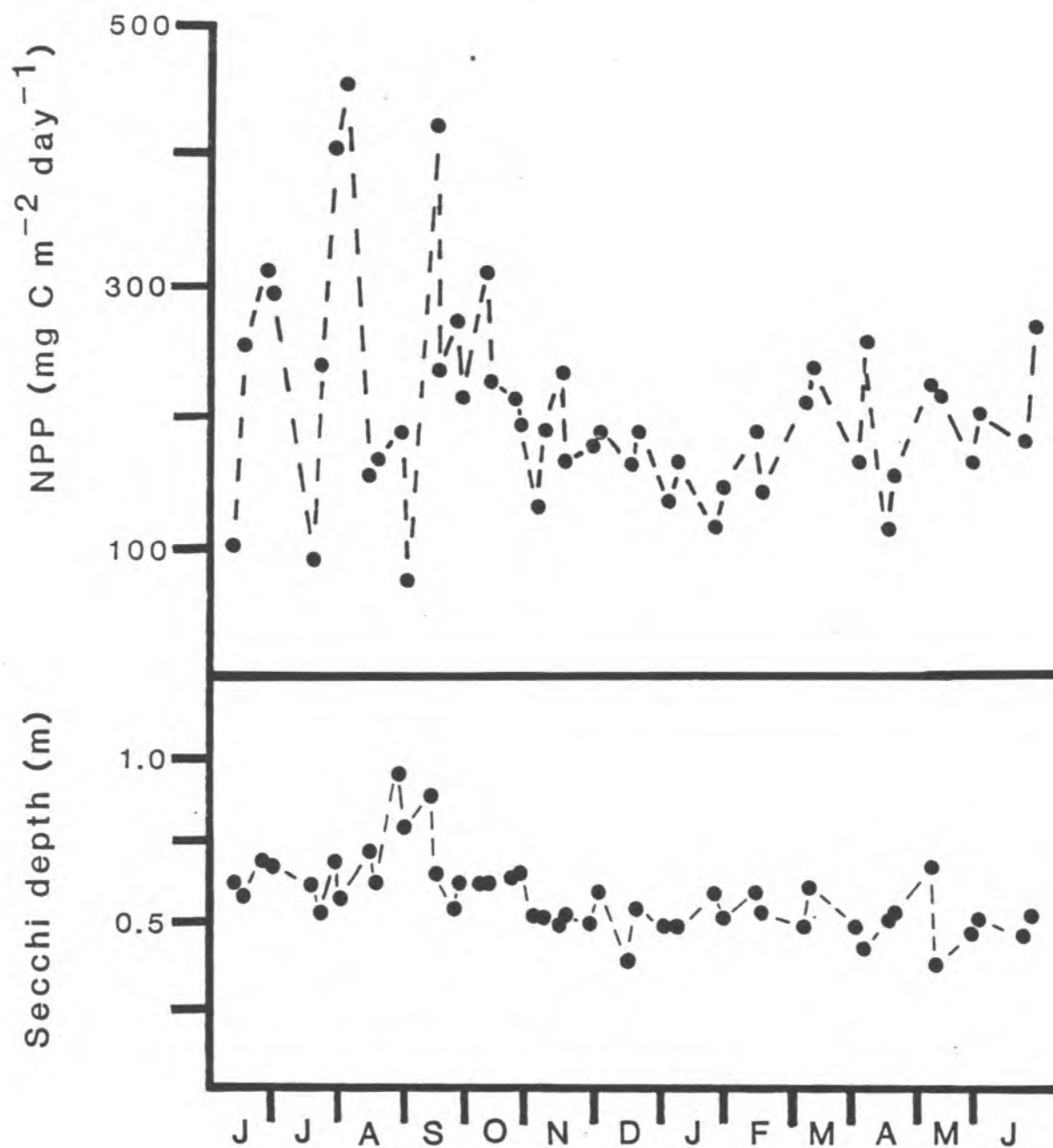


Figure 22. Seasonal pattern of net daily phytoplankton productivity (NPP) and Secchi depth at station 15.

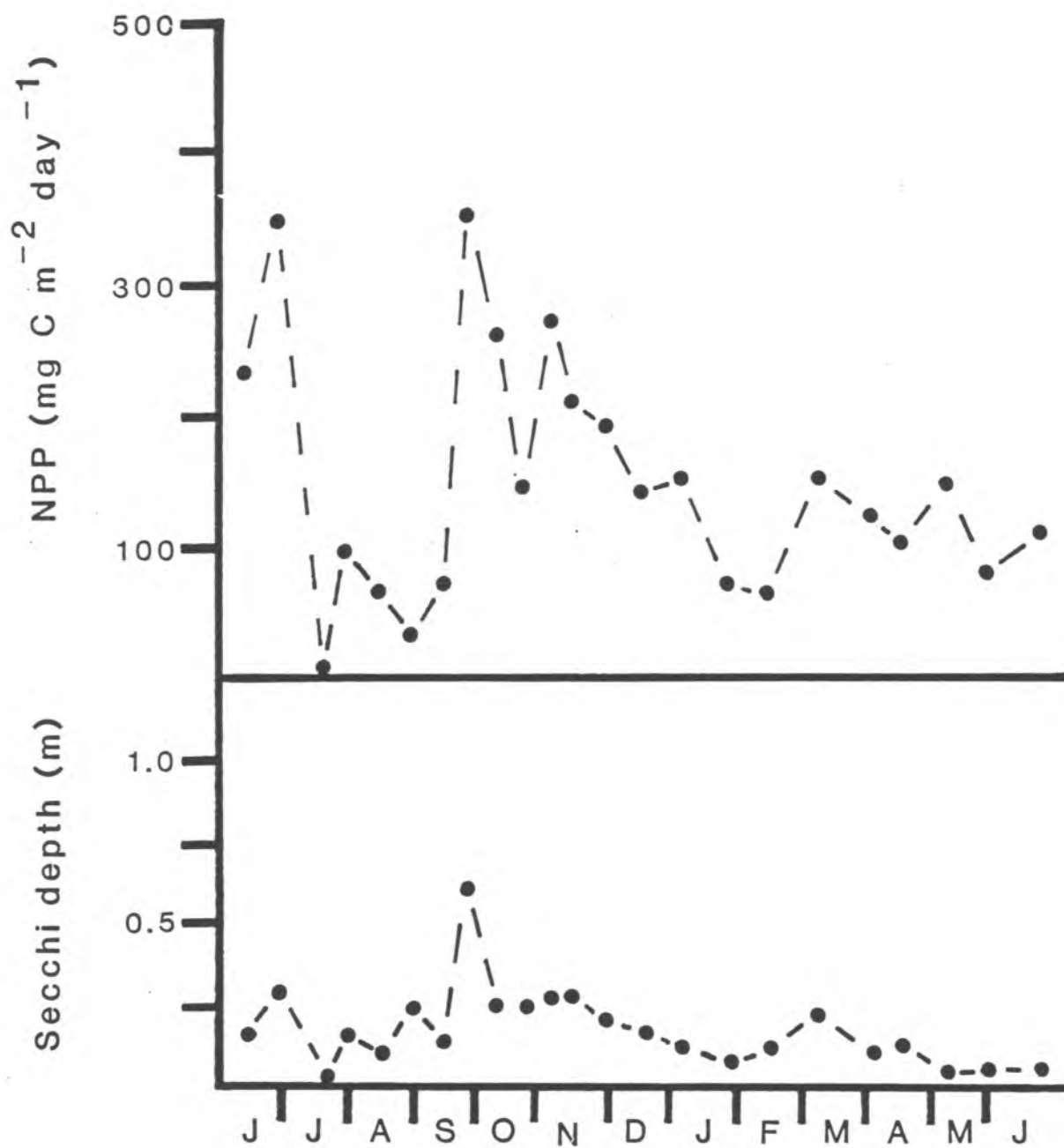


Figure 23. Seasonal pattern of net daily phytoplankton productivity (NPP) and Secchi depth at station 26.

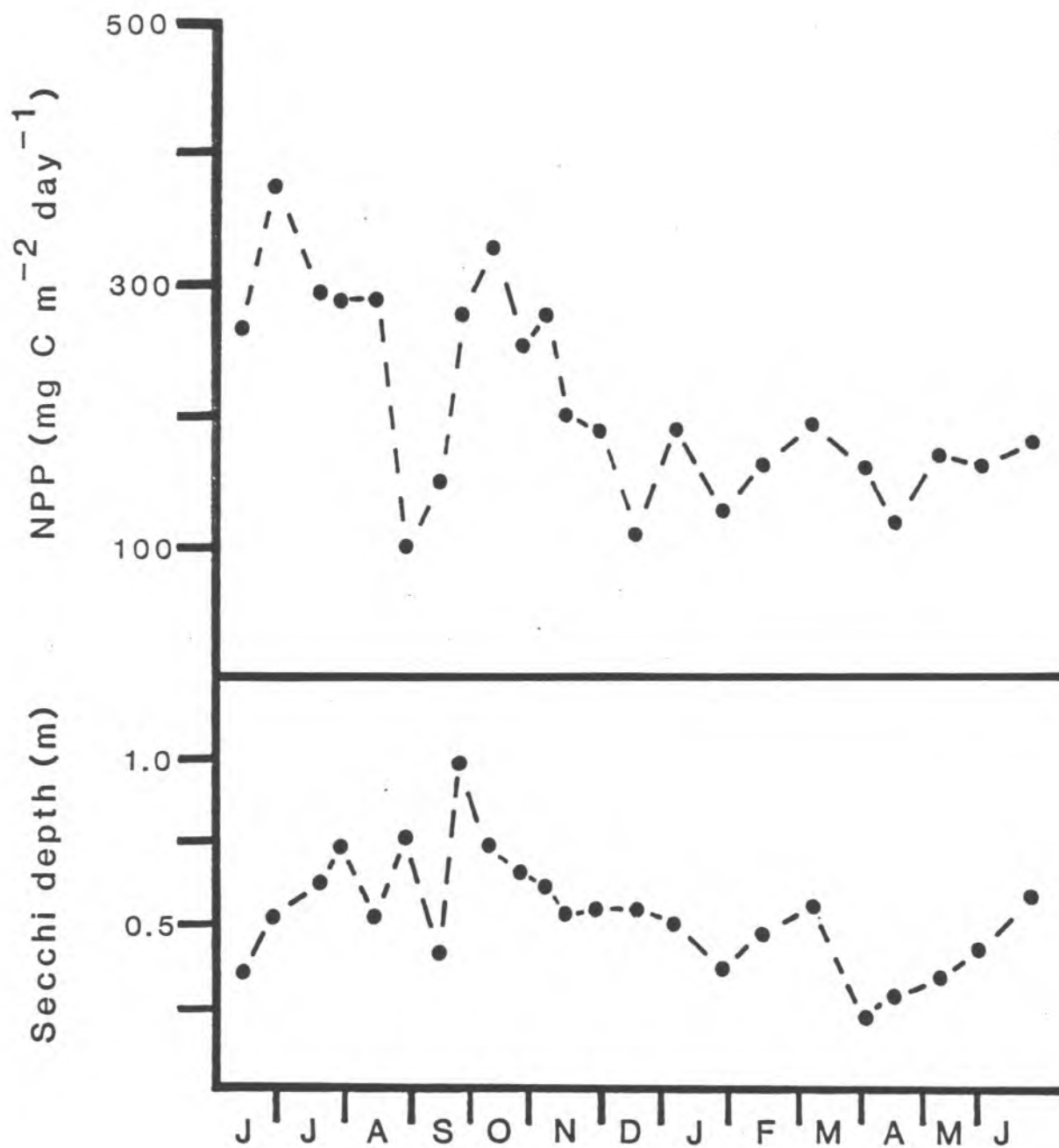


Figure 24. Seasonal pattern of net daily phytoplankton productivity (NPP) and Secchi depth at station 28.

Table 22. Two-tailed variance ratio test for differences in the coefficients of variation of NPP during the wet and dry seasons.

Station	Variance of the log of the C.V. (wet season)	Variance of the log of the C.V. (dry season)	F value	Degrees of Freedom (a,b)	F _{(.05),a,b}
03	0.037	0.019	1.947	11, 10	3.66
11	0.042	0.011	3.818 *	11, 10	3.66
15	0.038	0.009	4.222 *	23, 21	2.38
28	0.028	0.012	2.333	11, 10	3.66
26	0.235	0.034	6.912 *	11, 10	3.66
ALL	0.087	0.021	4.143 *	71, 65	1.62

* indicates F value is significant at the 0.05 level for the appropriate degrees of freedom

Table 23. Pearson correlation coefficients for phytoplankton productivity and biomass with selected physical, chemical, and biological parameters. Data presented as follows: [correlation coefficient / (n =) / p =].

STATION = ALL										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.6641 (132) P=0.000	0.4176 (135) P=0.000	-0.4355 (138) P=0.000	0.5521 (135) P=0.000	-0.0374 (138) P=0.332	-0.0716 (138) P=0.202	-0.1772 (138) P=0.019	-0.2316 (138) P=0.003	0.0278 (138) P=0.373	-0.0730 (137) P=0.198
NPP(eu)	-0.0693 (132) P=0.215	0.3784 (135) P=0.000	0.3348 (138) P=0.000	-0.2441 (135) P=0.002	0.3055 (138) P=0.000	0.2908 (138) P=0.000	-0.0045 (138) P=0.479	-0.0588 (138) P=0.247	0.1718 (138) P=0.022	0.3536 (137) P=0.000
NPP(mix)	-0.0559 (132) P=0.262	0.2453 (135) P=0.002	0.1963 (138) P=0.011	-0.1706 (135) P=0.024	0.2923 (138) P=0.000	0.2925 (138) P=0.000	-0.1345 (138) P=0.058	-0.0397 (138) P=0.322	-0.0086 (138) P=0.460	0.3304 (137) P=0.000
NPP(max)	-0.1348 (132) P=0.062	0.4820 (135) P=0.000	0.3295 (138) P=0.000	-0.3154 (135) P=0.000	0.3694 (138) P=0.000	0.3248 (138) P=0.000	-0.1250 (138) P=0.072	-0.0509 (138) P=0.277	-0.0048 (136) P=0.478	0.3833 (135) P=0.000
BIOMASS	-0.4840 (131) P=0.000	-0.0824 (134) P=0.172	0.5777 (137) P=0.000	-0.5280 (134) P=0.000	-0.0471 (137) P=0.292	-0.0086 (137) P=0.460	-0.0816 (137) P=0.172	0.0013 (137) P=0.494	0.1436 (137) P=0.047	1.0000 (137) P=0.000
STATION = 03										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.3546 (21) P=0.060	0.3790 (22) P=0.043	-0.3287 (23) P=0.065	0.2583 (22) P=0.126	0.0389 (23) P=0.431	-0.0683 (23) P=0.380	0.4256 (23) P=0.023	-0.0694 (23) P=0.378	-0.0991 (23) P=0.328	0.4474 (23) P=0.017
NPP(eu)	0.2453 (21) P=0.145	0.6208 (22) P=0.001	0.0712 (23) P=0.375	-0.0415 (22) P=0.428	0.3108 (23) P=0.077	0.2459 (23) P=0.132	0.2542 (23) P=0.124	-0.0019 (23) P=0.497	0.0765 (23) P=0.366	0.1475 (23) P=0.253
NPP(mix)	0.2999 (21) P=0.096	0.3788 (22) P=0.043	-0.2515 (23) P=0.126	0.1778 (22) P=0.217	0.2648 (23) P=0.114	0.2090 (23) P=0.172	0.3532 (23) P=0.051	0.0108 (23) P=0.481	-0.1704 (23) P=0.221	0.2353 (23) P=0.143
NPP(max)	-0.0763 (21) P=0.373	0.3889 (22) P=0.038	0.2122 (23) P=0.168	-0.2545 (22) P=0.129	-0.0088 (23) P=0.484	0.0980 (23) P=0.330	0.3136 (23) P=0.075	-0.1845 (23) P=0.202	-0.0186 (23) P=0.467	0.2489 (23) P=0.129
BIOMASS	-0.1474 (21) P=0.265	-0.2654 (22) P=0.119	0.0179 (23) P=0.468	-0.0076 (22) P=0.487	-0.4853 (23) P=0.010	-0.4301 (23) P=0.021	0.2403 (23) P=0.137	-0.3890 (23) P=0.035	0.1129 (23) P=0.306	1.0000 (23) P=0.000

Table 23. (continued)

STATION = 11										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.7360 (21) P=0.000	0.4714 (22) P=0.014	-0.5786 (23) P=0.002	0.6655 (22) P=0.000	0.3452 (23) P=0.055	0.3299 (23) P=0.064	0.2735 (23) P=0.106	-0.0422 (23) P=0.425	0.1387 (23) P=0.266	0.0363 (23) P=0.435
NPP(eu)	0.6490 (21) P=0.001	0.5875 (22) P=0.002	-0.3517 (23) P=0.052	0.4906 (22) P=0.011	0.3371 (23) P=0.060	0.3784 (23) P=0.039	0.2070 (23) P=0.174	-0.0557 (23) P=0.401	0.2160 (23) P=0.164	-0.0182 (23) P=0.468
NPP(mix)	0.6689 (21) P=0.001	0.4239 (22) P=0.026	-0.5376 (23) P=0.004	0.6120 (22) P=0.001	0.3768 (23) P=0.040	0.4218 (23) P=0.024	0.2280 (23) P=0.150	-0.0257 (23) P=0.454	0.0750 (23) P=0.368	-0.0544 (23) P=0.404
NPP(max)	0.4447 (21) P=0.023	0.5381 (22) P=0.005	-0.1143 (23) P=0.304	0.2511 (22) P=0.133	0.1602 (23) P=0.235	0.1909 (23) P=0.194	0.2532 (23) P=0.125	-0.2097 (23) P=0.171	0.1794 (23) P=0.209	0.0779 (22) P=0.367
BIOMASS	-0.2208 (21) P=0.171	-0.1312 (22) P=0.283	0.1896 (23) P=0.196	-0.1889 (22) P=0.203	-0.4366 (23) P=0.020	-0.4925 (23) P=0.009	0.5228 (23) P=0.006	-0.4133 (23) P=0.026	0.0884 (23) P=0.346	1.0000 (23) P=0.000
STATION = 15										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.4803 (44) P=0.000	0.4769 (45) P=0.000	-0.2066 (46) P=0.084	0.2038 (45) P=0.090	0.1451 (46) P=0.168	0.2054 (46) P=0.085	0.1085 (46) P=0.236	0.1073 (46) P=0.239	0.4059 (46) P=0.003	0.0908 (46) P=0.257
NPP(eu)	0.5513 (44) P=0.000	0.5270 (45) P=0.000	-0.2148 (46) P=0.076	0.2740 (45) P=0.034	0.2894 (46) P=0.026	0.3583 (46) P=0.007	0.1963 (46) P=0.096	0.1841 (46) P=0.110	0.4570 (46) P=0.001	-0.0891 (46) P=0.278
NPP(mix)	0.4290 (44) P=0.002	0.4430 (45) P=0.001	-0.2016 (46) P=0.090	0.1664 (45) P=0.137	0.2381 (46) P=0.055	0.3384 (46) P=0.011	-0.0007 (46) P=0.498	0.1367 (46) P=0.183	0.3540 (46) P=0.008	0.0395 (46) P=0.397
NPP(max)	0.4675 (44) P=0.001	0.6164 (45) P=0.000	0.0215 (46) P=0.444	0.0283 (45) P=0.427	0.3497 (46) P=0.009	0.3480 (46) P=0.009	-0.0783 (46) P=0.303	0.1705 (46) P=0.129	0.2251 (46) P=0.066	-0.0356 (46) P=0.407
BIOMASS	-0.3416 (44) P=0.012	-0.2263 (45) P=0.067	0.3075 (46) P=0.019	-0.3207 (45) P=0.016	-0.5034 (46) P=0.000	-0.4691 (46) P=0.000	-0.0607 (46) P=0.344	-0.5171 (46) P=0.000	0.1092 (46) P=0.235	1.0000 (46) P=0.000

Table 23. (continued)

STATION = 28										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.6576 (.23) P=0.000	0.6381 (.23) P=0.001	-0.2589 (.23) P=0.119	0.4134 (.23) P=0.026	0.3787 (.23) P=0.039	0.3462 (.23) P=0.055	0.0003 (.23) P=0.500	0.1848 (.23) P=0.202	0.0875 (.23) P=0.347	-0.0836 (.23) P=0.354
NPP(eu)	0.2351 (.23) P=0.143	0.3886 (.23) P=0.035	-0.0237 (.23) P=0.458	0.0729 (.23) P=0.372	0.5674 (.23) P=0.003	0.5012 (.23) P=0.008	0.0219 (.23) P=0.461	0.3589 (.23) P=0.048	0.1809 (.23) P=0.207	-0.0741 (.23) P=0.370
NPP(mix)	0.4833 (.23) P=0.010	0.5505 (.23) P=0.004	-0.1851 (.23) P=0.202	0.2485 (.23) P=0.129	0.5405 (.23) P=0.004	0.5632 (.23) P=0.003	-0.1677 (.23) P=0.225	0.3059 (.23) P=0.080	0.0091 (.23) P=0.484	-0.1182 (.23) P=0.298
NPP(max)	0.2969 (.23) P=0.087	0.6613 (.23) P=0.000	-0.0021 (.23) P=0.496	-0.0193 (.23) P=0.466	0.7278 (.23) P=0.000	0.6274 (.23) P=0.001	-0.0930 (.23) P=0.338	0.4512 (.23) P=0.016	-0.1408 (.23) P=0.274	-0.1657 (.23) P=0.228
BIOMASS	-0.2190 (.23) P=0.160	0.0327 (.23) P=0.442	0.1934 (.23) P=0.191	-0.3046 (.23) P=0.081	-0.2450 (.23) P=0.133	-0.0556 (.23) P=0.402	0.0434 (.23) P=0.423	-0.4560 (.23) P=0.015	-0.1434 (.23) P=0.259	1.0000 (.23) P=0.000
STATION = 26										
	SECCHI*IRRAD	IRRAD	EXT	SECCHI	TP	SRP	NO ₃	NH ₄	TN	BIOMASS
NPP	0.7979 (.23) P=0.000	0.4456 (.23) P=0.018	-0.7306 (.23) P=0.000	0.7390 (.23) P=0.000	-0.2821 (.23) P=0.099	-0.2929 (.23) P=0.090	-0.3871 (.23) P=0.036	-0.4110 (.23) P=0.027	-0.4366 (.23) P=0.020	0.0936 (.22) P=0.341
NPP(eu)	0.3343 (.23) P=0.062	0.3303 (.23) P=0.064	-0.4398 (.23) P=0.019	0.2864 (.23) P=0.095	-0.0996 (.23) P=0.328	-0.1543 (.23) P=0.244	-0.3634 (.23) P=0.046	-0.4267 (.23) P=0.022	-0.3777 (.23) P=0.039	0.0188 (.22) P=0.467
NPP(mix)	0.4423 (.23) P=0.018	0.2741 (.23) P=0.105	-0.5755 (.23) P=0.002	0.3939 (.23) P=0.033	0.1047 (.23) P=0.319	0.1078 (.23) P=0.314	-0.3456 (.23) P=0.055	-0.2623 (.23) P=0.116	-0.4443 (.23) P=0.018	-0.0077 (.22) P=0.487
NPP(max)	0.2744 (.23) P=0.105	0.6628 (.23) P=0.000	-0.3669 (.23) P=0.044	0.1284 (.23) P=0.282	0.2367 (.23) P=0.141	0.1433 (.23) P=0.260	-0.4070 (.23) P=0.028	-0.2790 (.23) P=0.101	-0.4070 (.23) P=0.028	0.1129 (.21) P=0.315
BIOMASS	-0.1447 (.22) P=0.263	0.0310 (.22) P=0.446	0.0453 (.22) P=0.422	-0.1914 (.22) P=0.200	-0.0015 (.22) P=0.497	-0.0258 (.22) P=0.455	-0.5816 (.22) P=0.002	-0.3521 (.22) P=0.056	0.0935 (.22) P=0.341	1.0000 (.22) P=0.000

Table 24. Multiple Stepwise Regression analysis of NPP with selected physical and chemical parameters.

Station	Variance explained by:	Cumulative r-squared	Regression Equation
All	Secchi depth (X1)	.31	$Y = -80.6 + 101.2(X1) + 4.9(X2) + 3.8(X3)$
	Irradiance (X2)	.44	
	Biomass (X3)	.53	
03	Biomass (X1)	.26	$Y = -47.6 + 6.1(X1) + 5.8(X2) + 0.1(X3)$
	Irradiance (X2)	.54	
	Nitrate-N (X3)	.61	
11	Secchi depth (X1)	.41	$Y = -223.9 + 160.5(X1) + 6.6(X2) - 1.0(X3) + 0.3(X4)$
	Irradiance (X2)	.53	
	Ammonia-N (X3)	.65	
	Soluble-P (X4)	.73	
15	Irradiance (X1)	.23	$Y = -6.8 + 4.8(X1)$
28	Irradiance (X1)	.32	$Y = -138.7 + 4.9(X1) + 77.0(X2) + 0.2(X3)$
	Secchi depth (X2)	.52	
	Soluble-P (X3)	.61	
26	Secchi depth (X1)	.55	$Y = -85.0 + 172.8(X1) - 0.04(X2) + 4.2(X3) + 0.1(X4)$
	Nitrate-N (X2)	.67	
	Irradiance (X3)	.79	
	Soluble-P (X4)	.85	

The most important variables in these equations were those associated with the underwater light climate. Nutrient concentrations and phytoplankton biomass were less important in determining phytoplankton productivity.

The predictive ability of these equations is improved substantially by including the factor $NPP(max) * \text{photic depth}$ (Table 25). This factor then becomes the most important factor in each equations and improves the r^2 to near 90%.

Results of the two laboratory bioassays with natural phytoplankton populations indicate that significant changes occurred in the phytoplankton biomass during the course of the experiments (Table 26, Table 27). In fact, under the artificial light conditions of incubation, each experimental group, including controls, showed increases in phytoplankton biomass. However, the increases in the experimental groups enriched with phosphorus or micronutrients were not different from the increase in the control group. Addition of nitrogen, either as nitrate or ammonia, caused an increase in phytoplankton biomass greater than the increase in the control group. The group enriched with ammonia nitrogen showed a greater increase in biomass over controls than did the group enriched with nitrate nitrogen (Table 28).

Table 25. Multiple Stepwise Regression Analysis of NPP with (NPP(max)*photic depth) and selected physical and chemical parameters

Station	Variance explained by:	Cumulative r-squared	Regression Equation
All	NPP(max)*photic depth (X1) Temperature (X2) Irradiance (X3) Nitrate Nitrogen (X4)	.81 .88 .89 .90	$Y = -19.4 + 0.44(X1) + 0.74(X2) + 1.54(X3) - 0.01(X4)$
03	NPP(max)*photic depth (X1) Irradiance (X2)	.67 .76	$Y = -24.9 + 0.33(X1) + 3.30(X2)$
11	NPP(max)*photic depth (X1) Temperature (X2)	.80 .91	$Y = -19.4 + 0.55(X1) + 1.20(X2)$
15	NPP(max)*photic depth (X1) Temperature (X2) Irradiance (X3)	.75 .88 .89	$Y = -23.0 + 0.47(X1) + 0.70(X2) + 1.36(X3)$
28	NPP(max)*photic depth (X1) Irradiance (X2) Temperature (X3)	.76 .86 .93	$Y = -36.3 + 0.33(X1) + 3.38(X2) + 0.76(X3)$
26	NPP(max)*photic depth (X1) Temperature (X2) Irradiance (X3)	.98 .98 .99	$Y = -9.19 + 0.43(X1) + 0.18(X2) + 0.82(X3)$

Table 26. Nutrient bioassays of natural phytoplankton populations showing initial and final nitrogen concentration and chlorophyll fluorescence.

Date	Treatment (n=3)	Initial Values			Final Values (after 6 days)		
		NO ₃ -N (ug l ⁻¹)	NH ₄ -N (ug l ⁻¹)	Fluorescence	NO ₃ -N (ug l ⁻¹)	NH ₄ -N (ug l ⁻¹)	Fluorescence
October 08, 1983	Control	420	40	19.03 ± 0.55	<10	35	43.07 ± 4.02
	Phosphorus	420	40	19.03 ± 0.55	<10	30	42.50 ± 3.00
	Micro nutrient Solution	420	40	19.03 ± 0.55	<10	32	37.43 ± 0.71
	Nitrate Nitrogen	820	40	19.03 ± 0.55	<10	36	84.13 ± 5.40
	Ammonia Nitrogen	420	440	19.03 ± 0.55	<10	43	94.60 ± 6.26
November 01, 1983	Control	150	30	13.43 ± 0.32	20	14	28.87 ± 0.12
	Phosphorus	150	30	13.43 ± 0.32	16	14	28.60 ± 0.36
	Nitrate Nitrogen	550	30	13.43 ± 0.32	185	37	66.87 ± 3.97
	Ammonia Nitrogen	150	430	13.43 ± 0.32	23	26	79.17 ± 3.01

Table 27. One-way analysis of variance testing for differences in phytoplankton biomass (chlorophyll fluorescence) among experimental treatments.

Date	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Significance
08 October	within groups	188.5	12	15.7	164.4	p < .0000
	between groups	12910.6	5	2582.1		
01 November	within groups	50.2	10	5.0	472.0	p < .0000
	between groups	9474.6	4	2368.6		

DISCUSSION

Our understanding of the dynamics of the phytoplankton communities at low latitudes is poor. This is due to a lack of data on tropical lakes. Until recently, intensive investigations of the limnology of these lakes were rare (Serruya and Pollinger 1983; Schindler 1978a). With only a few well studied tropical lakes, it is exceedingly difficult to distinguish differences due to latitude and those due to local limnological conditions (Talling, 1965b). Phytoplankton production data from Lake Chapala, Mexico helps answer three basic questions concerning tropical lakes.

First, are tropical phytoplankton communities highly productive? Brylinski and Mann (1973) have shown a negative relationship between latitude and phytoplankton production. That is, tropical lakes are more productive than temperate ones. However, Hammer (1980) concludes that in tropical lakes, the high rates of photosynthesis theoretically possible due to high solar irradiance, are very often not realized because of poor nutrient supply or high turbidity. Results from this investigation support the latter opinion.

That is, on this tropical lake, the phytoplankton productivity was low due to poor light penetrance.

Second, is the productivity of tropical phytoplankton communities constant throughout the year? Some tropical lakes have been shown to have unusually stable phytoplankton biomass and productivity (e.g., Lake George and Lake Titicaca). However, the absence of seasonality of these lakes now appears to be the exception and not the rule for tropical lakes (Melack 1979a). Data show that phytoplankton productivity and biomass in tropical Lake Chapala are decidedly seasonal.

Third, is the phytoplankton production of tropical lakes limited by nitrogen? Odum and Pigeon (1970, cited by Goldman and Horne, 1983) concluded that tropical rainforests are usually deficient in nitrogen. Early investigations of phytoplankton ecology in tropical lakes also implicated nitrogen as the limiting factor (Prowse and Talling 1958, Talling 1965a). However, others have shown that numerous tropical lakes are phosphorus rather than nitrogen limited (Kalff 1983, Peters and MacIntyre 1976). This investigation found that nitrogen was much more important than phosphorus in limiting the phytoplankton community. However productivity in Lake Chapala is apparently primarily limited by light rather than nitrogen.

Because Lake Chapala is a tropical lake, I expected it to: 1) have high phytoplankton productivity, 2) have a constant rate of phytoplankton production throughout the year, and 3) be primarily limited by nitrogen. Furthermore, I expected a gradient of phytoplankton productivity over the lake, being highest near the nutrient inputs of the Rio Lerma inflow and lowest at the west end of the lake.

Factors Regulating Phytoplankton Productivity

The mean daily phytoplankton productivity on Lake Chapala was low in comparison to most lakes (Table 29). Those lakes with lower phytoplankton productivity were either deep oligotrophic ones (Castle and Crater Lakes), or shallow turbid ones (Sorell, Crescent, and Lac Hertel). Many of the tropical lakes in Table 29 for which the mean daily productivity is less than $1000 \text{ mg C m}^{-2} \text{ day}^{-1}$ are reported to be light limited.

Phytoplankton production on Lake Chapala is probably also light limited during most of the year. Three lines of evidence directly support this conclusion. First, net phytoplankton productivity m^{-2} at each station is significantly positively correlated to the physical variables determining the underwater light climate (e.g., Secchi depth and irradiance) (Table 23). Second, multiple stepwise regression analysis showed these variables to be

Table 29. Comparison of mean phytoplankton productivity of several lakes with that of each station on Lake Chapala. Lakes are arranged in order of increasing productivity per m².

LAKE	Mean Daily Productivity (mg C m ⁻² day ⁻¹)	Mean Depth (m)	Photic Depth (m)	Mean Productivity In Photic Zone (mg C m ⁻³ day ⁻¹)	References
Sorell, Tasmania	44	shallow	ca. 2.0	ca. 22	Cheng and Tyler 1976
Crescent, Tasmania	115	shallow	1.5-2.0	ca. 60	Cheng and Tyler 1976
Castle Lake, USA	207 (annual)		30	4.2	Goldman et al. 1973
Chapala, station 26	207 (ice free)			6.9	This study
Crater Lake, USA	151	1.9	0.6	245	Larson 1972
Chapala, station 15	192 (summer)	325	200	1.0	This study
Chapala, station 28	209	6.9	1.8	120	This study
Lac Hertel, Canada	213	5.2	1.8	133	This study
Memphremagog, Canada/USA	220	6	4.5	49	Kalff 1972
Chapala, station 03	219	7.0			Ross and Kalff 1975
Chapala, station 11	249	4.4	1.9	134	This study
Herbert, Canada	281	6.9	2.1	137	This study
George, Uganda	330	13.0	10.0	33	Fabris and Hammer 1975
	375 (net)	2.5	ca 0.65	ca. 575	Ganf 1972
	4500 (gross)			ca. 6900	
Clear Lake, USA	438				Goldman and Wetzel 1963
Izabal, Venezuela	1440 (gross)	11.6			Brinson and Nordlie 1975
Coragulac, Australia	680	2.0	ca. 1	ca. 680	Hammer 1981
Tapacura, Brazil	767	17	1 - 2.5	ca. 380	Hartman et al. 1981
Sibaya, South Africa	808	21	12	67	Allanson and Hart 1975
Castanho, Brazil	815	2 - 12	ca. 1	ca. 815	Schmidt 1973b
Waco, USA	890 (main res.)	16	3.3	270	Kimmel 1969
Tanganyika, East Africa	1000	700	28	36	Hecy and Fee 1981
Lucerne, Switzerland	1140	43	15	76	Bloesch et al. 1977
Titicaca, Peru	1300	134	15 - 20	ca. 76	Widmeyer et al. 1975
Rotsee, Switzerland	1400	9	5	280	Bloesch et al. 1977
Victoria, East Africa	1080 - 4200	40			Talling 1965b
Sylvan Lake, USA	1564				Wetzel 1966
Chad, Chad (1969)	1575	3.2	ca. 0.5	ca. 3150	Lemoalle 1983
	1012 (1975)	3	ca. 0.75	ca. 1500	
Kinneret, Israel	1700	25			Berman 1978
Lanao, Philippines	1700	60	8 - 20	ca. 120	Lewis 1974
Naivasha, Kenya	1840	4.6	ca. 3.5	ca. 525	Melack 1979b
Crescent Island, Kenya	1990	11.1	ca. 10.0	ca. 199	Melack 1979b
Corangamite, Australia	2080	4.9	ca. 2.5	ca. 830	Hammer 1981
Valencia, Venezuela	2148	18			Lewis and Weibezahn 1976
Januaca, Brazil	2208	2.5	ca. 1	ca. 2208	Fisher 1979
Winamguluf, Kenya	2213	6.0	ca. 2.5	ca. 885	Melack 1979b
Nakuru, Kenya	2370	2.3	ca. 1	ca. 2370	Melack and Kilham 1974
Manyara, Kenya	2400	3.7	ca. 0.5	ca. 4800	Melack and Kilham 1974
Oldien, Kenya	3040	5.6	ca. 2	ca. 1520	Melack 1979b
McIlwaine, Rhodesia	3918	9.4	ca. 3	ca. 1300	Roberts 1979
Hartbeespoort, South Africa	4027	9.6	5 - 8	ca. 620	Roberts 1984
Red Rock, Australia	6000	2.0	ca. 1	ca. 6000	Hammer 1981

more important than nutrient concentrations or phytoplankton biomass in determining daily productivity (Table 24). Finally, among stations there exists a positive relationship between mean daily phytoplankton productivity and mean Secchi depth (Figure 25). That is, the clearer waters are more productive.

Light limitation may be determined by the ratio of $Z(\text{mix})$ to $Z(\text{eu})$. Talling (1971) considered lakes to approach the "critical depth" for light limitation only when the ratio of $Z(\text{mix})$ to $Z(\text{eu})$ was higher than 5. On Lake Chapala this ratio is rarely that high and the mean annual ratio is below 4.0 at all stations (Table 9). This suggests that some factor besides this simple ratio must be important in determining light limitation. The rate of circulation within the mixing zone may be such a factor. It seems unlikely, in terms of its effect on phytoplankton physiology, that a $Z(\text{mix}):Z(\text{eu})$ ratio on a shallow lake subject to high wind stress would be comparable to a similar ratio on a much deeper lake.

Inorganic nitrogen may play a secondary role in limiting phytoplankton productivity at certain times of the year. The very low TN:TP ratio on Lake Chapala indicates that nitrogen should become limiting before phosphorus. Results of the natural phytoplankton population bioassays support this contention. These experiments show that under the non-limiting light conditions of incubation, additions

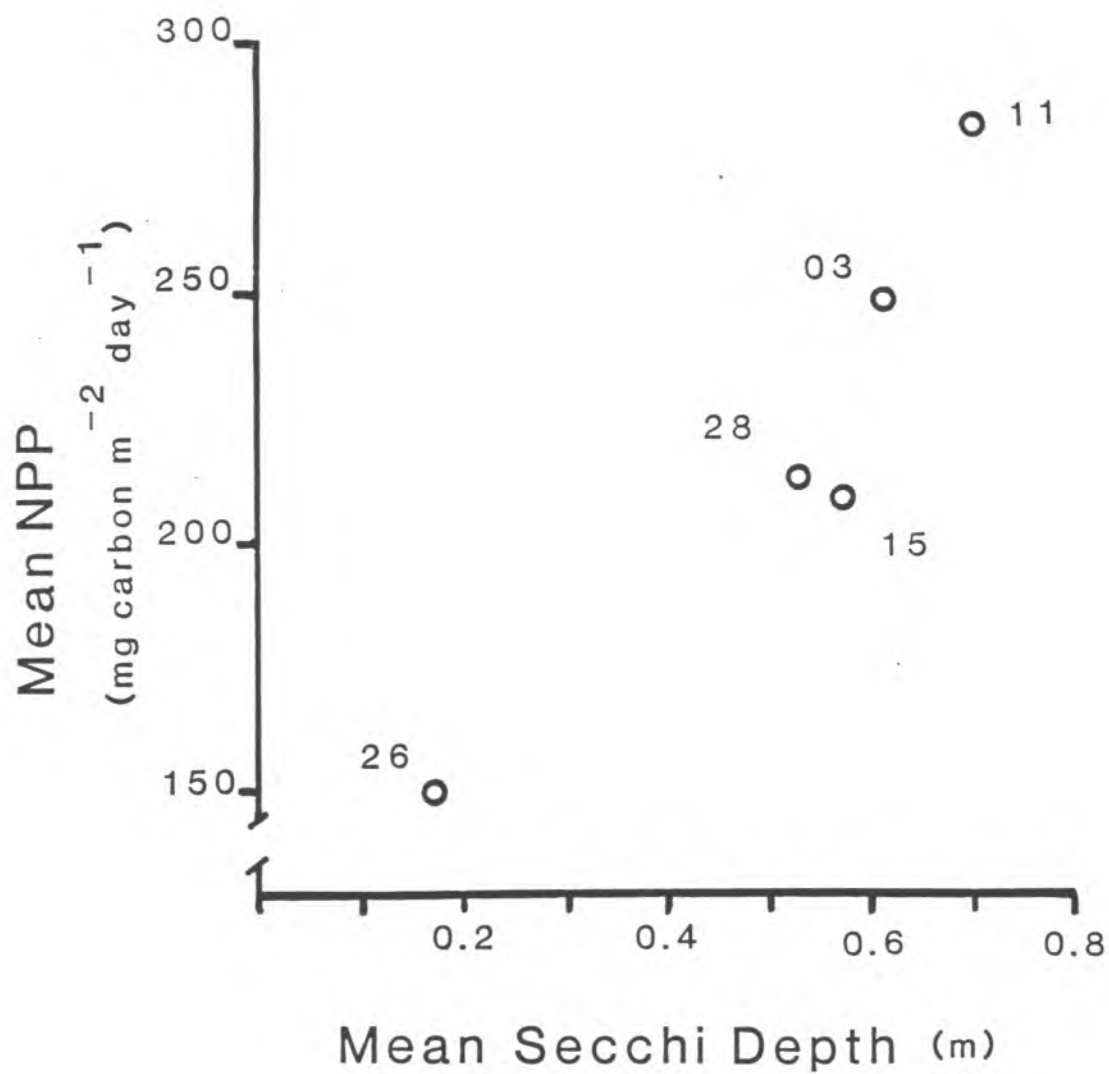


Figure 25. Relationship between mean NPP and mean Secchi depth among the five sampling stations.

- of inorganic nitrogen enhances phytoplankton growth while additions of phosphorus or micronutrient solution do not (Table 28).

Also of importance in the bioassays is the fact that phytoplankton biomass in the control bottles was significantly higher at the end of the experiment than at the beginning. This increase in biomass was accompanied by a dramatic decrease in inorganic nitrogen. This suggests that the lake water had sufficient nutrients to support higher phytoplankton biomass than was present in the lake. If so, some other factor, such as light, must have been the primary limiting factor. This agrees with Schelske et al.'s (1978) opinion that if a nutrient is present in measurable quantities, it most likely does not limit phytoplankton growth. Following this line of reasoning, in situ nitrogen limitation would occur only when inorganic nitrogen concentrations were very low. On Lake Chapala, this situation may occur during the dry season, especially at Stations 03 and 11 (Figures 15, 16).

Although natural phytoplankton population bioassays were conducted only twice, there is little doubt that nitrogen is always the essential nutrient in least supply. The TN:TP ratio on the lake was always below 4. More importantly, concurrent laboratory bioassays using Selenastrum capricornutum as a test organism were conducted throughout this study using water collected from Station 03,

11, 15 and 28. In all of the experiments, inorganic nitrogen stimulated S capricornutum growth while additions of phosphorus or micronutrient solution did not (Davalos, personal communication).

Additional evidence of the relative importance of nitrogen and phosphorus is seen in the seasonal patterns of these nutrients. On Lake Chapala, phosphorus behaves essentially like a conservative factor such as alkalinity. The seasonal pattern of these variables are predominantly determined by rainfall. During the rainy season the ambient concentrations are diluted by the seasonal influx of water, only to be reconcentrated later in the year by evaporation (Figures 10-14, Table 20). This pattern implies very little change due to biological processing. Nitrogen, on the other hand, is much more dynamic. During the rainy season, nitrogen is brought into the lake by surface runoff in the form of ammonia. This initial ammonia pulse is followed by one of nitrate. After this, inorganic nitrogen concentrations fall and remain relatively low throughout the dry period. The peaks in inorganic nitrogen are almost always followed by peaks in phytoplankton biomass (Figures 15-19) implying a direct relationship between these two variables.

From the experimental design employed it was impossible to evaluate the effects of diel thermal stratification upon net phytoplankton productivity. Since water samples were always collected early in the morning when the lake was isothermal in vertical profile (Table 5), it is not surprising that there was little variability in phytoplankton biomass or nutrient concentration with depth (Table 7). On Lake George, Uganda, the phytoplankton are usually evenly distributed throughout the water column in the early mornings. However, with the onset of thermal stratification, complex vertical patterns soon appear. These patterns make accurate estimation of phytoplankton productivity difficult (Ganf 1975). If similar biomass stratification occurred on Lake Chapala in response to thermal stratification, it would not have been detected by the sampling regime used. However, because Lake Chapala is almost constantly subject to wind mixing, and calm days with pronounced thermal stratification are relatively few, biomass stratification is probably rare.

Horizontal Variability in Phytoplankton Productivity and Biomass

A chemical gradient was apparent in the lake. Station 26 had a significantly greater concentration of all forms of nitrogen and phosphorus. The mean nutrient concentrations at Stations 03 and 11 were usually significantly less than

any other station. Stations 15 and 28 often had intermediate nutrient concentrations (Table 14).

Phytoplankton productivity was also variable across the lake (Table 15). Differences among stations in NPP were not related to nutrient concentrations, as hypothesized, but to differences in water transparency (Figure 25). Station 11, which normally had the least available inorganic nitrogen (Figure 16, Table 12), but which had the clearest water (Figure 21, Table 9), consistently has the highest productivity (Figure 21, Table 15). Station 26, which was the most nutrient rich and the most turbid, had the lowest NPP.

However, on a volume basis, net phytoplankton productivity was not related to water transparency. Station 26 had the highest NPP(max), the highest NPP(eu), and the highest NPP(mix) (Table 15). The reason for this is probably best seen in the photosynthetic profiles of each station (Table 18). Station 26 has a very shallow photic zone and therefore low NPP. However, the photosynthetic rate within that small photic zone is very high. This unusually high photosynthetic activity gives Station 26 significantly higher NPP(max) and NPP(eu). Also, because this station is very shallow, the NPP(mix) is also high. On Lake Chapala, this high photosynthetic rate at Station 26 is due to the unusually high phytoplankton biomass there (Figure 26). Kimmel (1969) also found that the turbid areas

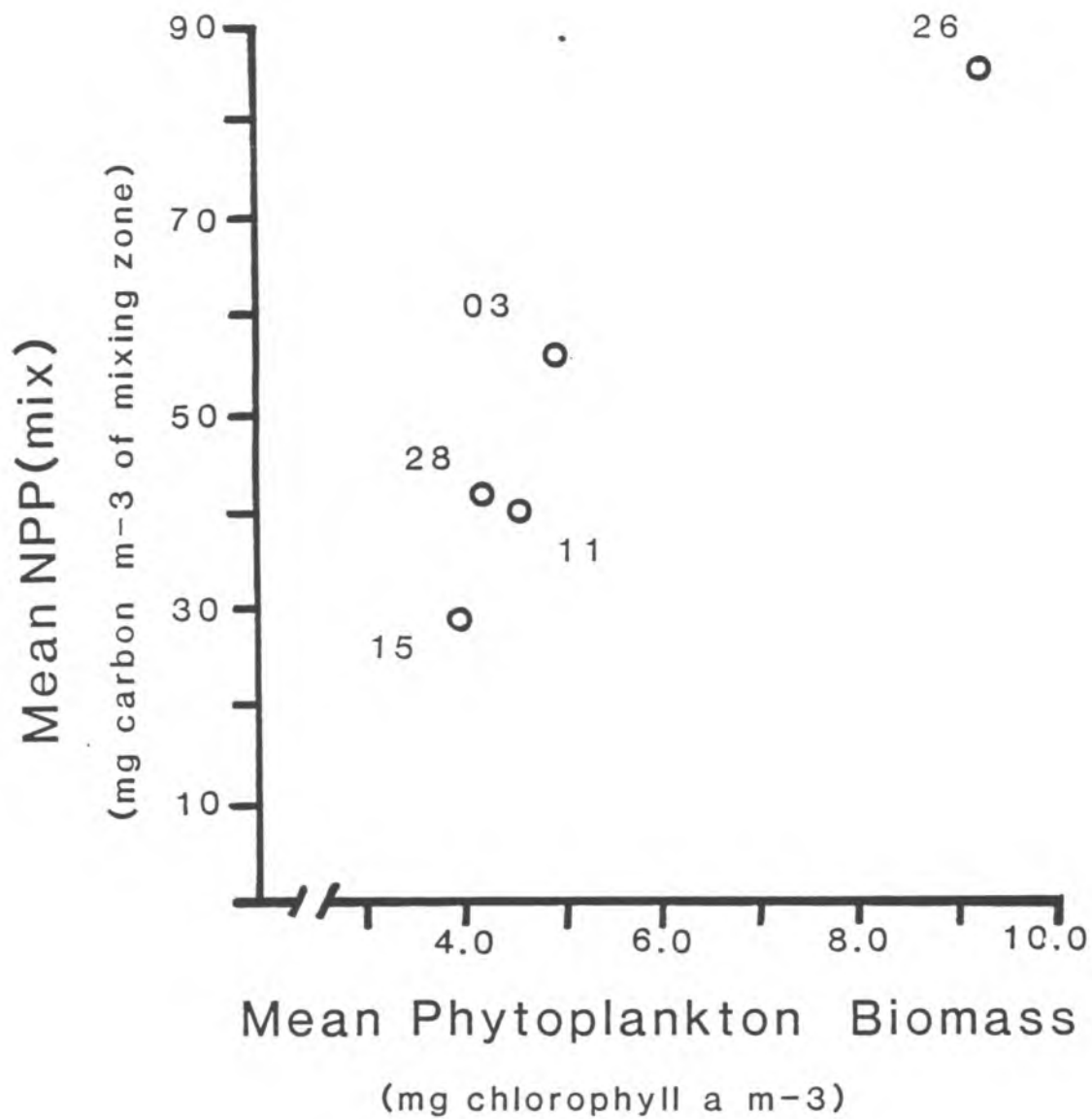


Figure 26. Relationship between mean NPP(mix) and mean phytoplankton biomass among the five sampling stations.

near river inflows of a reservoir have significantly lower areal phytoplankton productivity due to greatly reduced euphotic zones. And yet those same areas had higher phytoplankton production rates within that small euphotic zone and supported more phytoplankton biomass than the clearer area of the reservoir.

Although Station 26 is the most turbid station (i.e., small $Z(eu)$), it is also the most shallow (i.e., small $Z(mix)$) (Table 9). Consequently, the $Z(mix):Z(eu)$ ratio there is no greater than at most of the other stations on the lake (Table 11, Figure 8). This means that this station should be no more light limited than any other on the lake. Perhaps the abundant nutrient supply at this station (Table 12, Figure 18) and the presumably short circulation time of a given algal cell through the very shallow mixing zone allow for the relatively high phytoplankton biomass characteristic of this station.

Temporal Variability of Phytoplankton Productivity and Biomass

The annual C.V. of NPP shows that Lake Chapala is a lake with pronounced seasonal fluctuations (Melack 1979a). This seasonality is related to changes in the light penetrance into the lake between the wet and dry seasons. During the wet season, the lake is clearer and more

productive than during the dry season (Figures 20-24, Table 21). Cheng and Tyler (1976) and Hare and Carter (1984) show similar increases in water transparency during the rainy season for Australian and African lakes, respectively. Schmidt (1973b) reports increased phytoplankton production in the riverine lakes of central Amazonia during the rainy season, when water transparency is high.

The only exception to this generalization of higher productivity during the rainy season is seen at Station 26. Between July 23, and September 15, 1983, this station was exceptionally turbid due to inflowing waters from the Rio Lerma. This resulted in very low daily phytoplankton productivity during this period. However, once the turbidity decreased, NPP increased (Figure 23). Similarly, Fisher and Parsley (1979) show that the annual flooding of some riverine lakes of the Amazon serves first to decrease phytoplankton productivity by increasing turbidity. However, this turbid phase is followed by increased transparency and increased productivity as the phytoplankton take advantage of the high nutrient concentrations.

On some tropical lakes the day to day variations in productivity are as large as seasonal ones (e.g., Lake George, Uganda). This was not true on Lake Chapala. Day to day variations in productivity at Station 15 was only about half of the annual variability. The mean C.V. for consecutive days at that station was only 21.5% compared to

an annual C.V. of 38.0%. This implies a relatively stable environment that is subject to greater changes on a seasonal rather than day to day basis.

The higher daily variability of NPP during the wet season (Table 22) is probably due to more variable cloud cover and nutrient concentrations on the lake at that time. Similarly, the relatively high variability at Station 26 is undoubtedly due to the influence of the Rio Lerms's flow.

SUMMARY AND CONCLUSION

Lake Chapala is best described as meso-oligotrophic. During the study phytoplankton production was low. Mean annual phytoplankton production for the entire lake was $76.4 \text{ g C m}^{-2} \text{ year}^{-1}$ ($209 \text{ mg C m}^{-2} \text{ day}^{-1}$). Phytoplankton biomass was also low. As measured by chlorophyll a concentration, it averaged only $5.4 \text{ mg chlorophyll a m}^{-3}$.

Phytoplankton productivity was primarily limited by light. NPP was most highly correlated with the factors controlling the underwater light climate. Among stations, NPP was always highest at the clearer stations.

The very low TN to TP ratios on Lake Chapala indicate that nitrogen should become limiting before phosphorus. In fact, nitrogen may have been an important limiting factor of phytoplankton productivity during part of the dry season, when environmental concentrations of inorganic nitrogen were low.

Phytoplankton biomass did not correlate well with any physical or chemical parameters. However, peaks in biomass always followed peaks in inorganic nitrogen.

Like most tropical lakes studied, phytoplankton productivity on Lake Chapala was decidedly seasonal. NPP was significantly higher during the rainy season (June - October), the time of greatest water transparency. Phytoplankton biomass, on the other hand, showed a steady increase throughout the rainy season, but did not reach a peak until November.

Barring any major hydrologic changes, Lake Chapala should continue to be relatively stable in the years to come. Because the lake is not primarily limited by nutrients, it should suffer minimal impact from increased anthropogenic uses. However, this same fact makes Lake Chapala a poor candidate for management. For example, fertilization would be of no value in trying to increase annual fish yields.

Because Lake Chapala is so shallow, sustained changes in the water balance would have serious consequences. If the lake becomes more shallow, the phytoplankton community may be released from the condition of light limitation and increase productivity until it is limited by nitrogen. Under such conditions blue-green algae should flourish. Lake managers, therefore, should concentrate on maintaining an adequate supply of water to the lake and manage the fisheries for sustained yields on the primary production base currently available in the lake.

APPENDICES

APPENDIX A

CALIBRATION OF ^{14}C CARBON INNOCULUM

APPENDIX A

CALIBRATION OF ^{14}C CARBON INNOCULUM

The $\text{Na}_2^{14}\text{CO}_3$ solutions used in this study came from four different sources. Three batches were from New England Nuclear Co and one from G. M. Mfg. and Inst. Co. These concentrates were diluted according to labeled concentrations to a presumed specific activity of 1.0 uci ml^{-1} . Volumetric glassware, previously rinsed in the alkaline dilution solution, was used for all dilutions (Lind 1979). To determine the exact specific activity of this dilution, 2-3 ml samples were ampulated, sterilized, and returned to Baylor for calibration.

Calibration was made using Beckman Ready-Solv HP water tolerant fluor. However, direct addition of the $\text{Na}_2^{14}\text{CO}_3$ solution to this fluor resulted in significant loss of activity. This was probably due to the acidic nature of the fluor (pH ca. 5.5). To avoid this problem, a 5 μl sample was placed on the underside of a dry vial cap. This very small drop remained in place by surface tension. The cap was then placed on a vial full of fluor and securely capped. This procedure ensured that the $\text{Na}_2^{14}\text{CO}_3$ solution did not come into contact with the acidic fluor until after the vial was capped, thereby preventing the loss of ^{14}C as CO_2 . An internal spike of

efficiency of this procedure at 94.4%.

Results of this calibration showed that the actual specific activity of the dilute radioactive solution ranged from 0.30 to 1.00 uci ml⁻¹. This variability might be due to two sources. First, there may have been a loss of activity when the concentrated Na₂¹⁴CO₃ solutions were diluted. However, since all glassware used for this dilution was pre-rinsed in alkaline dilution solution, it is unlikely that this loss is due to acidification of the radioactive solution. More probably there was variability in the original concentrates. Dilutions made using ¹⁴C received from New England Nuclear showed specific activities close to the expected 1.00 uci ml⁻¹ (range = 0.82 - 1.00 uci ml⁻¹). However, dilutions made from the ¹⁴C solution from G.M. Mfg. and Inst. Co. ranged from 0.30 to 0.35 uci ml⁻¹.

This variability of specific activity used does not compromise the accuracy of the production data. As long as the specific activity of the Na₂¹⁴CO₃ solution used for each series is known, accurate calculations of phytoplankton production is possible.

APPENDIX B

RELATIONSHIP BETWEEN TOTAL DAILY PRODUCTION AND
PRODUCTION DURING INCUBATION PERIOD

APPENDIX B

Relationship Between Total Daily Production and Production During Incubation Period

In this study, phytoplankton samples were incubated for two hours in the period between 11:00 A.M. and 2:00 P.M. Normally this incubation was from 11:30 A.M. to 1:30 P.M. In order to estimate the percentage of the total daily phytoplankton production taking place during the incubation period, two full day series were conducted in November, 1983. These series consisted of sequential incubations from shortly after sunrise to sunset.

Four-liter water samples were collected at station 11 from the surface, 0.5 m, 1.0 m, and 2.0 m. These samples were returned to the on-shore work station and kept at lake temperature at about 50% of surface light intensity. Aliquots were taken from those samples for the sequential ^{14}C incubations (see Methods)..

Mean phytoplankton productivity was calculated for each incubation period (Figure B-1). Results show that the incubation period between 11:30 A.M. and 1:30 P.M. accounted for 31% of the total daily phytoplankton production.

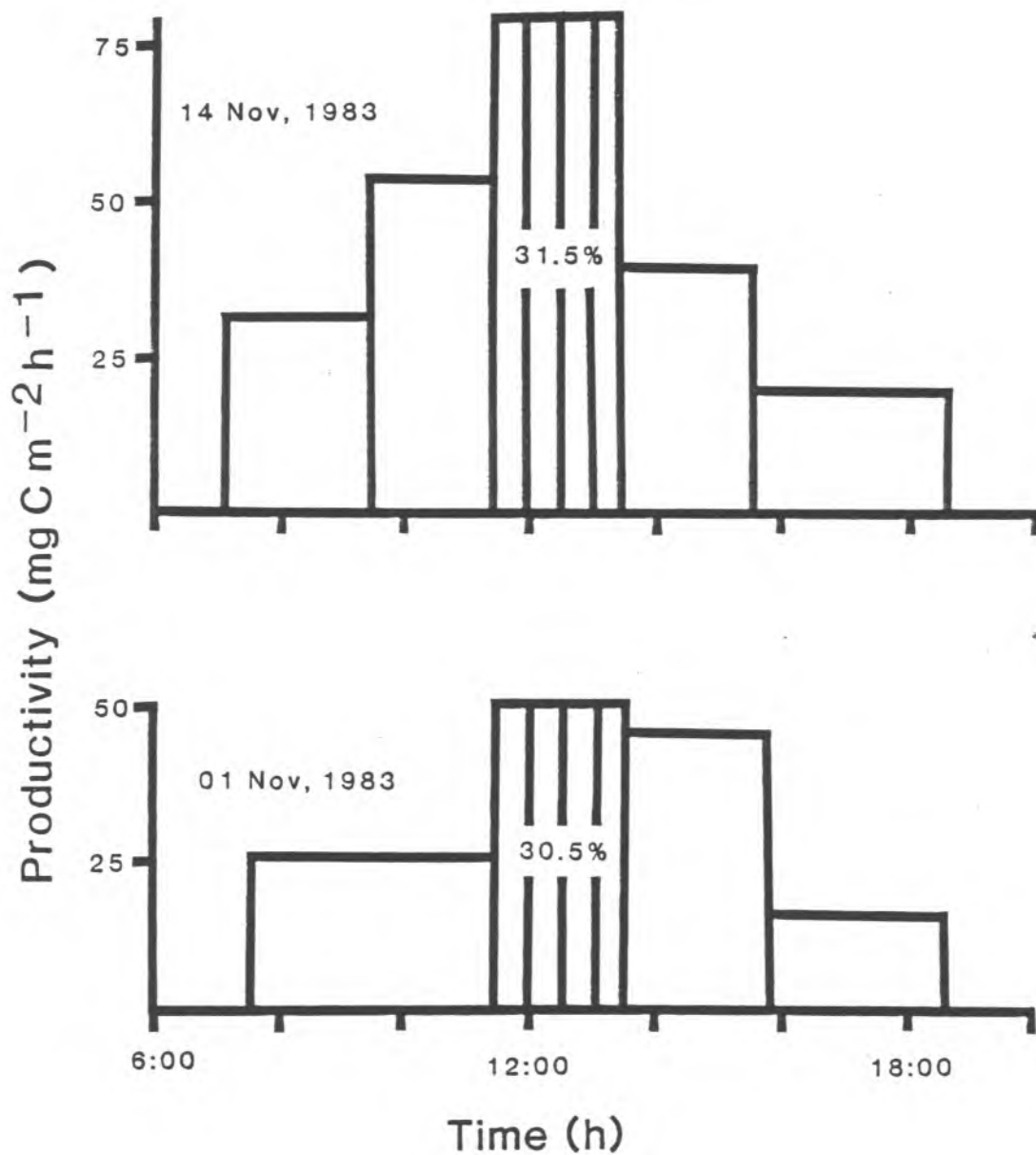


Figure B-1. Diel pattern of photosynthesis showing the percentage of the total daily production occurring during the two-hour incubation period (11:30 A.M. - 1:30 P.M.)

APPENDIX C

POSITION EFFECT OF FILTERS

APPENDIX C

Position Effect of Filters

The membrane filters used for determination of phytoplankton productivity were placed in liquid scintillation vials so that they lined the inner wall of the vial with the algal coating towards the inside. In the large vials (20ml), the edges of the filter did not meet, while in the small vials (7.5ml), the edges overlapped slightly. Either way produced a non-uniform coating of algae. To see if the relative position of the filter within the vial affected the performance of the liquid scintillation counter, the following test was made.

A 4-liter water sample was collected in a polyethylene container, inoculated with ^{14}C , and incubated at about 75% of surface light for four hours. Twenty-six aliquotes were filtered through 0.45 μ membrane filters. Thirteen were placed into small scintillation vials and 13 into large ones. The filters were then dried in a dessicator for three days. The vials were then filled with scintillation fluor (see methods) and capped. A small mark was made on each cap on the side where the filter edges met. The samples were

direction and counted. The vials were next the rotated 1/4 turn to the right and recounted. This was repeated until all vials were counted in four different positions.

A complete randomized block design analysis was run to test for differences among filter positions. For this analysis, each vial was considered a block and tested at four levels (positions). Results indicate no significant differences existed among the four positions for either size vial (Table C-1).

Table C-1. Test for difference in counting efficiency among four filter positions. Analysis design was complete randomized block.

Vial Size	Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Sm	Within sample	18366	36	510		
	Position	2203	3	735	1.44	0.25
Lg	Within sample	23436	36	651		
	Position	2578	3	859	1.32	0.31

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