THESIS

PHYTOPLANKTON DYNAMICS UNDER ICE-COVER IN A SUBALPINE LAKE

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY SARAH A. SPAULDING ENTITLED "PHYTOPLANKTON DYNAMICS UNDER ICE-COVER IN A SUBALPINE LAKE" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

PHYTOPLANKTON DYNAMICS UNDER ICE-COVER IN A SUBALPINE LAKE

The temporal dynamics of phytoplankton, as well as factors potentially controlling the dynamics, were examined in The Loch, a subalpine lake (3110 m above sea level) in Rocky Mountain National Park over the winter seasons of 1987-88 and 1988-89. The Loch (area = 4.98 ha, z_m = 4.7 m) was ice covered from early November until early May. The lake was sampled twice monthly at three discrete depths for the duration of ice cover.

The formation of ice resulted in freeze concentration of lake water. Because of The Loch's large surface area to volume ratio, between 40 and 80% of the lake volume became frozen. The exclusion of impurities as ice formed led to increased concentrations of dissolved constituents in the remaining lakewater. Although not all ions increased, pH, Ca, Na, K, SO_4, and alkalinity showed a significant increase ($P < 0.05$). The increases may have had an enriching affect on algal growth. However, nutrient concentrations were not measureably increased. Phosphorus (as ortho-phosphate) remained below dectection limits (3 - 6 $\mu g\ l^{-1}$), nor did nitrate increase significantly with freeze concentration.

Conservative ions changed only slightly over the winter season and with depth in the water column. However, there were changes in nutrient concentrations. Nitrate fluctuated with no discernable pattern during the first year and showed a clear decline the second year. Nitrate values were high (0.044 to 1.240 mg l^{-1}) compared to other high

elevation Colorado lakes, and concentrations were probably not limiting to the phytoplankton. Silica concentration ranged from 1.3 to 3.6 mg l^{-1} and also had late winter minima. The decline was attributed to depletion by the diatom *Asterionella formosa* Hass..

Values for pH ranged between 5.8 and 6.7 but did not show any trends over the season. Alkalinity ranged from 28 to 165 μeq l^{-1}. Oxygen concentrations were between 2.2 mg l^{-1} and 10 mg l^{-1} and varied over the season and with depth in the water column. Light impinging on the lake surface was at a minimum in January due to low aspect of the sun and shading of the lake by high ridges in the watershed. A low percentage of incident light transmitted through the ice surface was attributed more to low aspect of the sun, than ice thickness or snow accumulation. Light transmitted through the ice was rarely greater than 10 % of incident radiation.

The winter zooplankton assemblage was composed nearly exclusively of cyclopoid copepods and rotifers. The copepods (*Eucyclops agilis* Koch and *Acanthocyclops* sp.). were low in number, with maximum densities of 6 organisms l^{-1}. The rotifers (*Keratella hiemalis* (Carlin), *Notholca squamula* (O.F. Müller) and *Polyarthra* sp.) reached greater abundances, the latter attaining maximum values of 700 organisms l^{-1}.

The pattern of phytoplankton biomass during ice cover was consistent between the two years. The pattern was characterized by an early winter peak, followed by a minimum in January. A second maximum occurred in February / March, followed by a decrease until late May / April, and then a slight increase in May, when the ice melted. The pattern of algal biomass, and it resulted principally from the contribution of *A. formosa*. The dominant phytoplankton species in terms of biomass were *A. formosa*, *Dinobryon sertularia* Ehrenb., *Cryptomonas ovata* Ehrenb., and *Peridinium cinctum* (Müll.) Ehrenb.. Dominant species collectively contributed from 10 to 90 % of the total cells.

Algal composition changed throughout the season and individual species varied in abundance with depth. Although the same dominant (and most of the rare) taxa were present in both years, they varied in time of occurrence and abundance. Chlorophytes, cryptophytes, and cyanobacteria were all important components of the phytoplankton, but they did not occur at the same time in both seasons.

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INTRODUCTION

Temperate lakes generally have low primary productivity and biomass during the winter because of low temperature and solar radiation (Saija and Sakamoto, 1964; Lewis, 1974), a tendency one would expect to be exaggerated in ice-covered lakes. Such lakes have water temperatures close to zero and ice cover that may reduce incident light. Yet, Rodhe (1955) found algal populations of several million cells per liter beneath ice and snow in Swedish lakes. Although the light intensity was too low for photosynthesis, algal populations were maintained. He suggested that micro-algae under the ice were heterotrophic. Wright (1964) found a large and diverse winter phytoplankton population in a Massachusetts lake. Phytoplankton photosynthesized beneath the ice cover until snow accumulation blocked the transmission of light. Primary productivity under ice in a hypereutrophic lake was found to contribute a substantial proportion of the total annual carbon fixation (Wetzel, 1966). In lakes of the Colorado Front Range, Keefer and Pennak (1977) and Herrmann (1978) documented high winter populations of filamentous blue-green algae. Peak primary productivity occurred in December and January while the greatest phytoplankton densities occurred in May under ice cover. These examples indicate that both eutrophic and oligotrophic lakes can experience development of winter phytoplankton populations.

Phytoplankton communities undergo continuous change in taxonomic composition and relative abundance. This seasonal succession has been well documented and the focus of numerous freshwater and marine studies (Smayda, 1980; Reynolds, 1984; Harris, 1986). However, most studies of phytoplankton succession are conducted during the open water period. There has been little documentation of the

changes that occur during winter, under ice cover. The seasonal succession of the algae is attributed to variations in the physical, chemical, and biotic components of the environment and their interactions (Reynolds,1984). This changing environment affects the specific growth and loss rates of the algae. Wind induced mixing, and the associated changes in nutrient regime and light climate, is an important driving variable of succession during the open water period (Lewis, 1974). Under ice cover, mixing by wind is absent. The resulting stability of the water column leads to conditions that are very different from the open water period. Consequently, the winter seasonal succession is expected to be driven by factors other than mixing and the associated changes in nutrients and light regime.

Numerous oligotrophic lakes are found in glacial basins at high elevation in Colorado where an extended period of ice cover is a characteristic feature. The majority of limnological studies in this region have been restricted to the open water season (Pennak, 1944; 1945; 1955, Brinley, 1950; Schmitz, 1959; Koob, 1966; Reed, 1970; Toetz and Windell, 1983; McKnight et al., 1986; 1988; 1990). Few studies have been conducted during winter because of the remote location of the lakes and difficult access (Pennak, 1968; Keefer and Pennak, 1977; Herrmann, 1978; Ellsworth, 1983). Yet, in the Colorado Front Range most lakes above 3200 m above sea level are ice covered for more than 230 days of the year (Keefer and Pennak, 1977).

Due to the difficulties in studying high elevation lakes, less is known about them than about more accessible low elevation lakes. The potential for ecological change due to increases in acidic deposition is of special concern in the alpine and subalpine lakes of the Colorado Front Range because such lakes are often most sensitive to acid precipitation. Not only are they low in alkalinity due to limited buffering capacity of granitic bedrock and thin soils (Norton, 1980; Baron et al., 1984), they also tend to receive more acidifying substances than low elevation lakes (Lewis et al., 1984). Although acidic precipitation events have been recorded (Baron et al., 1984), there has at

yet been no evidence of the effects of acidification in Colorado. Acidification of lakes will initially affect phytoplankton. Schindler et al. (1985) emphasized that shifts in phytoplankton community composition are reliable indicators of acidification.

Long-term acidification of lakes has been recognized and well documented in Sweden, Denmark, Great Britain, Czechoslovakia, Greenland, Canada, and the eastern United States (reviewed in Charles and Norton, 1986; Battarbee, 1984; Battarbee et al., 1986). In areas where acidification has already occurred, paleolimnological reconstructions are the only way of estimating original phytoplankton communities. Reconstructions are based on sedimentary diatom and chrysophyte remains, only a portion of the algal community. This study provides a record of the phytoplankton community in a lake unimpacted by acidification. The understanding of phytoplankton seasonality and relationship to water chemistry may aid in the interpretation of previous paleolimnological work (Charles and Norton, 1986).

Research Objectives

The goal of this study is to determine the importance of factors that interact to influence the winter phytoplankton community of a subalpine lake. To achieve this goal, the following objective were addressed:

1. Determine the temporal dynamics of the phytoplankton of a subalpine lake by examining changes in species composition, abundance, diversity, and biomass throughout the winter season.

2. Examine concomitant dynamics of selected physico-chemical factors.

3. Examine concomitant abundance and diversity of the zooplankton.

4. Assess the relationship between winter phytoplankton dynamics, selected physico-chemical factors, and zooplankton dynamics.

Characterization of lakes during winter

Physical and chemical characterization

In most temperate lakes, conditions during the winter differ significantly from those that prevail during the rest of the year. Ice seals lakes from the influence of their surroundings and the water column becomes relatively stable. Ice-covered lakes become inversely thermally stratified, with 0° C water immediately below the ice and bottom water near 4° C. In contrast to open water lakes, little mixing occurs between the thermally stratified layers because ice seals the water column from the stirring action of wind (Wright, 1964). Ice cover also precludes mixing caused by seiches, Langmuir currents, and surface waves (Seaburg et al., 1983) and exchange of gases with the atmosphere. Nevertheless, the water column is rarely hydrologically static (Likens and Hasler, 1962) but the circulation currents are weak compared to those in the epilimnion during the summer (Wright, 1964). Ice cover also acts as insulation to reduce heat exchange between the air and the water column. Further stability results from decreased, or nonexistent stream inflow and outflow during winter, and the subsequent increase in water renewal time. As a consequence of ice cover, some physical conditions are remarkably stable when compared to the open water period.

With the formation of ice cover, there are associated changes in the wavelength and intensity of incident light that a lake receives. During the winter, total solar input is at its lowest ebb in the yearly cycle. Light available for photosynthesis is further reduced by the formation of ice and the accumulation of snow. While clear ice has a transparency close to that of water, ice with bubbles or particle inclusions increases the attenuation of light (Wetzel, 1983). Wright (1964) demonstrated that 20 to 40% of incident light penetrated a lake's ice surface. After a light snowfall, however, light reaching the water was reduced to 5.0%; with additional snow, light was reduced to

0.2% of incident light. Transmission of light is the most important factor limiting photosynthesis under ice cover (Wright, 1964; Maeda and Ichimura, 1973; Nebaeus, 1984).

The formation of ice cover seals a lake from the two-way exchange of atmospheric gases. The ice sheet reduces diffusion and allows oxygen to be depleted or to build up to high concentrations in the water column. The oxygen concentration depends on the balance between photosynthetic production of oxygen, respiration of higher trophic levels and decomposition processes. In a hypereutrophic lake, entrapped oxygen built up to concentrations of 25 mg/l (185% saturation) (Wetzel, 1966). When the ice was penetrated, the supersaturated water effervesced with the release of oxygen. As the winter season progressed, oxygen was consumed in the hypolimnion and anerobic conditions developed. In the Antarctic, many lakes have permanent ice cover (Parker et al., 1982). In such lakes oxygen concentrations build up to 40-45 mg l^{-1}, many times the saturation value. On the other hand, oxygen depletion may also occur under ice cover. This is the commonly known cause of winterkill of fish populations (Greenbank, 1945; Halsey, 1968). Fish mortality often occurs in shallow eutrophic lakes with 3 to 4 months of ice and snow cover. In some Colorado alpine lakes, photosynthesis did not proceed at a rate high enough to maintain the initially high winter oxygen concentrations (Pennak, 1968). As a result, oxygen decreased from supersaturated conditions at the formation of ice cover to anerobic conditions.

Studies have shown that ionic concentrations are generally higher in winter under ice cover than during summer (Greenbank, 1945; Barica, 1977; Canfield et al., 1983; Ellsworth, 1983). As ions are excluded from the ice they are concentrated in the remaining water. If the water volume of the lake is small in comparison to the ice volume, this "freezing out" process may alter ionic concentrations. Accordingly, Canfield et al. (1983) found that when ice melted, lake water was diluted. However, "freezing out" should not be confused with the release of dissolved material from bottom

sediments as oxygen concentrations and redox potentials decrease, because both processes may simultaneously occur in ice-covered lakes.

Biological characterization

Several investigators have examined winter primary productivity and biomass values in ice-covered lakes. Under clear ice, algal growth is often similar or higher than growth in open seasons. For example, in Arctic lakes much of the annual algal production takes place beneath the ice (Hobbie, 1973; Kalff et al., 1975). Several lakes in Sweden have experienced winter algal blooms in spite of low incident solar radiation (Rodhe, 1955; Nebaeus, 1984). In central Japan, daily primary production under the ice was comparable to that during the open season (Saijo and Sakamoto, 1964; Maeda and Ichimura, 1973). Although rates of carbon fixation under ice in hypereutrophic Sylvan Lake were lower than the peak summer rates, they were less variable and contributed a significant portion of the total annual productivity (Wetzel 1966). Willén (1961) reported that peak phytoplankton densities occurred under ice and snow. In Lake Baikal, the vernal algal maximum was reached before the break-up of ice cover (Kozhov, 1963 as cited by Lund, 1965). In Colorado alpine lakes, phytoplankton densities were similar under clear ice and open water (Keefer and Pennak, 1977; Herrmann, 1978). These authors also report "blooms" of nanoplankton that occurred even following heavy accumulation of snow on the ice surface.

The large planktonic algal populations in ice-covered lakes can partially be attributed to stability of the water column. In open water, a considerable portion of the euphotic zone is subject to continual or intermittent mixing. As the organisms are mixed, they experience fluctuating light regimes to which they rarely fully acclimate (Harris et al., 1980). In contrast, because ice covered lakes are stratified and stable, the phytoplankton may be better adjusted to their light environment than the phytoplankton in turbulent waters. Indeed, several investigators have found that stability of the water

column leads to extremely efficient utilization of light (Pechlaner, 1971; Tilzer, 1973; Maeda and Ichimura, 1973).

Planktonic algae may adjust to low light conditions in two ways: by modifying their photosynthetic metabolism (Tilzer and Schwarz, 1976) or by increasing the amount of the light harvesting pigment, chlorophyll (Wetzel, 1983). Algae may modify the quantity of electron transport carriers in their cells (Vincent, 1980). Cells form only the quantity of redox components necessary under the light conditions. The time necessary to regulate photosynthesis in this manner is on the order of hours to days. Thus, in a constant light climate cells may be most economical in the production of molecules for photosynthesis. In conditions of low light, this results in photosynthesis being light saturated at lower light intensity. Maeda and Ichimura (1973) found that light saturation occurred at unusually low levels of incident light under ice. Seaburg et al. (1983) determined that phytoplankton in amictic Antarctic lakes are more photosynthetically efficient than lakes in other areas of the world. They attributed this efficiency to the stability of the water column. However, they were not able to discern whether the Antarctic algae were more efficient at trapping light or at utilizing light energy. Availability of nutrients affect a cell's ability to modify its photosynthetic metabolism. The fact that the phytoplankton in Char Lake, a Canadian Arctic lake, did not exhibit increased light efficiency, may relate to low phosphorus levels (Kalff and Welch, 1974).

Some algal species adjust to dim light by increasing chlorophyll relative to total cell biomass. Algal cells grown in culture at low light intensities have a higher chlorophyll *a* content per cell than those at high light intensities (Wetzel, 1983). In nature, the highest pigment to weight ratios were observed in phytoplankton living in low light (Kalff and Holmgren, 1972; Tilzer and Schwarz, 1976). Higher chlorophyll content does not, however, necessarily increase photosynthetic rates (Maeda and Ichimura, 1973).

In open water and under clear ice cover, high light intensities near the surface may be damaging to algae and may inhibit photosynthesis. Wright (1964) showed that the phytoplankton in a small Massachusetts lake were inhibited by light directly below the ice. Nevertheless, whether light intensity is bright or dim, within a stable water column the phytoplankton may be more likely to occupy preferred depths or adapt physiologically.

Light and temperature are closely related in their effects on photosynthesis and growth (Wetzel, 1983). Maeda and Ichimura (1973) determined that optimal temperatures for algal growth were 10 to 15 °C higher than the winter water temperature of the lake from which the phytoplankton were taken. In addition, they found that microflagellates had a lower temperature optimum than that of diatoms. They concluded that it may be the general nature of the winter algae that the temperature optimum is far higher than the temperature of the habitat. Although temperature may not be optimum under ice cover, it is not known to what extent it limits algal distribution. Nabaeus (1984) found that most of the cyanobacteria species that occurred in winter also were found in summer at high temperatures. Wright (1964) could not attribute the distribution of algae in the water column to differences in temperature.

A stable, light-limited water column favors certain algal morphologies and nutritional strategies. Flagellates and small cells are common in ice covered lakes (Wright, 1964; Keefer and Pennak, 1977; Vincent, 1981). The motile phytoplankton are able to select their preferred light conditions.For example, Maeda and Ichimura (1973) found that under clear ice, microflagellates were abundant throughout the water column. When snow accumulated on the ice surface, the microflagellates migrated to the upper portion of the water column. In a permanently ice-covered Antarctic lake, flagellates underwent diel migrations to obtain light in upper waters and nutrients in the depths. In the absence of turbulence, flagella prevent sinking into the aphotic zone. Small sized

algae are also resistant to sinking. In addition, a high surface to volume ratio favors light capture and nutrient absorption.

In the absence of light, heterotrophy has been suggested as a means of nutrition (Rodhe, 1955). Wright (1964) found that some algal species disappeared when heavy snow cover remained on the ice surface. Other species maintained their populations at large enough numbers to allow rapid colonization when the light conditions became more favorable. In Lapland, Rodhe (1955) found that under thick ice and snow *Cryptomonas pusilla* reached densities of 36,000 cells per liter.

Phytoplankton have different nutritional strategies. The understanding of these strategies may provide insight into how algae survive in the absence of light. Hutchinson (1967) assigned chlorophyll containing algae into five categories based on nutritional requirements. Autoauxotrophic phototrophs obtain all energy and matter by photosynthesis and dissolved inorganic matter. Most freshwater algae are believed to be included in this category. Autoauxotrophic phototrophs that are facultatively heterotrophic are believed to be capable of living in the dark indefinitely on dissolved organic substances such as acetate and glucose. Wright (1964) was able to culture *Cryptomonas marsonii* , *Cryptomonas borealis* , and *Cryptomonas* sp. in the dark when supplied with acetate. In dim light, *C. borealis* and *C.* sp. were able to supplement autotrophic growth with heterotrophic assimilation. In addition, many of the green algae of the orders Volvocales and Chlorococcales have this type of nutritional strategy. Alloauxotrophic but obligate phototrophs are unable to obtain major sources of carbon from organic compounds. They are dependent on an external source of vitamins. Hutchinson suggests that dinoflagellates, chrysophytes, and some diatoms will be found to have this type of nutrition. Alloauxotrophic and facultatively heterotrophic algae require an external source of vitamins. They can obtain energy and matter from dissolved inorganic substances in the light of from dissolved organic sources in the dark. Pigmented euglenophytes belong to this group as well as a few diatoms and green algae.

Alloauxotrophic but partly obligate heterotrophic algae are unable to obtain all their nutrition requirements by photosynthesis. Such a strategy includes phagotrophy, the ingestion of bacteria or other algae. Some members of the divisions Chrysophyta, Pyrrophyta, and Cryptophyta have been reported to be phagotrophic (Sanders and Porter, 1988). This nutritional strategy is particularly suited to persistence in low light conditions (Sangren, 1988). The division Chrysophyta appears to have the most taxa that are capable of phagotrophy. In fact, a large number of genera have been shown to ingest particles. Under low light, *Dinobryon* sp. obtained 50 percent of its total carbon intake by bacterial grazing (Bird and Kalff, 1986; 1987). Not only does *Dinobryon* ingest bacteria at rates similar to those of nonphotosynthetic microflagellates, but because of the size of the populations *Dinobryon* consumed more bacteria than crustacean, rotifer and ciliate communities combined.

Zooplankton

Zooplankton growth is known to be directly related to algal food supply and temperature (Hutchinson, 1967). There have been few studies of zooplankton populations under ice cover. In those conducted in Colorado alpine lakes during the winter season, variability seems to be the rule. Keefer and Pennak (1977) found short term fluctuations in zooplankton population densities and extreme temporal differences between and within lakes. Pennak (1968) found that in some Colorado alpine lakes, copepods were ten times as dense in summer as compared to winter. This was despite an abundance of seston and nannoplankton under ice. In contrast, Long Lake which had similarly high algal resources had the greatest abundance of copepods in January though May (Keefer and Pennak, 1977). Likewise, in some lakes the winter density of rotifers was remarkably high (Pennak, 1968), in some cases greater than during the summer. The maximum populations were found in early or mid winter. But in Long Lake, rotifers were sparse or absent (Keefer and Pennak, 1977).

DESCRIPTION OF STUDY AREA

The study was conducted in the Loch Vale Watershed (LVWS) in northern central Colorado (Figure 1). It is the site of a long-term research study established by the National Park Service in 1981. The primary objective of the long-term research conducted at the site is to determine the biogeochemical processes that would be influenced by increasing acidic deposition in Rocky Mountain National Park (Baron et al., 1984). The project is also part of the National Acid Precipitation Assessment Program (NAPAP).

The LVWS encompasses an area of 660 ha that ranges in elevation from 3109 m to 4120 m above sea level on the east slope of the Continental Divide (Figure 2). The watershed is characterized by glacial cirques and U-shaped valleys that were formed in the Pleistocene (Madole, 1976). The bedrock consists of Precambrian biotite gneiss and schist with intrusions of Silver Plume granite. Slow weathering feldspars, quartz, and plagioclase are the dominant minerals. Roughly 80% of the watershed is exposed bedrock and talus (Walthall, 1985).

The vegetation is classified as subalpine and alpine tundra (Marr, 1961). Within the subalpine in Loch Vale, forest coniferous species consist of Engelmann spruce (*Picea engelmannii* Parry) , subalpine fir (*Abies lasiocarpa* (Hook.)Nutt.), and occasional limber pine (*Pinus flexilis* James). In general, the vegetation is characteristic of the subalpine in the Front Range (Peet, 1981). At approximately 3290 m above sea level spruce and fir take on the krummholtz growth form, and disappear entirely above 3320 m above sea level. The limit to tree growth is caused by a combination of low summer

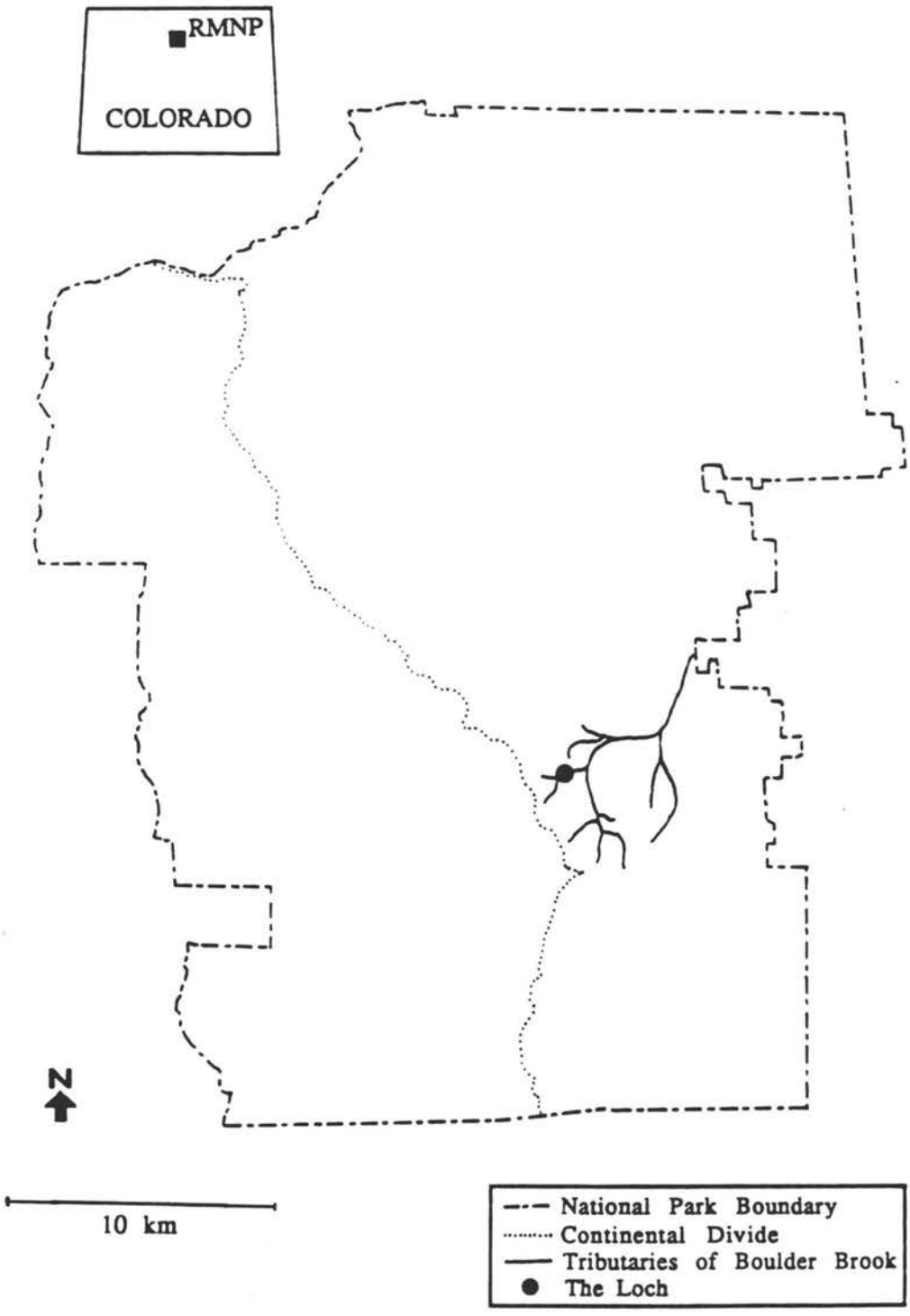


Figure 1. Rocky Mountain National Park (RMNP) showing the location of the study lake (The Loch) and the tributaries of Boulder Brook.

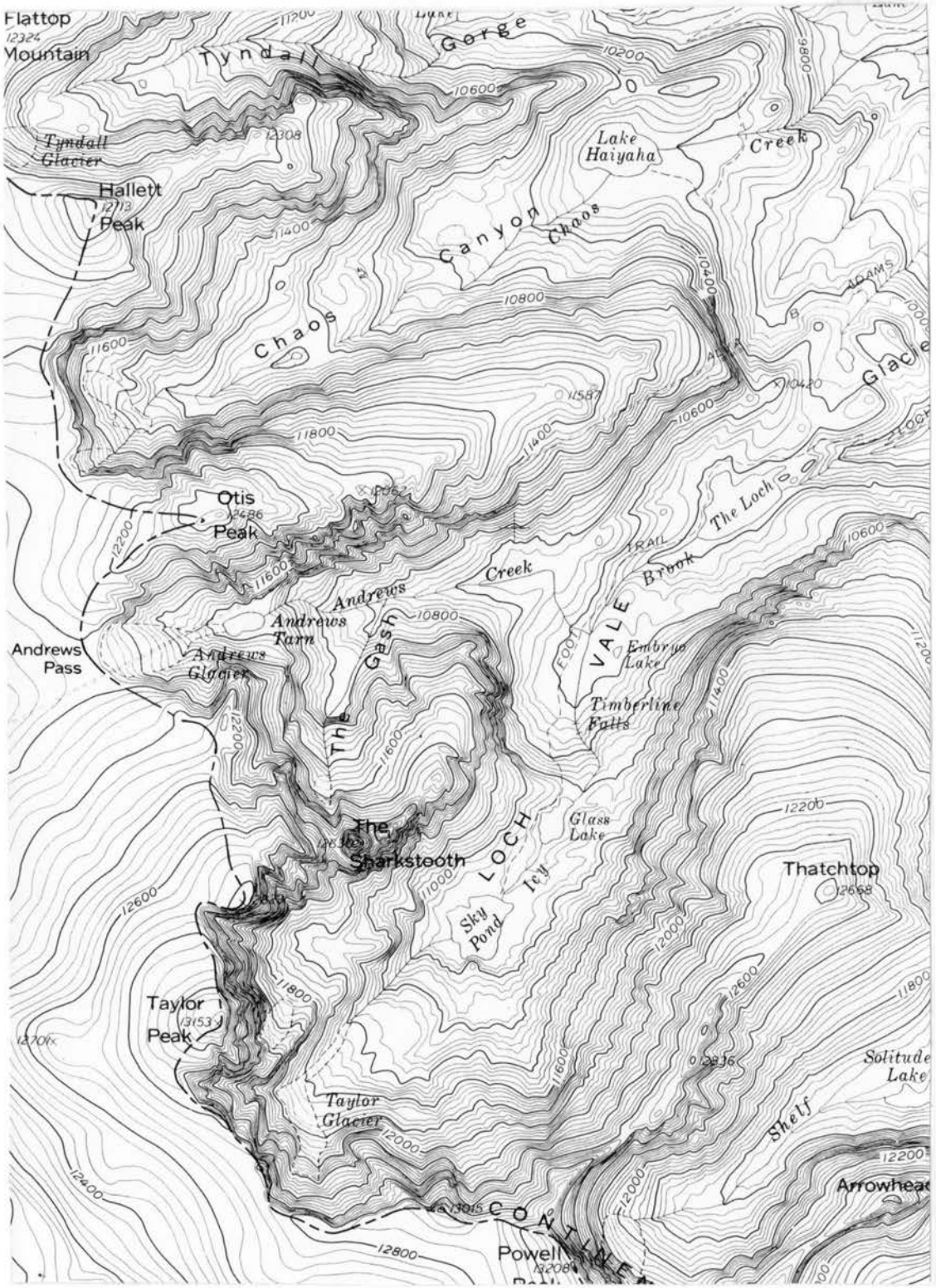


Figure 2. Contour map of the Loch Vale Watershed and surrounding area. (From U.S. Geological Survey 7.5 Series, Scale 1:24000, Contour Interval = 40 ft, McHenry's Peak quadrangle, Colorado)

temperatures, dry winter winds, and late lying snows that delay seedling development (Wardle, 1968). Above treeline, tundra vegetation consists of several associations of low perennial woody shrubs, sedges, grasses and forbs (Komárková and Webber, 1978). Marr (1961) determined that patterns of wind and distribution of snow are major abiotic factors determining the tundra vegetation on Niwot Ridge (approximately 20 k south of Loch Vale).

The range of weather conditions at high elevation in Colorado is extreme. Strong winds are characteristic of high elevation in the Front Range (Marr, 1961). Extreme gusts at Niwot Ridge occurred in October through February (Barry, 1973). Likewise, in Loch Vale winds reach their greatest force in winter months. Two minute average wind speeds were regularly greater than 8 m sec^{-1} and peaked at speeds of 17 m sec^{-1} (Bigelow et al., 1990).

The mean annual temperature at Niwot Ridge was -3.8°C, with temperatures above freezing 59 days of the year (at Como Creek, 3048 m a.s.l.). The distribution of precipitation varies with season with the highest precipitation at 3750 m from November to April. From June to September the greatest precipitation was found between 3050 and 3750 m a.s.l.. At the LVWS meteorological station, precipitation ranged from from 75 to 110 cm for the years 1985 through 1989 (Baron, in press). More than fifty percent of the annual precipitation occurs as snow. Two types of snowfall occur in the Front Range: cold "dry" snow that originates in Pacific air masses and heavy "wet" snow that originates in the Gulf of Mexico (Wardle, 1968). The wind redistributes the fine dry snow into deep drifts, while exposed sites are left wind swept and bare. The bulk of the water is from heavy snowfalls that occur in March and April. Dense spring snow is less prone to drifting.

Barry (1973) found that with increasing elevation there was no increase in solar radiation, on an annual basis. However, on a seasonal basis, there were at times

increasing inputs of radiation with elevation. During the winter, clouds reduced total solar radiation at higher elevations.

There are four lakes (Sky Pond, Glass Lake, Andrews Tarn, and The Loch) in LVWS (Figure 3 and Table 1). All the lakes are oligotrophic. Water temperatures range from 0 to 4°C during the winter and up to 12°C during summer months. None of the lakes thermally stratify during the open water season due to their shallow depths, short water residence times, and strong winds that promote mixing. The Loch contains a single deep channel with a maximum depth of 4.7 m (Figure 4). During the winter a large percentage of the lake is frozen to the sediment. Thus, the liquid water is confined to the single depression near the outlet.

Icy Brook flows from the headwaters of the watershed draining Sky Pond and Glass Lake. It is joined with Andrews Creek before it flows into The Loch. Icy Brook flows most of the year, but flow ceases in winter months. A single major snowmelt takes place in the spring that controls the hydrologic regime of the lakes. Thus, snowmelt dominates the runoff that contributes to the lakes and streams. Snowmelt dominates not only the pattern of discharge, but exerts primary control on the chemical composition and concentration of lakewater (Baron and Bricker, 1987).

McKnight et al. (1986; 1988; 1990) studied phytoplankton populations in three Loch Vale lakes for the period 1984 through 1986. The period of open water was characterized by a recurrent pattern of algal composition. During the spring, a bloom of *Asterionella formosa* Hass., a common diatom of temperate lakes, occurred in 1984 and 1985. Often, the deeper Sky Pond with longer hydrologic retention had nearly ten-fold more algal biomass than The Loch. In The Loch peak cell densities were between 3,000 and 9,000 *A. formosa* cells ml^{-1} while in Sky Pond they ranged from 10,000 to 30,000 cells ml^{-1}. The rapid net growth rates of *A. formosa* allowed high populations to occur despite rapid lake water turnover caused by peak runoff from snowmelt. Growth rate estimates ranged from 0.15 to 0.49 per day. Primary productivity measurements for one

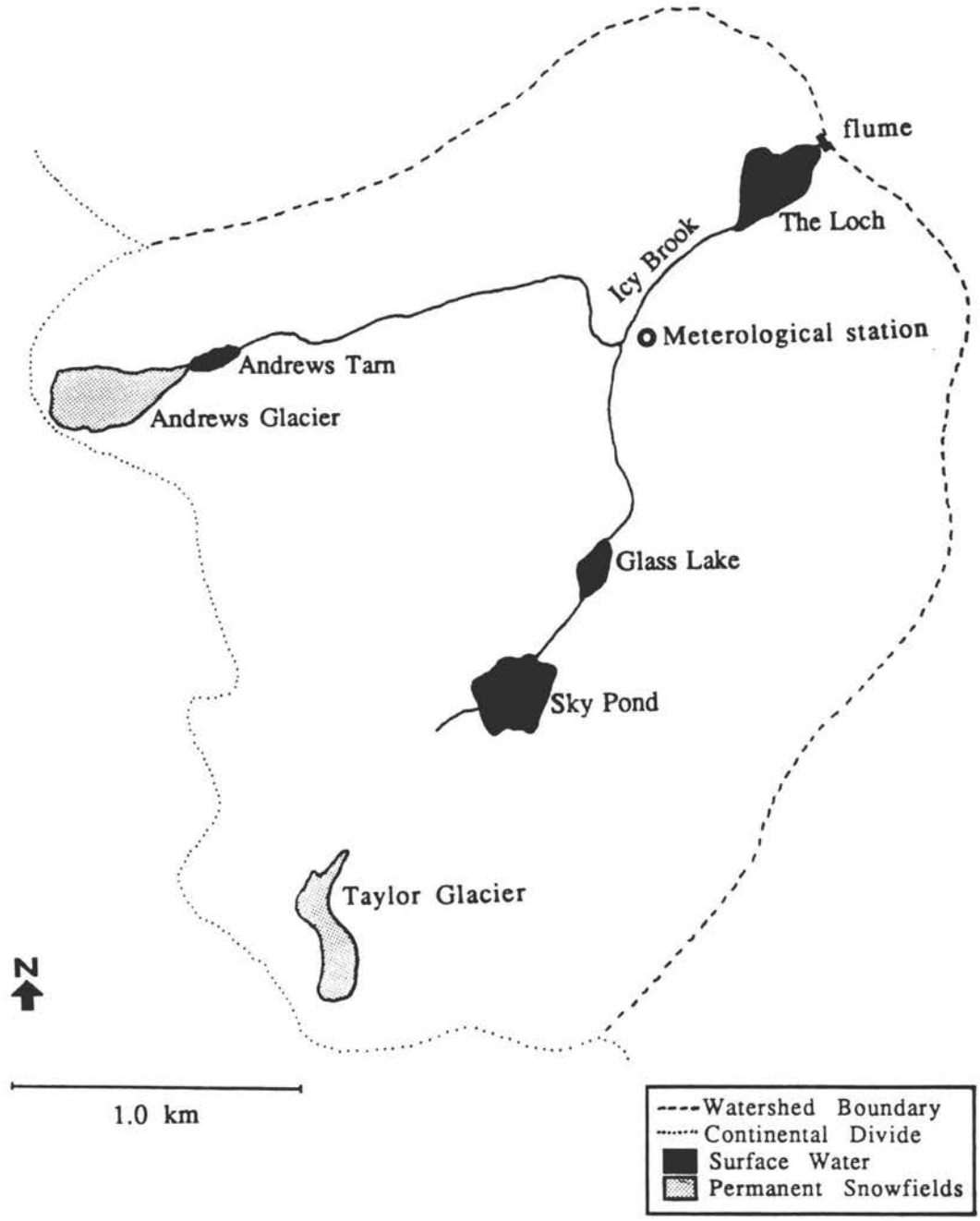


Figure 3. Detail map of the Loch Vale Watershed (LVWS).

Table 1. Morphometric characteristics of the four lakes in the Loch Vale Watershed (Baron et al., 1984).

Lake	Elevation (m.a.s.l.)	Lake area (ha)	Volume (m^3)	Average depth (z) (m)	Maximum depth (z_m) (m)
Sky Pond	3,320	3.03	121,680	4.5	7.3
Glass Lake	3,290	1.01	25,690	2.8	4.7
The Loch	3,050	4.98	61,100	1.5	4.7
Andrews Tarn	3,470	0.97	no data	no data	no data

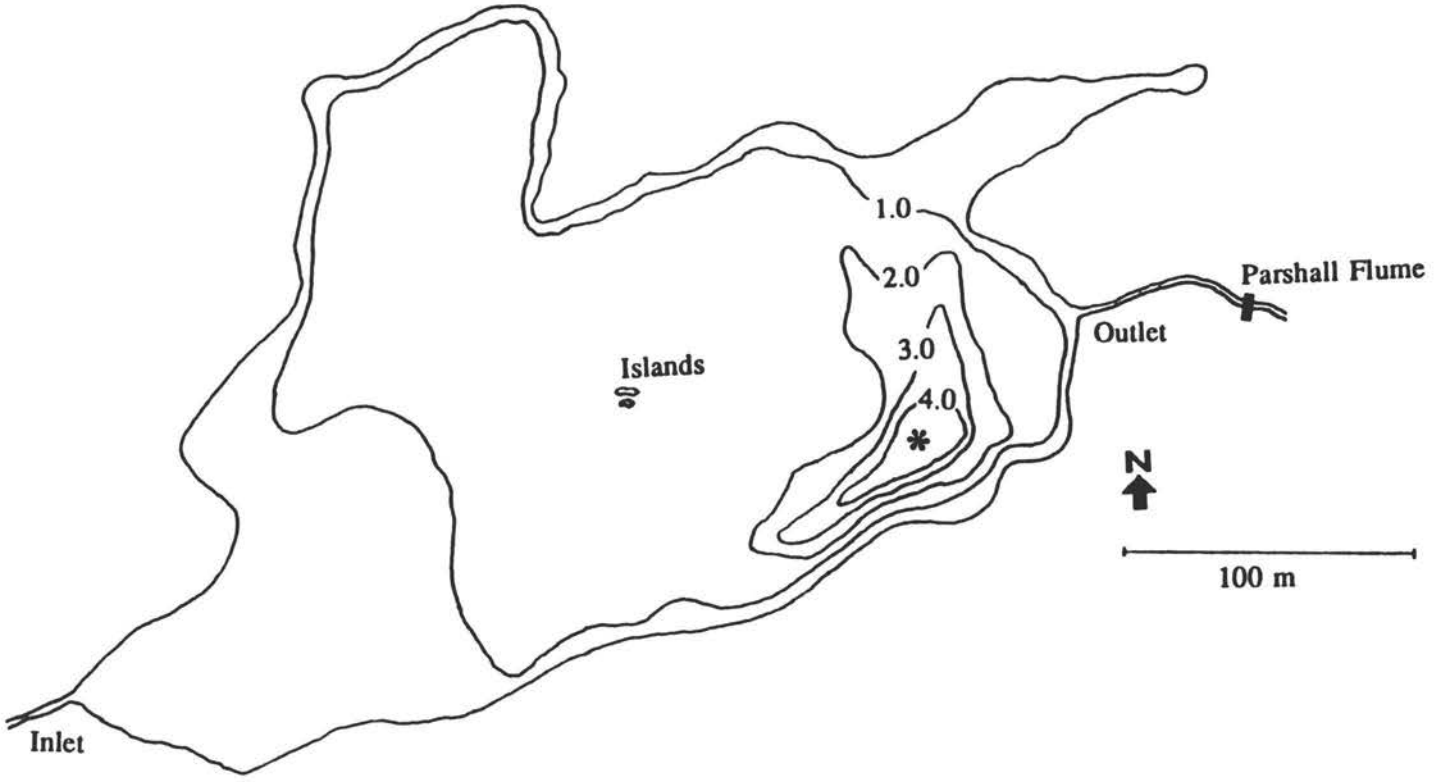


Figure 4. Bathymetric map of The Loch with 1.0 m contour intervals. Samples were always collected at the maximum depth (✱).

date in the spring ranged from 61 μg C l^{-1} h^{-1} at the 1 m depth to 9 μg C l^{-1} h^{-1} at the 2 m depth. Koob (1966) conducted a three year study of plankton populations in six subalpine lakes of the Rawah Wilderness Area in northern Colorado. Two of the lakes developed *A. formosa* blooms of between 100 and 1000 cells ml^{-1} during spring and summer.

The Loch and Sky Pond were also found to have large populations of the cyanobacterium, *Oscillatoria limnetica* Lemm. during the low stream flow period of autumn, when densities reached a maximum of 250,000 cells ml^{-1} in Sky Pond. The fall photosynthetic rates estimated at 7 μg C l^{-1} h^{-1} were lower than the spring rates. In general, algal concentrations in The Loch were much lower than in Sky Pond and reflect the shallow depth and high flushing rate of The Loch during the open water season.

MATERIALS AND METHODS

The Loch was sampled during the 1987-88 and 1988-89 seasons of ice cover. Ice may form as early as September, but a solid covering of ice does not form until November. In both years sampling began as soon as the ice was thick enough to support weight. In 1987 this was in early December and in 1988, mid November. The site was visited as close to every two weeks as possible. Sampling continued until early to mid May when the ice could no longer support weight.

The lake was always sampled at the deepest point in the lake (Figure 4), which varied between 3.5 and 4.5 meter depth during the study. Sample collection took place between 11:00 A.M. and 1:00 P.M. The first year two 25 cm diameter holes were drilled side by side with a manual ice auger. A spud bar, a iron bar with a sharpened end, was used to remove ice that joined the two holes. The ice opening was then large enough to accommodate sampling equipment. The second year a sampling tube was permanently set into the ice that could be readily accessed.

Snow depth at the sample site and areal extent of snow cover on the lake surface were estimated. Ice thickness was measured by lowering the spud bar into the hole to the depth of ice cover, retrieving the spud bar, and then measuring the marked distance with a meter tape. The ice hole was then filled with snow to prevent phytoplankton or zooplankton from responding to the increased light levels and congregating at the ice opening.

The lake depth was measured by lowering a weighted meter tape to the lake bottom. A temperature profile was measured with a Yellow Springs Instruments

temperature meter. The temperature meter was calibrated in the laboratory and verified in the field by measuring the surface temperature with a hand held thermometer.

Light profiles were measured using a Licor data logger (LI-1000) attached to a spherical quantum sensor (LI-193SA). The sensor was attached to a lowering frame and readings were taken every 0.5 m both as the sensor was lowered to the lake bottom and as it was raised. Attempts to complete a light profile under constant ambient light conditions were not always possible, as clouds could rapidly appear across the sky.

Water samples were collected with a Black and Decker jackrabbit pump. This hand-operated peristaltic pump was flushed with water from each sample depth before the samples were collected.

Three replicate samples for phytoplankton identification and enumeration were collected at each of three depths: 0.5 m below the ice surface, at mid depth (2.0-2.5 m), and 0.5 m above the sediment. Samples were collected in 250 ml opaque bottles shielded from direct sunlight and prevented from freezing. In the laboratory, phytoplankton samples were preserved with ten percent acid Lugol's solution (Standard Methods for the Examination of Water and Wastewater, 1965). Subsamples were concentrated in settling chambers ranging in volume from 5 ml to 100 ml, depending on the abundance of cells. Volume of the settling chambers was adjusted so that at least 100 cells of the most common taxa could be counted in two strip counts. Algae were identified and enumerated using a Leitz Diavert inverted microscope (Lund et al., 1958; Untermöhl, 1958). Identifications were made with the guidance of R.G. Dufford and were primarily based upon keys by Prescott (1962) and Tikkanen (1986). After counts were made, phytoplankton subsamples were archived in vials and preserved in formalin.

Cell volumes were estimated for the most common genera by measuring the dimensions of 100 individuals from samples taken on a given date. Measurements were also made on twenty cells of the same genera on four to five additional dates. Volume was estimated with formulas given in Willén (1976) and Tikkanen (1986). For less

common taxa, volume estimates were made from fewer cell measurements or from literature values. Cell volume may be converted to biomass by multiplying by algal specific density, most often assumed to be equal to the specific density of water (1 g ml^{-1}). However, there are cautions to using volume estimates. Sicko-Goad (1977) showed significant differences between algal species in cell contents. For example, diatoms may contain more than 40 % of the cell as empty vacuole. For the purposes of this study, chlorophyll *a* and biovolume were used as independent estimates of biomass and their results were compared.

Two replicate samples at each of three depths were collect in opaque 500 ml bottles for chlorophyll analysis. In the laboratory, sample water was filtered through Whatman GF/C 25 mm filters. One drop of 1 N $MgCO_3$ was added to the filter to aid in the preservation of chlorophyll. Enough water was filtered to obtain a well colored filter, usually between 100 and 500 ml. Filters were wrapped in aluminum foil, stored in individual petri dishes, and frozen until analysis. Analyses were completed within one week of collection the first year and within 2 months the second year.

Chlorophyll extractions were made in 95% ethanol using a modified method of Jesperson and Christoffersen (1987). Filters were macerated in a tissue grinder (carried out in dim light to prevent photodegredation) and extracted in ethanol for 12 to 18 hours. Extracts were centrifuged in 10 ml centrifuge tubes and the supernatant measured in a Turner Designs Model 10 Flourometer. The flourometer was calibrated using chlorophyll *a* from Sigma Chemical Company (No. C-6144) and verified with quality control samples obtained from the U.S. Environmental Protection Agency Monitoring and Support Laboratory, Cincinnati. Samples were measured, acidified with one drop of 1 N HCl, and remeasured to correct for phaeopigments.

Two replicate samples of zooplankton were collected at each of three depths using a Guzzler bilge pump equipped with 6.35 cm diameter tubing. The large diameter and powerful suction was used to overcome zooplankton avoidance. The bilge pump

was used to fill a 22 liter bottle, the contents of which were poured through a 35 μm mesh plankton net. The zooplankton were washed into collecting bottles and preserved in ethanol. In the laboratory, the entire sample was counted for adult copepods and cladocerans. One ml subsamples were taken from a 20 ml concentrated volume using a Henson-Stempel pipet and placed in a Sedgwick Rafter chamber for enumeration of nauplii and rotifers. Determinations were made using Edmondson (1959), Stemberger (1979), and Pennak (1978).

Two replicate samples for dissolved oxygen were collected at each of three depths. Samples were collected in 300 ml glass stoppered bottles and analyzed by the Winkler method with azide modification. The samples were collected by placing the peristaltic pump hose in the bottom of the bottle and flushing water approximately two times bottle volume. In the field, the reagents alkaline iodide-azide and manganous sulfate (Hach Chemical Company) were added to fix the dissolved oxygen present. The titrations were completed in the laboratory. A comparison of titrations completed in the field and in the lab was performed and no significant differences were found ($n = 6$, $P < 0.05$).

Water samples for pH measurement were collected in Luer-Loch syringes to avoid equilibration of the sample with atmospheric CO_2. The samples were then analyzed for pH using a closed cell chamber. Measurements were made with an Altex 3500 meter with a Beckman combination electrode (Model 39835). The meter was calibrated against pH 4 and 7 buffers and checked with dilute HNO_3 at pH 4.30. If the reading of the check sample was off by greater than 0.10 of a pH unit, the meter was recalibrated or a different electrode used until there was agreement. The electrode was allowed to equilibrate in an aliquot of each sample for one minute. The final reading was taken when the reading stabilized in a fresh aliquot.

Specific conductance was measured using a Beckman meter and electrode. The meter was calibrated weekly against a 22 and 75 $\mu S\ cm^{-1}$ standard.

Samples for dissolved organic carbon (DOC) were collected in 300 ml glass bottles. The bottles and aluminum foil lid seals were placed in a muffle furnace at 500° C for five hours. In the laboratory, samples were filtered through pre-combusted Whatman GF/C filters using filtration apparatus that had undergone the same muffle furnace treatment. DOC samples were sent to the U.S. Geological Survey Central Laboratory, Arvada, Colorado, for analysis.

Samples for additional chemical analysis were collected in 2 liter acid washed bottles. Bottles were rinsed 3 times with water from the sampling depth before filling. Ten percent of these chemical samples were replicate samples. The samples were collected at the surface (0.5 m below the ice) and bottom (0.5 m above sediment) depths once per month. In the laboratory, sample water was filtered through 0.4 μm Nucleopore polycarbonate membrane filters. Aliquots for cation and metals analysis were filtered into 250 ml bottles and preserved with 1 ml of reagent grade HNO_3. Aliquots for NH_4 and PO_4 were filtered into opaque bottles and preserved with reagent grade $HgCl_2$. All samples were shipped on ice to the Central Laboratory for analysis. A summary of methods used by the Central Laboratory is given in Table 2. Relative standard deviation of replicate samples and values of blank field samples varied by chemical constituent (Table 3). Analytical accuracy was verified by computing charge balance calculations for samples with complete analyses (Denning, 1988). Ion percent difference, the difference between total cations and total anions divided by the sum of all ions, in Loch Vale samples were skewed toward positive values (mean percent ion difference = 2.6, standard deviation = 4.9). The discrepancy may be due to different analytical techniques in the measurement of cations and anions. In addition, a positive charge imbalance may also result from the presence of unmeasured organic anions.

Phosphorus, an important nutrient to the phytoplankton was higher in field blank samples (0.010 mg l-1 as orthophosphate) than in replicate samples (0.0063 mg l-1) (Table 3). It was not possible to detect changes in phosphorus.

Table 2. Chemical analyses performed by the U.S. Geological Survey Central Laboratory, Arvada, Colorado.

Variable	Reporting Units	Analytical Method(s)
Acid Neutralizing Capacity	$\mu eq\ l^{-1}$	Titration
Ca	$mg\ l^{-1}$	AAS & ICP
Mg	$mg\ l^{-1}$	AAS & ICP
Na	$mg\ l^{-1}$	AAS & ICP
K	$mg\ l^{-1}$	AAS
NH_4	$mg\ l^{-1}$	AWC
SO_4	$mg\ l^{-1}$	IC
NO_3	$mg\ l^{-1}$	IC
NO_2	$mg\ l^{-1}$	AWC
PO_4	$mg\ l^{-1}$	IC & AWC
Cl	$mg\ l^{-1}$	IC
F	$mg\ l^{-1}$	IC
Br	$mg\ l^{-1}$	IC
SiO_2	$mg\ l^{-1}$	ICP
Al	$\mu g\ l^{-1}$	DCP
Fe	$\mu g\ l^{-1}$	ICP
Mn	$\mu g\ l^{-1}$	ICP
DOC	$mg\ l^{-1}$	Wet Oxidation
Color	Pt-Co	Platinum-Cobalt
Acidity	$mg\ l^{-1}$ as H	Titration

ABBREVIATIONS:

AAS	Atomic absorption spectrophotometry
ICP	Inductively coupled plasma spectrophotometry
DCP	Direct current plasma spectrophotometry
IC	Ion chromatography
AWC	Automated wet chemistry

Table 3. Mean and percent relative standard deviation of replicate samples taken in LVWS in 1988 and mean and standard deviation of field blanks taken in LVWS lakes in 1983-1987 (J. Baron, unpublished data).

Variable	Units	Mean of Replicates	Relative Std Dev of Repl.	Mean of Blanks	Std Dev of Blanks
ANC	$\mu eq\ l^{-1}$	69.1	2.4 %	5.0	7.0
Ca	$mg\ l^{-1}$	1.73	3.2	0.014	0.009
Mg	$mg\ l^{-1}$	0.24	2.5	0.022	0.018
Na	$mg\ l^{-1}$	0.62	2.9	0.162	0.085
K	$mg\ l^{-1}$	0.21	4.1	0.016	0.011
NH_4	$mg\ l^{-1}$	0.017	15.1	0.100	0.133
SO_4	$mg\ l^{-1}$	1.84	3.0	0.025	0.020
NO_3	$mg\ l^{-1}$	0.81	5.5	0.036	0.018
NO_2	$mg\ l^{-1}$	0.0083	14.1	0.003	-
PO_4	$mg\ l^{-1}$	0.0063	12.2	0.010	0.007
Cl	$mg\ l^{-1}$	0.18	6.6	0.024	0.031
F	$mg\ l^{-1}$	0.13	12.0	0.018	0.011
SiO_2	$mg\ l^{-1}$	2.12	2.6	0.63	1.33
Al	$\mu g\ l^{-1}$	40.8	8.8	11.0	6.6
Fe	$\mu g\ l^{-1}$	45.3	15.5	15.8	13.6
Mn	$\mu g\ l^{-1}$	3.72	19.4	1.24	0.36
DOC	$mg\ l^{-1}$	2.24	14.2	0.30	-

ABBREVIATIONS:

ANC Acid Neutralizing Capacity

Ice cores for chemical analysis were obtained using a modified SIPRE (Anon., 1958) corer. Cores were transported frozen to the laboratory. Upon melting, they were treated for analysis following the procedure for water samples.

RESULTS AND DISCUSSION

Physico-chemical Parameters

Freeze Concentration

As ice forms, it excludes ions and impurities. Freeze concentration is the successive increase in dissolved constituents in lake water during freezing. The concentration of ions in lakewater in winter is determined by the pattern of discharge, the ratio of lake surface area to volume, and the degree of freeze concentration. Stream discharge in the mountains of Colorado is dominated by snowmelt as most precipitation falls in the winter as snow. The onset and rate of snowmelt in the spring and summer is controlled by air temperatures and solar radiation. The pattern of stream discharge reflects the variability in weather patterns from year to year (Baron, in press). For example, successive warm days in spring can cause an early peak in stream discharge, in which case much of the snow is removed from the watershed early in the year. Conversely, cool cloudy days can delay snowmelt into the summer producing a more even hydrograph. During the late spring and summer, The Loch is rapidly flushed by dilute snowmelt which has little interaction with bedrock and soils. In times of peak discharge, the lake volume is replaced every 2-3 days (McKnight et al., 1990). In fact, during this period The Loch is more like a wide spot in the stream than a lake. By late summer in most years, streamflow is maintained by a few permanent snowfields. Discharge continues to decline into the fall as cooling temperatures reduce the melting of remaining snowfields. In winter, The Loch has much longer water renewal times as inflow and outflow virtually cease.

With the onset of winter, discharge of Icy Brook into The Loch is so low that the lake level decreases. As winter progresses, there is a continual reduction in the lake level so that eventually, instead of a maximum depth of 4.7 m, the Loch has a maximum depth of about 3.5 m (Table 4 and Figure 5). This "loss" of water may occur by groundwater seepage; flow several hundred meters below The Loch outlet has been observed in winter, when the outlet itself is dry. In 1988-89 the lowest maximum depth occurred in December and January. However, by January 20, the lake level had increased to 4.1 m and remained at about that level until the period of ice out. Thus, under the cover of ice, the lake level first drops, and then rises. The source of the inflow was not visible at the inlet to The Loch, suggesting a subsurface source.

At the same time the volume of The Loch was decreasing, ice was forming on the surface. The Loch is very shallow, with over 70% of its area less than 2 m deep. In a lake with a large surface area to volume ratio, ice takes up a large proportion of the total water volume. By the end of January approximately 75 cm of ice had formed (Figure 5). If the ice formed on the lake without any subsurface loss, 80 % of the lake would be taken up as ice. In reality, these two processes proceed concurrently and result in some intermediate value of the total volume of water included in the frozen state. The end result is a liquid volume that is much less than that during the open water season.

Furthermore, the remaining water is more chemically concentrated. As ice freezes, it excludes dissolved constituents. To test whether ions were being excluded from the ice rather than trapped within it, two ice cores were taken in February of 1989. The ice concentrations were close to the blank values of deionized water or only slightly higher (Table 5). The largest differences between the blank and ice concentrations were found for sulfate. Sulfate concentrations in snow range from 0.30 to 0.45 mg l^{-1} (J. Baron, unpublished data). Dry deposition of atmospheric sulfate in snow occurs to some extent, and may be similarly deposited on the ice surface. However, the ice

Table 4. Depth of The Loch at the sample site for the years 1987-88 and 1988-89. [1]

Date	Lake Depth (m)
6 Dec 87	3.8
21 Dec 87	-
5 Jan 88	3.5
24 Jan 88	3.5
9 Feb 88	3.4
21 Feb 88	3.7
6 Mar 88	3.5
20 Mar 88	3.4
6 Apr 88	3.4
19 Apr 88	3.6
4 May 88	3.6
15 May 88	4.1
13 Nov 88	4.5
2 Dec 88	3.5
20 Dec 88	3.5
4 Jan 89	3.5
20 Jan 89	4.1
10 Feb 89	4.0
26 Feb 89	4.1
11 Mar 89	4.0
27 Mar 89	4.0
8 Apr 89	-
26 Apr 89	4.4

[1]During the first year the sample location may have varied up to 10 m laterally. The second year the sample location was fixed at a single point.

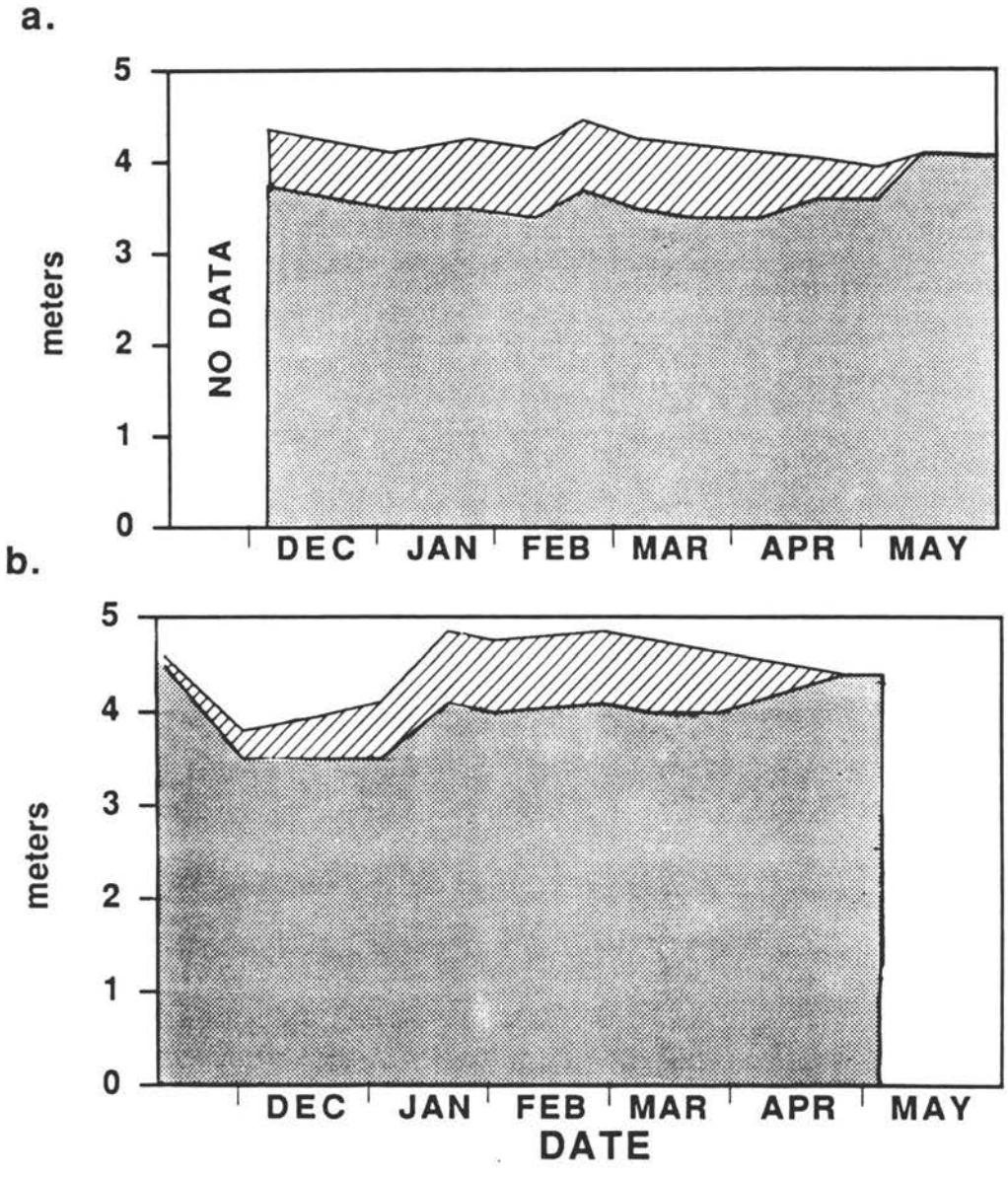


Figure 5. Thickness of ice cover and distance from the sediment (sediment = 0.0 meters) in The Loch in a) 1987-88 and b) 1988-89. Ice layer is hatched.

Table 5. Concentrations of dissolved species in two ice cores taken 2/26/89 compared with a deionized water blank.

Variable	Units	Blank	Core #1	Core #2
pH	-	5.6	5.3	5.5
Conductance	$\mu S\ cm^{-1}$	3	2	3
Ca	$mg\ l^{-1}$	<0.01	0.02	0.15
Mg	$mg\ l^{-1}$	<0.02	<0.02	0.02
Na	$mg\ l^{-1}$	0.01	0.03	0.09
K	$mg\ l^{-1}$	<0.01	0.02	0.04
ANC	$\mu eq\ l^{-1}$	6	3	4
SO_4	$mg\ l^{-1}$	<0.01	0.18	0.20
NO_3	$mg\ l^{-1}$	<0.01	0.04	0.07
Cl	$mg\ l^{-1}$	<0.01	0.07	0.08
PO_4	$mg\ l^{-1}$	<0.01	<0.01	<0.01
Al	$\mu g\ l^{-1}$	5	14	15
Fe	$\mu g\ l^{-1}$	<10	<10	10
Mn	$\mu g\ l^{-1}$	<10	<10	<10
NH_4	$mg\ l^{-1}$	<0.05	<0.05	<0.05
F	$mg\ l^{-1}$	<0.01	<0.01	<0.01
DOC	$mg\ l^{-1}$	2.3	2.3	2.5
SiO_2	$mg\ l^{-1}$	<0.02	<0.02	0.04

formed is primarily frozen from lakewater. The surface is often blown clear of snow, so it would not be expected that the ice core chemistry would be similar to snow chemistry. Nitrate, chloride, and aluminum concentrations were slightly higher in the ice cores than the blank. Dissolved organic carbon (DOC) concentrations were surprisingly high in both the deionized water blank and in the ice cores. I attribute the high values to analytical error. Such values were unusual for Loch Vale blank samples. Blanks typically range from 0.20 to 0.30 mg $l^{-1}$and lake water samples have a mean concentration of 1.42 mg l^{-1} (Denning, 1988).

The percent change in concentration between the low flow periods in August / September and December / January is significant at $P < 0.05$ for some chemical variables (Table 6). The percent change for the variables that were significant (pH, Ca, Na, K, SO_4, ALK) ranged from 32 % to 63 % increases in concentration as the lake surface froze (Figure 6). This range is comparable to the 40 % to 80 % increase I estimated based on lake morphometry. This concentration effect may have important implications for the phytoplankton dynamics. Phosphorus (as ortho-phosphate) was always below detection limits of 3-6 ug l^{-1}, and it may have been concentrated by freezing. Phosphorus is often a limiting nutrient to algal growth, so an increase of phosphorus by freeze concentration would be important to phytoplankton.

Ice cover does not provide a perfect seal for lakes. The weight of snowfall can cause the water (which is warmer than ice, if only by a degree or two) to melt holes through the ice and flow out onto the ice surface (Knight, 1987; 1988). Although the Loch did not accumulate heavy snowfall, melt holes similar to those reported by Knight were formed. Evidently the pressure resulting from the increase in volume of ice as it forms from liquid water causes periodic "water spouts" to melt through the ice allowing water to flow onto the ice surface until equilibrium is attained. Such spouts were observed on Sky Pond (K. Schoephflin and S. Denning, personal communication).

Table 6. Summary statistics for chemical variables in The Loch during the fall and early winter of 1987-88. Values for August and September are combined from all surface, mid-depth, bottom, and outlet samples. Values for December and January are from surface samples. (* significant at $P < 0.05$).

Variable		August and September		December and January		
	Units	Mean	Std. Dev.	Mean	Std. Dev.	
H^+	[M]	$2.39 * 10^{-7}$	$0.47 * 10^{-7}$	$7.59 * 10^{-7}$	$1.23 * 10^{-7}$	*
ALK	($\mu eq\ l^{-1}$)	43.48	3.38	101.78	11.04	*
Ca	($mg\ l^{-1}$)	1.03	0.20	2.30	0.19	*
Mg	($mg\ l^{-1}$)	0.17	0.02	0.34	0.03	
Na	($mg\ l^{-1}$)	0.39	0.07	0.92	0.08	*
K	($mg\ l^{-1}$)	0.15	0.03	0.24	0.02	*
NH_4	($mg\ l^{-1}$)	0.009	0.012	0.018	0.013	
SO_4	($mg\ l^{-1}$)	1.27	0.29	2.88	0.34	*
NO_3	($mg\ l^{-1}$)	0.69	0.12	0.89	0.19	
SiO_2	($mg\ l^{-1}$)	1.59	0.23	3.00	0.66	
Al	($\mu g\ l^{-1}$)	38.69	21.13	17.00	1.73	

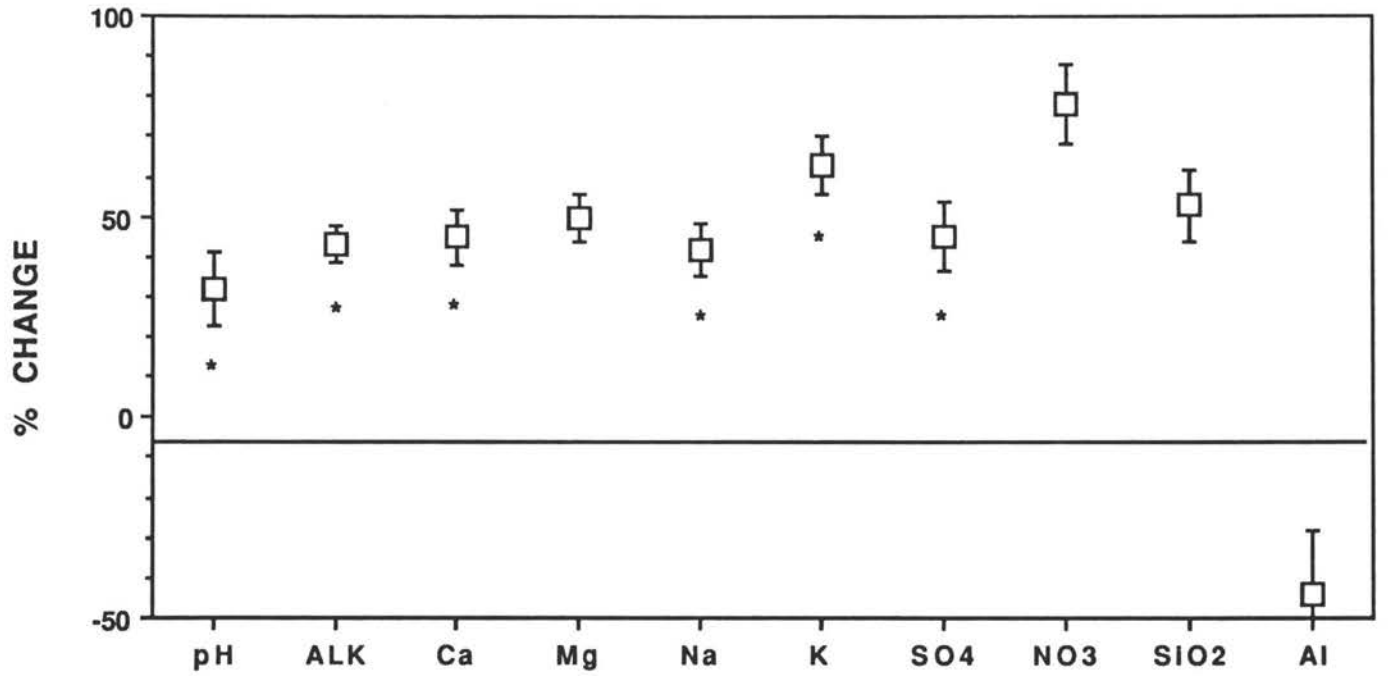


Figure 6. Percent change and relative standard deviation in concentration of major constituents in The Loch between the fall (August and September) and winter (December and January), 1987-88. (* significant at P<.05)

Visual evidence of these flows can be observed throughout the winter on many lakes including the surface of The Loch.

Temperature

The Loch experienced several periods of ice formation and melt from as early as September until early November when the season's solid ice formed. However, because such periods are hazardous to sample, temperature profiles were not recorded until later in winter. Temperature profiles of The Loch beneath ice cover varied between being inversely stratified to close to isothermal (Figure 7). There were slight fluctuations in temperature throughout the winter, with the region of greatest temperature change immediately below the ice surface.

Water is at its maximum density at 3.98°C. In an ice covered lake, under most conditions temperature will range from 0°C at the lower surface of the ice to close to 4°C at the lake bottom. However, there are instances in ice-covered lakes when inverse thermal stratification or isothermal profiles do not exist. Dilute meltwater immediately below the ice surface has been reported to reach temperatures as great as 6.1°C (Hill, 1967). Williams (1969) found that water temperatures under melting ice depended on the quantity of light transmitted through ice and solar heating of water. In shallow lakes of high salinity, temperatures increased above 4°C by solar heating and were maintained by dense, chemically stratified water (Rahal, 1990). In addition to solar radiation, other mechanisms have been suggested to explain temperatures warming beneath lake ice. Heat exchange between sediments warmed in summer months and overlying water may occur (Billelo, 1968; Welch and Bergmann, 1985a). Alternatively, inflow of warm surface waters, heat from oxidation of organic matter, and geothermal gradients have been proposed but have not been found to appreciably contribute to lake warming (Likens and Ragotzkie, 1965).

Temperature influences algae directly through effects on physiological mechanisms and indirectly by its relationship to stratification and water column stability.

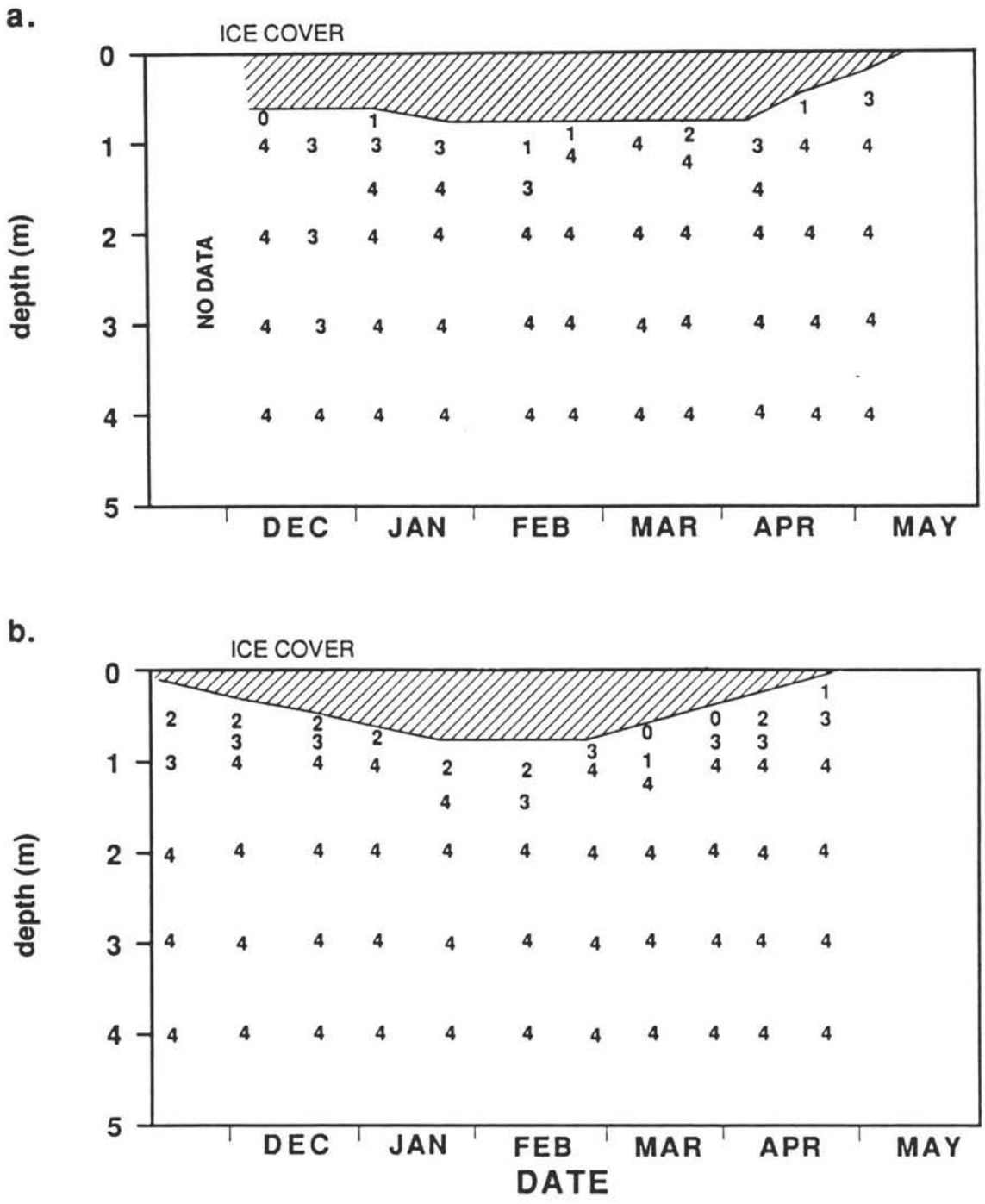


Figure 7. Water temperatures (°C) beneath the ice in The Loch for a) 1987-88 and b) 1988-89. Ice layer is cross hatched.

Historically, it was assumed that the physiological tolerance of algal species determined much of their seasonal distribution (Findenegg, 1943 as cited in Sommer, 1987). The spring maximum of diatoms and summer maxima of green and blue-green algae in many lakes may suggest that temperature is a decisive factor. However, algae associated with one season can flourish under some circumstances in another, suggesting the influence of multiple factors. It has been found that in the course of eutrophication of some lakes traditional "cold water" species have shifted to summer growth periods (Sommer, 1987). Sommer found that nearly all winter and spring algae of Lake Constance also had short growth pulses in summer. Algal species can vary in their optimal temperature range, but Lund (1965) considered no algae to be cold stenotherms. It is too simplistic to isolate one or two factors such as temperature and light as the only determinants of the seasonal occurrence of phytoplankton. Temperature changes concomitantly with other environmental changes such as nutrients, grazing, parasitism, and light and their direct and indirect interactions are inexorably linked to produce the planktonic environment.

Mixing

Temperature and chemical stratification can give some indication of the stability of the water column and its resistance to vertical mixing. Obviously, wind is not able to mix the water under ice cover. Currents and circulation that take place in The Loch during winter are largely unknown, but some evidence indicates that mixing does occur. As a lake is freeze-concentrated, excluded salts are released at the lower ice surface. If there were no vertical movement of the concentrated water, water of higher ionic strength would remain immediately below the sub-ice surface (Welch and Bergmann, 1985a). In fact, the concentrations of ions in The Loch were distributed uniformly throughout the water column. Welch and Bergmann found that denser water formed by freeze concentration sinks and is transported laterally. Near shore, denser water sinks and follows the slope to the lake bottom. Both density and temperature gradients contribute to the overall circulation of lake water under ice cover. In early spring, horizontal flow

immediately beneath the ice surface of The Loch was indicated by changes in pH and chlorophyll *a*. The surface water pH was lower than the rest of the water column (5.92 as compared to 6.01, standard deviation of replicate samples = 0.45 pH unit). The early melt causes a layer of low pH melt water to flow directly beneath the ice surface. The pH of snowmelt is typically lower than lakewater (Denning et al., in press). In addition, there were large differences in the amount of chlorophyll *a* between the surface water (~0.5 $\mu g\ l^{-1}$) and the rest of the lake water (~4.0 $\mu g\ l^{-1}$). This distinct surface layer had disappeared by the next sampling date two weeks later.

As a lake becomes inversely stratified as a result of temperature differences, the density layers are resistant to vertical mixing of the water column. However, at temperatures between 1°C and 4°C, the density change per degree lowering is less than at higher temperatures (Wetzel, 1983). Therefore, the inverse stratification in ice covered lakes may not be strong. In fact, even within lakes that are strongly vertically stratified, the water column is not hydrologically static (Likens and Hasler, 1962; Welch and Bergmann, 1984a). Likens and Hasler showed that relatively rapid horizontal water currents exist in ice-covered lakes. They also observed vertical motion, but at a slower rate than horizontal movements. The concept of winter stagnation was not supported by their results. They suggest that probable sources of energy to drive under-ice circulation include heat in bottom sediments and external changes in temperature and pressure affected by solar radiation and wind.

The degree of vertical mixing is of consequence to both growth and loss of phytoplankton. Hobbie (1964) found high primary productivity under the ice of an Arctic Alaskan lake. When the ice melted in June and July, production dropped sharply. Hobbie postulated that with the advent of circulation, the algae were no longer remaining in the photic zone. In a more stable water column, the algae are exposed to a relatively continuous light climate. In contrast, with mixing and turbulence, the cells experience rapidly fluctuating solar radiation as they are transported from surface to deeper waters

(Harris and Piccinin, 1980; Trimbee and Harris, 1984; Sephton and Harris, 1984; Harris and Trimbee, 1986). The short-term mixing regime can be of fundamental importance to the species composition and sequence of algal succession (Talling, 1966; Reynolds et al., 1983).

While a stable water column may be favorable to some algae, others may not be able to compensate for loss due to settling in the absence turbulence. For example, diatoms cannot regulate their position in the water column as well as flagellates or blue-green algae which utilize gas buoyancy regulation. In permanently ice-covered Antarctic lakes with strong chemical stratification, diatoms are infrequent in the water column even though they are abundant in littoral benthic algal mats (Parker et al., 1982; Vincent, 1981).

Circulation within ice-covered lakes has further ecological importance with the regeneration and mixing of nutrients. In addition to introducing essential nutrients into the photic zone, slow water movements at the sediment surface could reduce zones of oxygen depletion (Likens and Hasler, 1962). Water movements also play a role in removing toxic metabolic by-products and reducing substances liberated at the sediment-water interface (Coleman and Armstrong, 1987).

Light

The quantity of light penetrating the ice layer affects photosynthetic rates of the algae. It may also indirectly determine the species composition at any given time. Ice and snow cover can vary in thickness and opaqueness, causing variation in the attenuation of light. The ice thickness reached a maximum of about 75 cm in both years (Figure 7). Clear ice transmits light similarly to clear water (Wetzel, 1983), however, the inclusion of air in ice can greatly reduce light transmission. The ice on The Loch appeared to be mostly "black ice", or clear ice formed from lakewater with few air inclusions. "White ice", which forms from melted snow on the ice surface was absent, or present only to a limited extent.

The Loch receives high winds that reach gale force speeds during the winter. Consequently, the ice surface has very little snow accumulation (Table 7). However, on all dates (except February 9) the percentage of light transmittance immediately below the ice was less than 10 % of incident light (Figure 8). Furthermore, there was no relationship between snow cover and the percentage of light penetration ($r = -0.08$). This result is surprising and indicates that, contrary to my initial beliefs, the ice blocks out so much light that the effect of snow is insignificant. That is, the ice cover attenuates light to such an extent that the slight accumulation of snow has little effect on the total. These results are in contrast to other studies that report values of 80 % transmission through clear ice (Bolsenga, 1981). Bolsenga found that overcast skies can reduce the percent transmission by as much as 20 %.

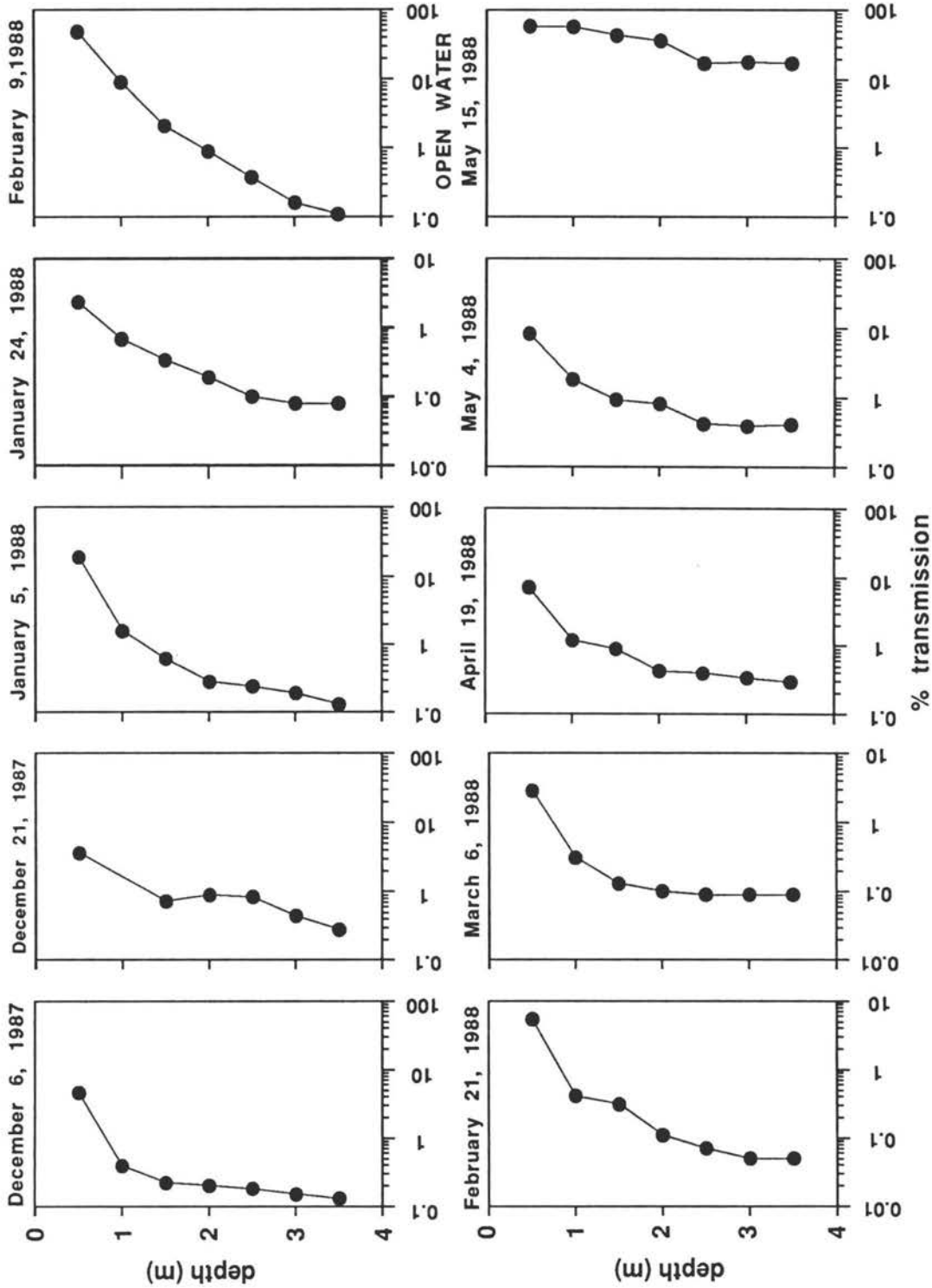
Daylength is shortest and the sun is at its lowest aspect in December. The total available incident radiation is lowest in December and progressively increases throughout the remainder of the season (Figure 9). Measurements of solar radiation were made at hourly intervals at a meteorological station approximately 0.5 km from The Loch. Areas within the Loch Vale watershed are often shaded because of steep, high ridges. The meteorological station and The Loch are shaded differently, based on their distinct orientations within the basin (Figure 2). Thus, daily solar radiation varies between the two sites. At The Loch on December 6 the lake sample site was shaded by the ridge of Thatchtop mountain until 1:00 PM. By March 6, the sample site received direct sun by 11:00 AM. The meteorological station is not as shaded to the south, so measurements at the station can not be indiscriminately applied to the total incident light on the lake surface.

Weather patterns cause large fluctuations in solar radiation on a daily and hourly basis. Nevertheless, a progressive increase in light penetrating to the 1.0 meter depth occurred from December to the period of ice out (Figure 10). Total incident radiation increased at both the lake surface and in the water column.

Table 7. Snow depth at the sample site and estimated areal extent of snow cover on The Loch surface during the winters of 1987-88 and 1988-89.

Date	Snow Depth (cm)	% Snow Cover	Comments
6 Dec 87	15	20	
21 Dec 87	8	40	
5 Jan 88	3	90	
24 Jan 88	30	95	
9 Feb 88	15	50	
21 Feb 88	13	50	
6 Mar 88	10	40	
20 Mar 88	8	40	
6 Apr 88	5	100	
19 Apr 88	5	100	slush
4 May 88	0	100	slush
15 May 88	0	-	open water
13 Nov 88	0	80	trace
2 Dec 88	0	5	
20 Dec 88	8	10	
4 Jan 89	0	5	
20 Jan 89	0	5	
10 Feb 89	30	20	
26 Feb 89	5	100	
11 Mar 89	5	30	
27 Mar 89	0	30	white ice
8 Apr 89	5	40	slush
26 Apr 89	0	-	open water

Figure 8. Profiles of percent of surface light transmission with depth in The Loch during 1987-88.


December 6, 1987
December 21, 1987
January 5, 1988
January 24, 1988
February 9,1988
February 21, 1988
March 6, 1988
April 19, 1988
May 4, 1988
May 15, 1988
OPEN WATER
depth (m)
% transmission

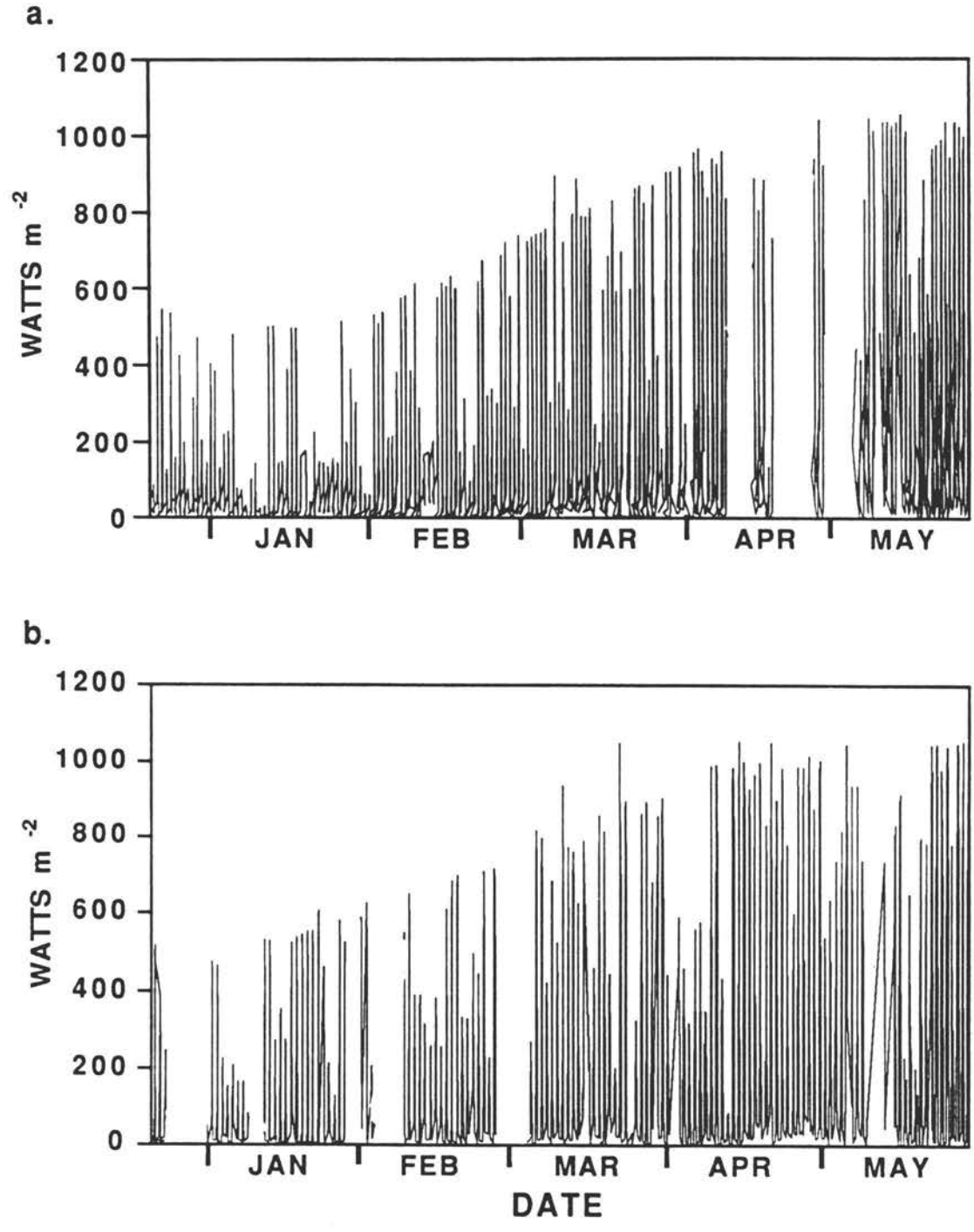


Figure 9. Solar radiation measured at the Loch Vale meteorological station for a) 1987-88 and b) 1988-89. Gaps indicate missing data.

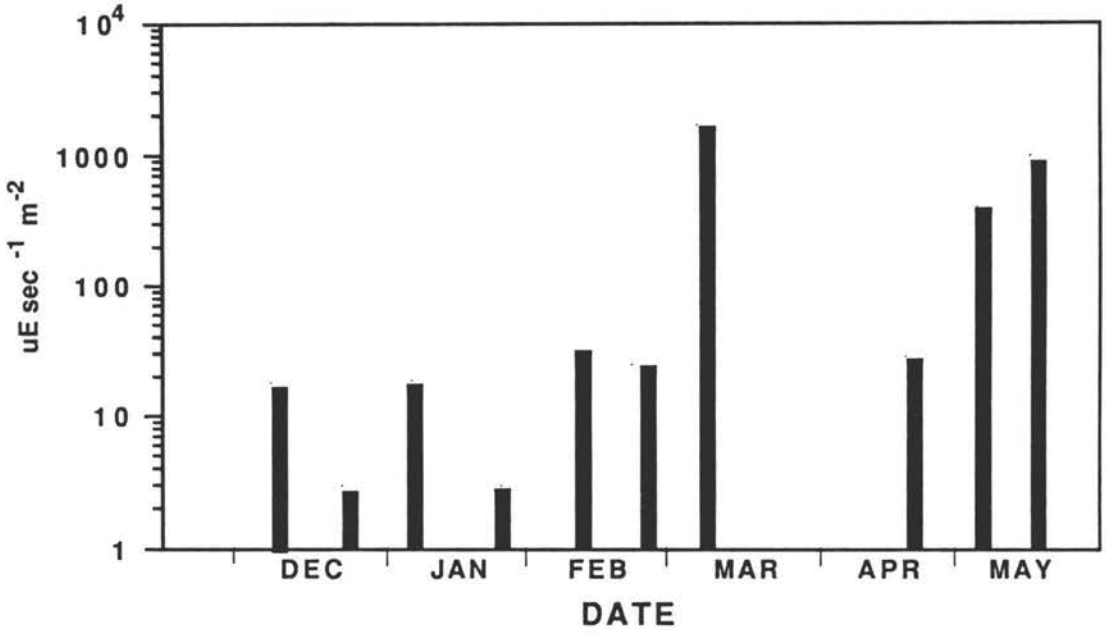


Figure 10. Total photosynthetically active radiation (PAR) measured at the 1.0 m depth in The Loch during the period of ice cover in 1987-88.

On the other hand, the percentage of incident light that reached the water column shows only slight changes throughout the winter season (Figure 8). It is generally considered that photosynthesis does not take place at less that 1% incident radiation. However, photosynthesis has been measured at light levels much less than 1%. For example, Rodhe (1962, as cited in Wright, 1964) found that photosynthesis took place in deep high mountain lakes at light intensities 0.06% of that at the surface. Wright (1964) reported that measurable photosynthesis occurred at 0.07% of incident radiation. In The Loch, the percentage of light reaching the 2 meter depth was never greater than 0.89% of incident radiation. I was surprised by these results because the lake has clear, black ice that is blown clear of snow for most of the winter. High reflectance of the ice surface may partly account for the low transmission of solar radiation.

Oxygen

Oxygen concentrations varied over the winter season and with depth in the water column (Figure 11). During December of both years, oxygen concentrations were high at all depths (between 6 - 10 mg l^{-1}) in December. Following theses high values was a general decreasing trend in January and February. After February a continual increase in oxygen concentrations occurred until ice break-up in May. Oxygen expressed as percent saturation in water showed a similar pattern (Figure 12). Values of 100% saturation were found only in December and just before the ice melted in spring. The concentration of oxygen at the 1.0 meter depth was always greater than the concentration 0.5 m above the sediment, although this did not necessarily hold for the percent saturation. Percent saturation of oxygen in water is dependent on temperature, which varied with depth.

The early winter high concentrations of oxygen may have reflected high levels of oxygen prior to ice formation, or they may have been generated by the large biomass of phytoplankton early in the season . The decrease in oxygen in January and February could have been the result of decomposition of the algal remains, despite the low water temperatures. The standing crop of zooplankton was minimal and the number of trout

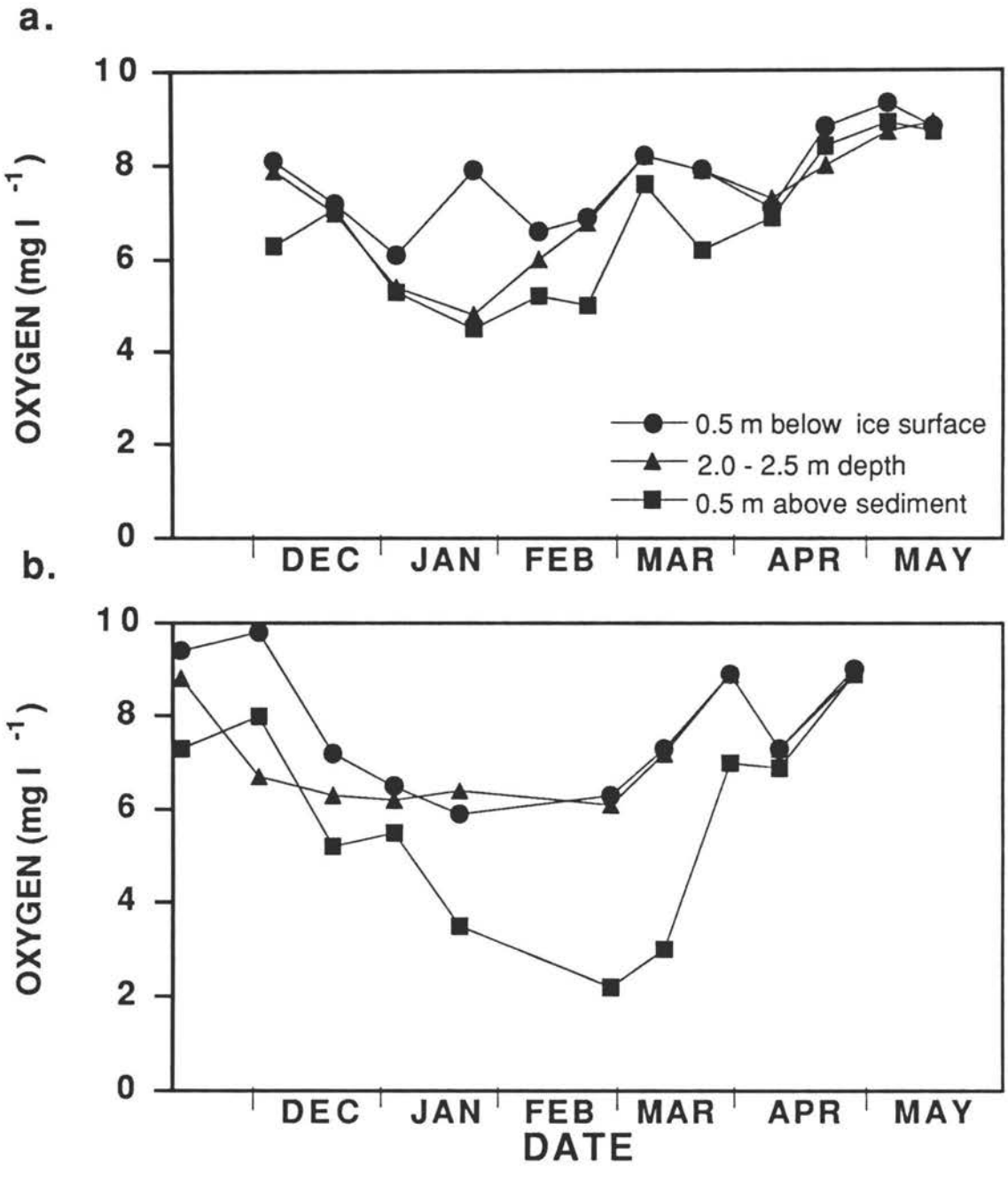


Figure 11. Oxygen concentrations (mg l^{-1}) in The Loch at three sample depths for a) 1987-88 and b) 1988-89. Each point represents the mean of two samples.

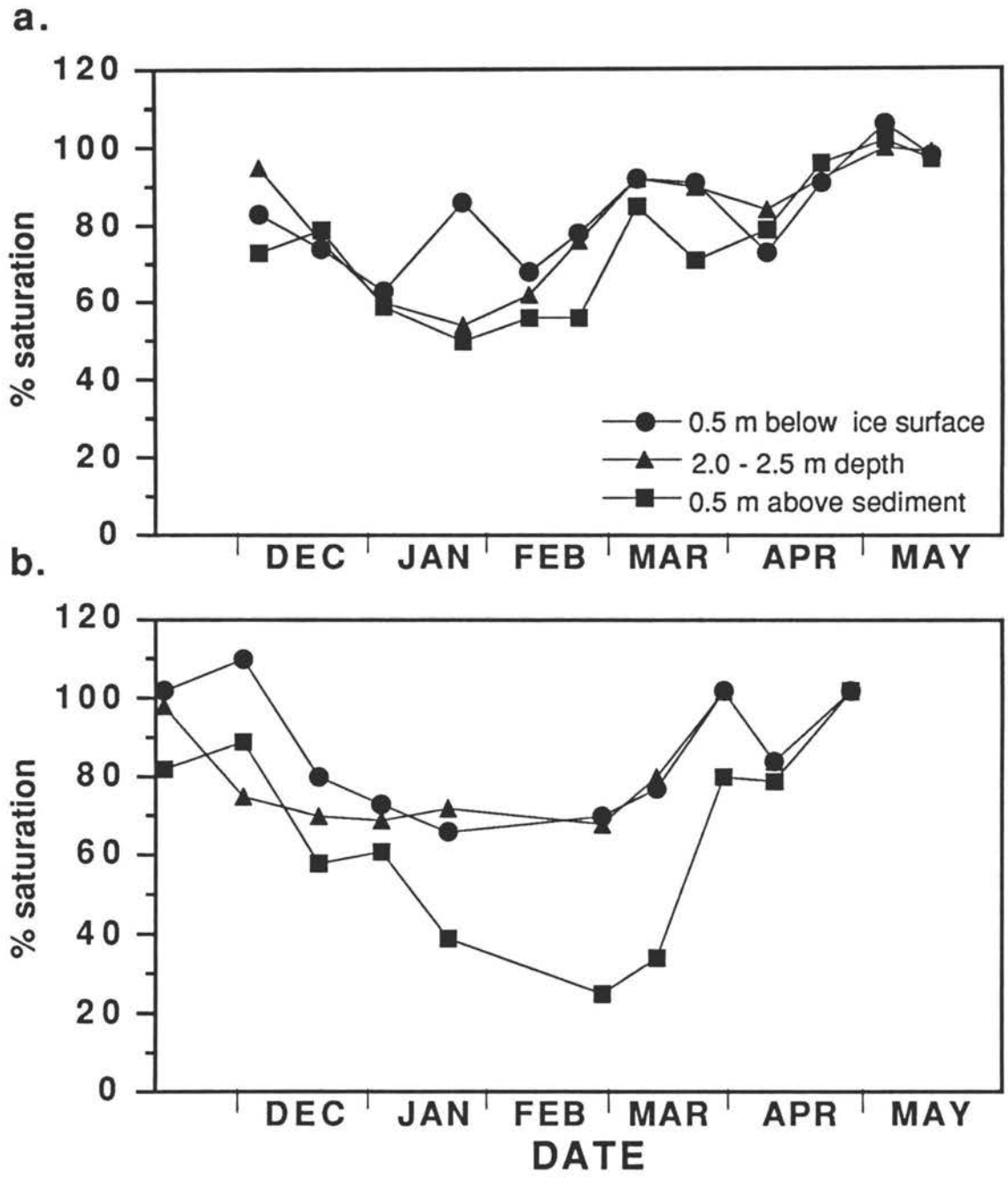


Figure 12. Percent saturation of oxygen in The Loch at three sample depths for a) 1987-88 and b) 1988-89. Each point represents the mean of two samples.

are thought to be low in The Loch. The increase in oxygen corresponded to the period when algal biovolume increased. However, oxygen concentrations continued to increase despite a waning algal biovolume. It is unlikely that a reduction in biomass would relate to increasing oxygen production. The explanation for the continued rise is speculative. Surface water flowing into the lake and causing the level to rise in the spring may be snowmelt that is saturated with oxygen. Alternatively, benthic algal production, which was not measured during this study, and which may provide a substantial portion of the total production during the period of open water, may begin to develop beneath ice cover, in late March and early April.

Oxygen concentration fluctuates based on the balance between photosynthetic production and consumption by respiration. In ice-covered lakes the presence of a barrier to gas exchange allows oxygen concentrations to either build up or become depleted in the water column. The depletion of oxygen leading to winter fish mortality is a well known example of the ability of ice to prevent gas exchange. The demand for oxygen is governed by microbial and respiratory metabolism and diffusion rates (Wetzel, 1983). Respiration in lake sediments leading to oxygen depletion has been shown to be inversely related to lake depth (Mathias and Barica, 1980). The sediment surface area was found to be more important than summer productivity in controlling winter respiration. Welch and Bergmann (1985b) found that a 50 % increase in annual primary productivity resulted in only a 19 % increase in winter respiration. They suggest that lake respiration is a integrative process that averages several years of productive output.

Alternatively, oxygen concentrations may increase under ice-cover. Welch and Bergmann (1985b) described the abiotic process of freeze concentration of oxygen with ice formation, as with ions in solution. Nearly 100 % of oxygen is excluded from ice leading to more oxygen in a smaller volume. Algal photosynthesis is the main source of oxygen increases under ice-cover. Wetzel (1966) found that oxygen trapped under ice

cover in a hypereutrophic lake reached concentrations of 24.5 mg l^{-1}, at 185% saturation. Bamforth (1958) found the highest dissolved oxygen concentrations in winter and spring under ice cover. The maximum oxygen concentrations corresponded to peaks in the phytoplankton population.

Other Chemical Parameters

" Natural waters acquire their chemical characteristics by dissolution and by chemical reactions with solids, liquids, and gases with which they have come into contact with during various parts of the hydrologic cycle" (Stumm and Morgan, 1981). To varying degrees, mineral weathering, soil processes, precipitation, terrestrial productivity and respiration, aquatic productivity and respiration, and microbial activity in sediments determine the chemical characteristics of lakes. Major cations, silica, and substances responsible for acid neutralizing capacity (ANC) are released into surface waters by weathering of granitic minerals that are common to Front Range watersheds (Turk and Spahr, 1990). However, the stoichiometric weathering of common granitic minerals can not account for lake chemistry (Turk and Spahr, 1990; Mast et al., 1990). These investigators found an apparent discrepancy between mineral composition and lake water concentrations, and suggest that atmospheric sources of minerals or preferential chemical weathering of bedrock influence surface water chemistry.

pH

The mean pH of The Loch under ice cover (6.14 at 2.0 m, n = 20) is slightly lower than the mean pH in the open water season (6.33, n = 44 for 1982-85) (Baron and Bricker, 1987). The range in pH for the duration of the current study was from 5.8 to 6.7 (Figure 13). The seasonal pattern of pH was generally that a higher pH occurs in early winter with lowest values immediately before the ice breaks up in the spring. The increase in pH in early winter may be the result of cryoconcentration, as discussed

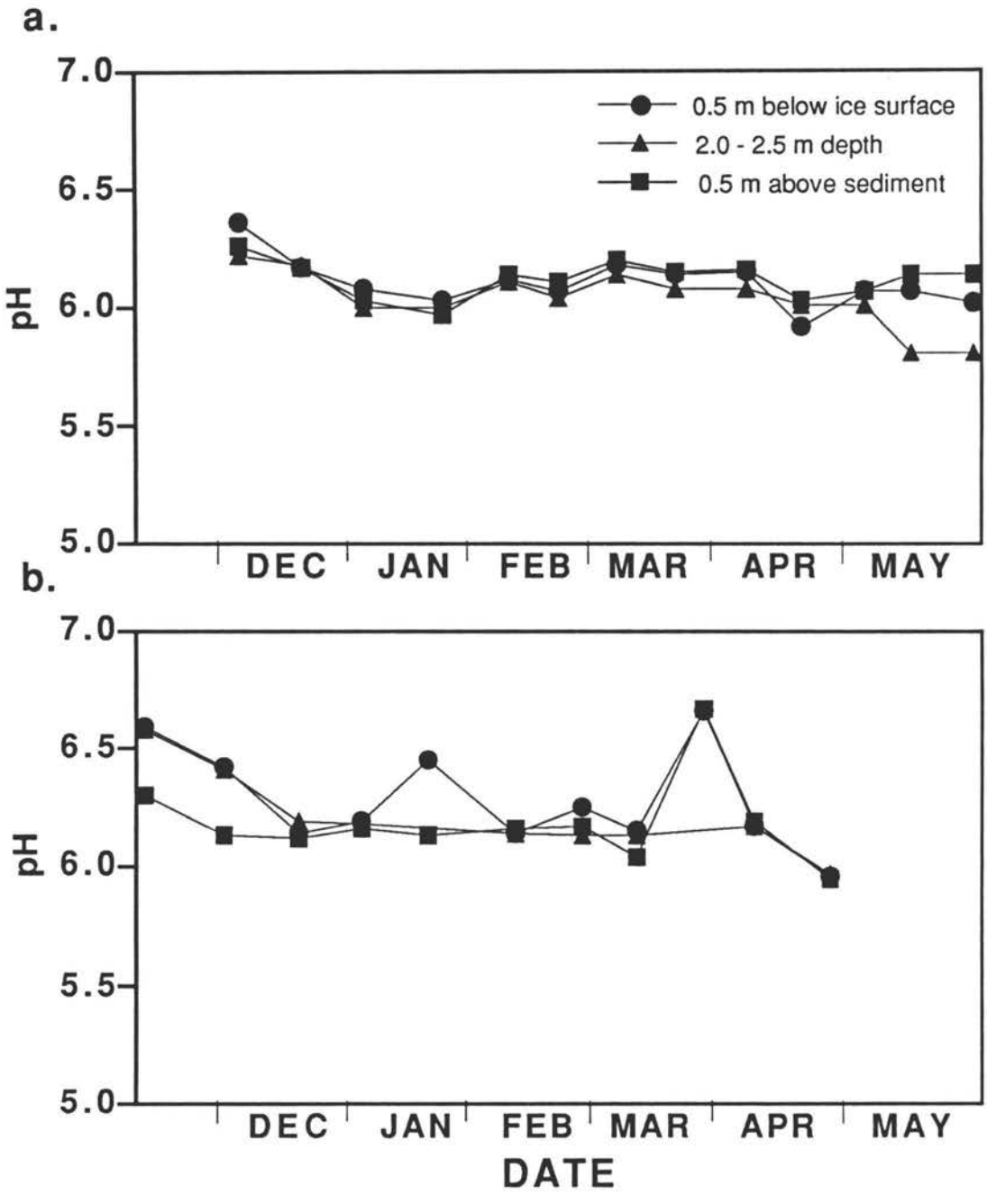


Figure 13. Values of pH in The Loch at three sample depths during a) 1987-88 and b) 1988-89.

earlier. The low pH values in spring may be due to the release of acidic ions in snowmelt.

In early spring, the first fraction of melt contains a disproportionate percentage of ions (Hultberg, 1977; Denning et al., in press). Johannessen and Henriksen (1978) showed that 75% of divalent and 58% of monovalent ions were removed from snow pack in the first 30% of melt water. The first fraction was an acidic salt-solution. Such episodic declines in pH may precede chronic acidification. Episodic acidification may occur during the brief period of snowmelt, when runoff does not interact sufficiently with rock or soil to be neutralized (Turk and Spahr, 1990). If the acidic snowmelt dilutes a lake or replaces an entire lake volume, a period of decreased pH and ANC may occur. Eposodic acidification has not been observed in the Loch Vale Watershed (Denning et al., in press).

As the pH of a lake changes, there are associated changes in species composition of the phytoplankton. Several investigators have documented the shifts in composition that occur with increasing acidity. Diatom species preference for defined pH levels is well known and has been used extensively in paleolimnological reconstructions of historical lake chemistry (Sullivan et al., 1990). A decrease in pH alters phytoplankton species richness, composition, and dominant species (Geelen and Leuven, 1986). In general, with decreasing pH there are decreased numbers of green and blue-green algae and diatoms. Kwiatkowski and Roff (1976) found that in lakes in Ontario, there were changes in species composition when pH dropped below 5.7. All major phytoplankton groups decreased in species number with increasing acidity. The effects of pH were also seen in the relative dominance of green and blue-green algae. Blue-green algae, or cyanobacteria, made up an increasing percentage of the population with increasing acidity. It is evident that certain algal species are correlated with changes in pH; however, the cause of the response is ambiguous. It is not clear whether the changes in algal communities result from pH itself, or from lowered concentrations of nutrients,

change in chemical speciation, toxic effects, or alterations in grazing pressure (Stokes, 1986).

Alkalinity

Alkalinity is defined as the equivalent sum of the bases that are titratable with strong acid (Stumm and Morgan, 1981). Alkalinity is a measure that represents the acid neutralizing capacity (ANC) of a lake or given body of water. In The Loch under ice cover, alkalinity had a mean of 93 $\mu eq\ l^{-1}$ (n = 10, at 1.0 m depth) and ranged from 28 to 165 $\mu eq\ l^{-1}$ (Figure 14). These values are typical for high elevation oligotrophic lakes in Colorado (Turk and Spahr, 1990; Landers et al., 1987). For most of the winter season the alkalinity is higher than during the open water season, when there was a mean value of 45 $\mu eq\ l^{-1}$ (n = 44, 1982-85) (Baron and Bricker, 1987). In both years alkalinity increased from December to a peak value in late February. Subsequently, alkalinity declined until ice out to values that were typical of the open water season.

There are several mechanisms that operate to regulate alkalinity. Alkalinity may be increased as ions are excluded in lake ice leading to concentration of remaining lakewater. Baron and Bricker (1987) suggest that the lack of flushing in winter allows the more concentrated groundwater to influence lake chemistry. In the Snowy Range of Wyoming, the alkalinity of some subalpine lakes increases substantially in winter, due to anoxic conditions that lead to sulfate reduction in the sediments (F. Vertucci, personal communication). In The Loch, however, the water column does not become anoxic. If sulfate reduction were occurring, one might expect that sulfate concentration in the water column would decrease. Such a decrease does not occur in The Loch. In fact, sulfate concentrations remained constant throughout the winter season (Figure 15). However, oxygenated conditions in the water column do not rule out the possibility that the sulfate reduction occurs in the sediments. Alkalinity may also be increased by photosynthesis. Photosynthesis results in a reduction of total dissolved inorganic carbon, increased pH,

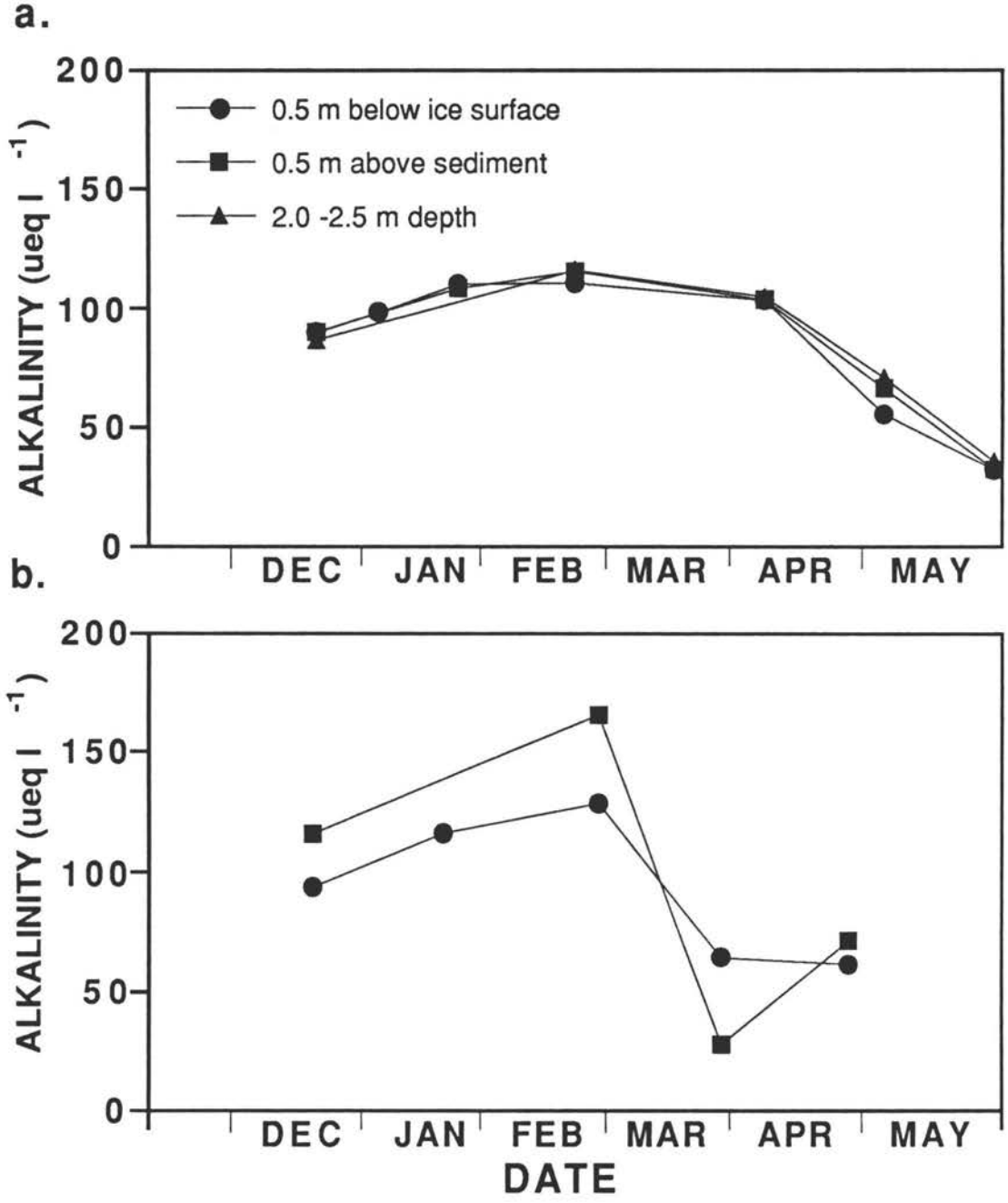


Figure 14. Total alkalinity (μeq l^{-1}) in The Loch at three sample depths during a) 1987-88 and for two sample depths during b) 1988-89.

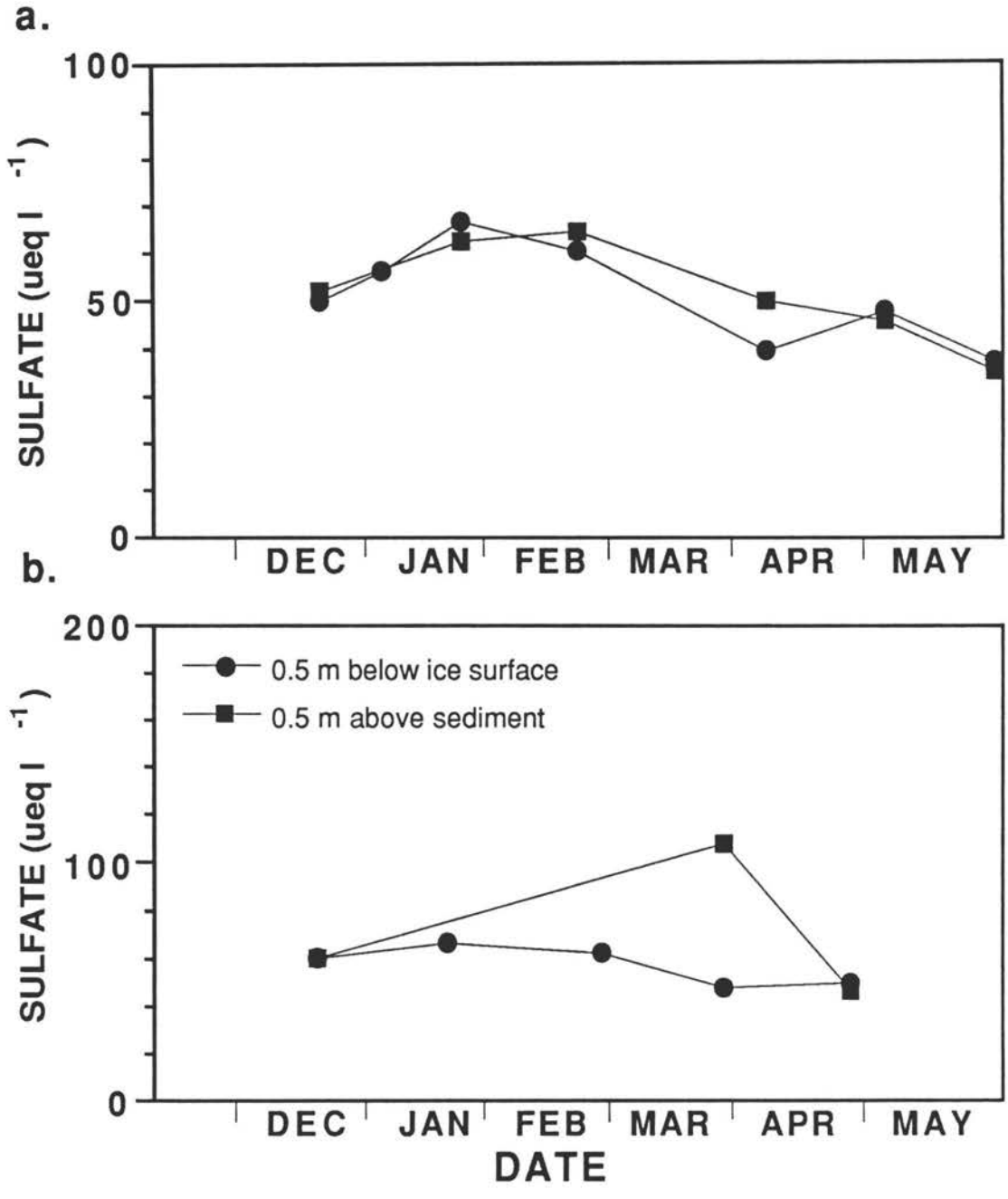


Figure 15. Sulfate concentrations ($\mu eq\ l^{-1}$) in The Loch at two sample depths during a) 1987-88 and b) 1988-89. Note different vertical scales.

and increased alkalinity with algal uptake of nitrate, as illustrated by the equation (Stumm and Morgan, 1981):

$$106\ CO_2 + 16\ NO_3^- + HPO_4^{2-} + 122\ H_2O + 18\ H^+ \rightarrow \{C_{106}H_{263}O_{110}N_{16}P\} + 138\ O_2$$

Algae in freshwater generally take up nitrogen as nitrate, rather than ammonium, which can lead to a decrease in alkalinity (Stumm and Morgan, 1981). However, in The Loch there were no concurrent changes in pH that would indicate a photosynthetic source. Carbon fixation rates in The Loch are low during the period of open water. They range from 1 to 46 $\mu g\ C\ l^{-1}\ h^{-1}$ (McKnight et al., 1990). It is likely that rates are even less under ice cover. Thus, photosynthesis is probably not a significant source of alkalinity. Turk and Spahr (1990) constructed a budget for a Rocky Mountain lake from the EPA Western Lakes Survey and concluded that a negligible amount of ANC could be attributed to processes involving ammonia, nitrate, sulfate, and hydrogen ion. They suggested that weathering products were responsible for alkalinity rather than lake processes or watershed transformations. Mast et al. (1990) determined the chemical composition of each mineral phase within the Loch Vale Watershed and concluded that primary weathering accounted for most of the total annual lake alkalinity. Nevertheless, it is important to remember that lakes can differ substantially within the region.

The decrease in alkalinity may be attributed to several processes operating singly or in concert. Gradual increases in the lake level began in January of 1989. This water may have originated as groundwater. Water in contact with minerals would be more concentrated and higher in alkalinity. Therefore, if groundwater was responsible for raising the lake level, the total alkalinity would not decrease as spring progressed. Alternatively, snowmelt in Loch Vale has no ANC (S. Denning, personal communication), but may infiltrate soils and and lead to increases in base cations and

ANC to some extent. Meltwater flushing through soils may a likely source of water that acts to increase The Loch volume and decrease alkalinity.

Aluminum and Dissolved Organic Carbon

The concentration of aluminum was relatively constant until late March or early April when it underwent a dramatic increase in both years (Figure 16). An increase in dissolved organic carbon (DOC) was concurrent with the rise in total aluminum. Denning showed that forest soils contribute aluminum and DOC to snowmelt water entering streams and lakes in Loch Vale (S. Denning et al., in press). Melt from the snowpack has a certain amount of exchange with soils. Early in the period of snowmelt surface water chemistry is largely determined by soil solutions.

Calcium and Magnesium

Calcium and magnesium are both considered conservative ions; they are not taken up to the extent in biological reactions that total concentrations are reduced. Magnesium is an essential component of chlorophyll, but as one of the major cations, there is little evidence that it limits phytoplankton production (Lund, 1965). Within the lake, they can be used to trace hydrologic processes. Both calcium and magnesium increased in early winter as The Loch became freeze concentrated (Figure 17). After February, both ions decreased in subsequent samples. It appears that both ions are freeze concentrated followed by dilution.

Iron and Manganese

Iron and manganese are similar in their chemical reactivity in freshwater. Both may undergo redox reactions in lacustrine systems mediated by microbial activity (Wetzel, 1983). Iron exists in solution in either the ferrous (Fe^{2+}) or ferric (Fe^{3+}) state. The amount of dissolved iron and manganese in natural waters is controlled by pH, redox potential (Eh), and temperature. Manganese is found in the reduced form (Mn^{2+}) at pH values below 7. Above this value, manganese may form hydrated oxides with mixed valency states (Lindsay, 1979). Under oxidized conditions, concentrations of

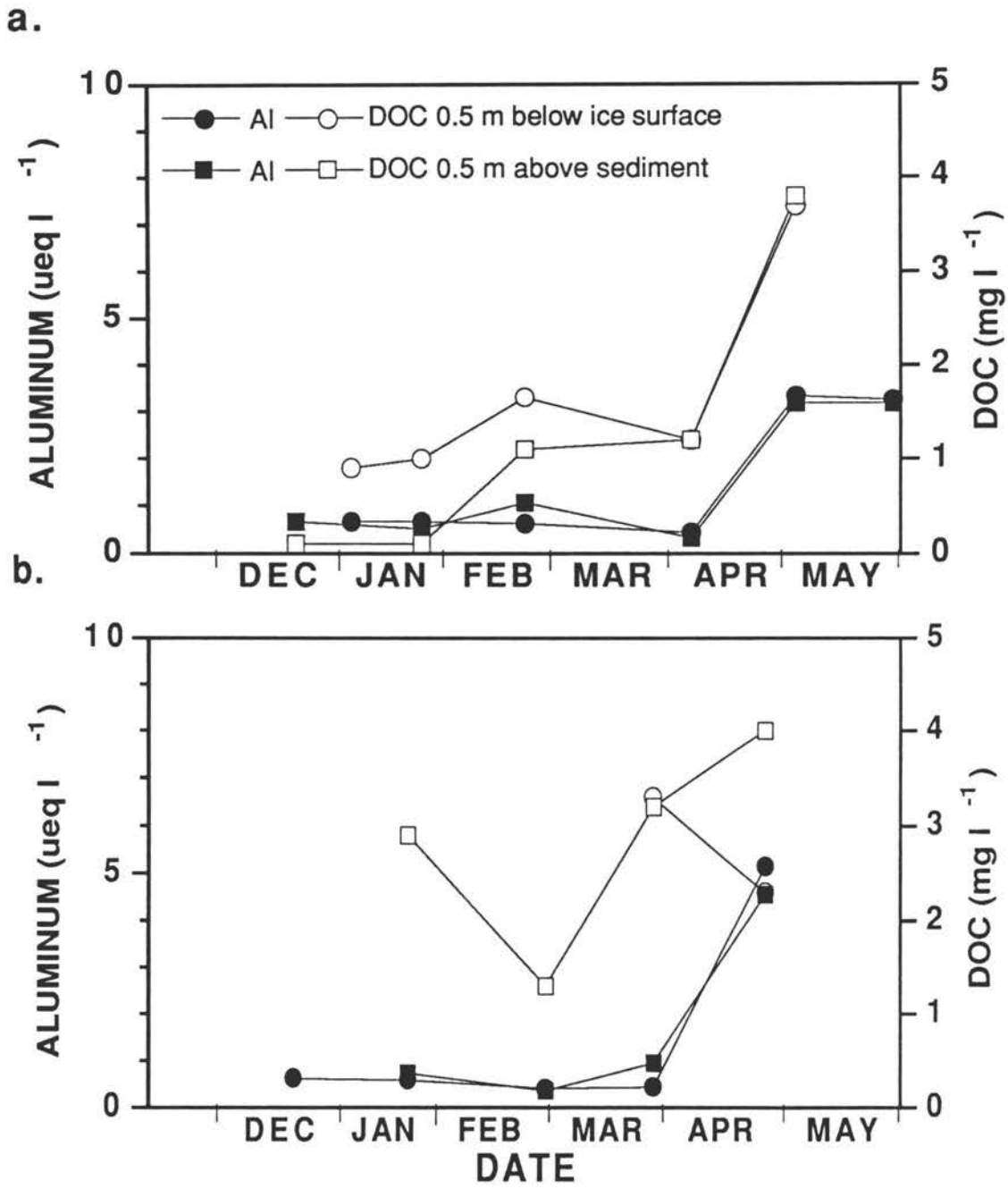


Figure 16. Total aluminum concentrations (μeg l^{-1}) and dissolved organic carbon concentrations (DOC) (mg l^{-1}) in The Loch at two sample depths for a) 1987-88 and b) 1988-89.

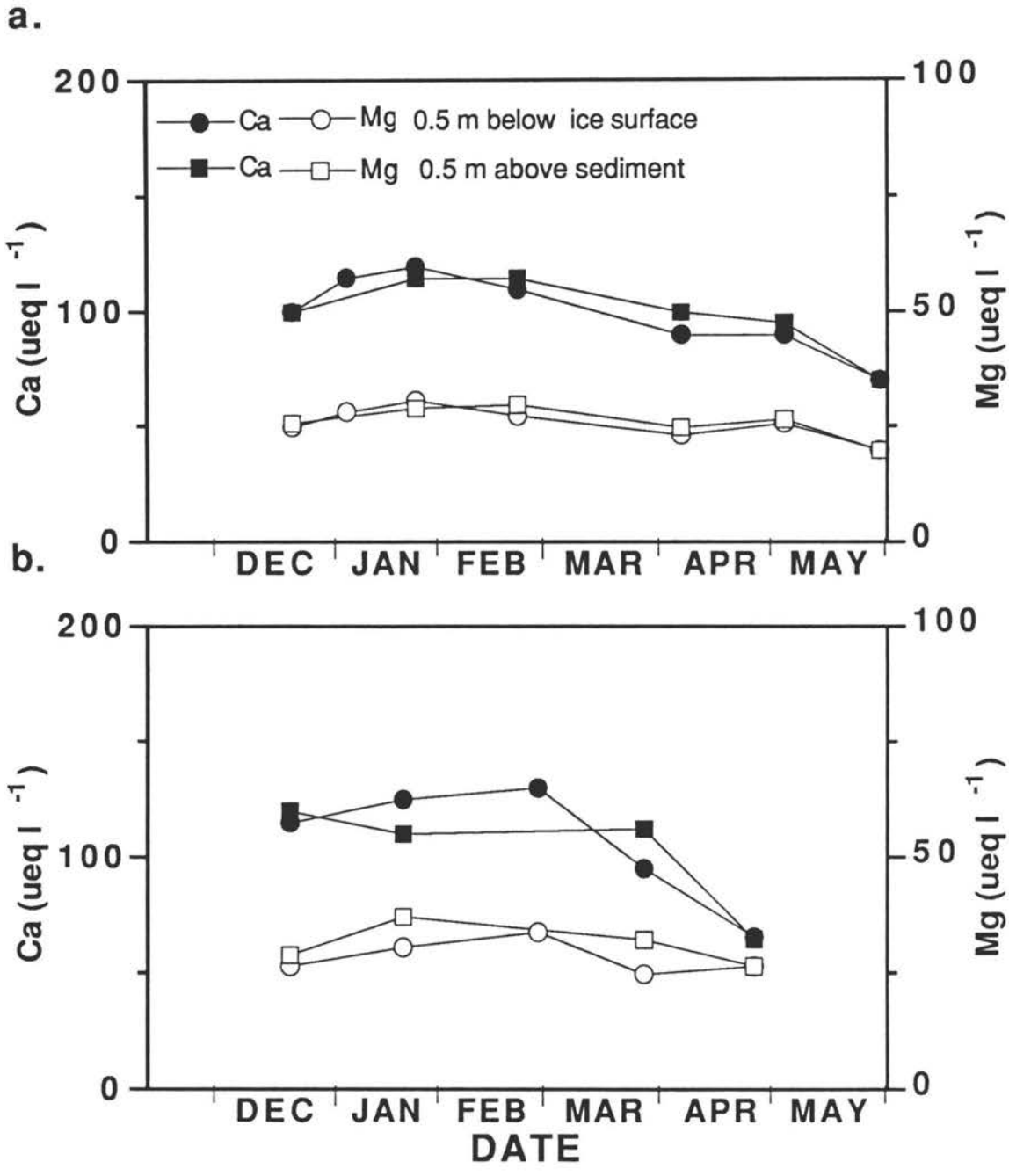


Figure 17. Calcium and magnesium concentrations ($\mu eq\ l^{-1}$) in The Loch at two sample depths for a) 1987-88 and b) 1988-89.

iron are low. Manganese is slightly more soluble and may exceed iron concentrations. Diffusion of Mn^{2+} from sediments occurs at redox potentials slightly greater than that of Fe^{2+} of above 200 mv (reviewed in Wetzel, 1983). The solubility of manganese complexes is exceeded prior to that of iron complexes as anoxic conditions develop. Total dissolved iron concentrations (filtered through 0.45 μm) ranged from approximately 0.4 to 9.0 μeq l^{-1} (Figure 18). Although concentrations immediately below the ice remained relatively constant throughout the season, there were fluctuations in the concentrations of water 0.5 m above the sediment. In the first year iron concentrations in the bottom sample increased from December at 1.3 μeq l^{-1} to a maximum of 3.2 μeq l^{-1} in late February. The second year there were fewer data, but a maximum of 8.8 μeq l^{-1} occurred in late February. The peak value represents only a single data point so it may be subject to question. The sample, however, was both split and replicated so that the high values were verified by two separate laboratories (USGS Central Lab and CSU Soil Testing Lab). The increased values of iron correspond to the changes in oxygen concentration (Figure 11). The bottom waters were most depleted of oxygen, with minimum values occurring in January and February. There was a greater depletion of oxygen in the second year to a minimum of (2.2 mg l^{-1}). As oxygen values increased, iron concentrations in the bottom waters decreased. The elevated concentration of iron near the sediments was probably caused by the release of Fe^{3+}. It would have later precipitated, as the redox potential increased and exceeded the solubility of Fe^{2+} complexes, such as iron hydroxide.

Similarly, manganese concentrations fluctuated throughout the winter season (Figure 19). Manganese ranged from a low of 0.02 μeq l^{-1} to a maximum of 1.1 μeq l^{-1}. However, unlike iron, manganese concentrations in the surface water also fluctuated. Manganese can remain soluble up to oxygen concentrations of 50 % (Burns and Nriagu, 1976). Such a distribution of solutes further indicates that there was some mixing beneath the ice cover. In the first year, manganese in the surface waters was higher than

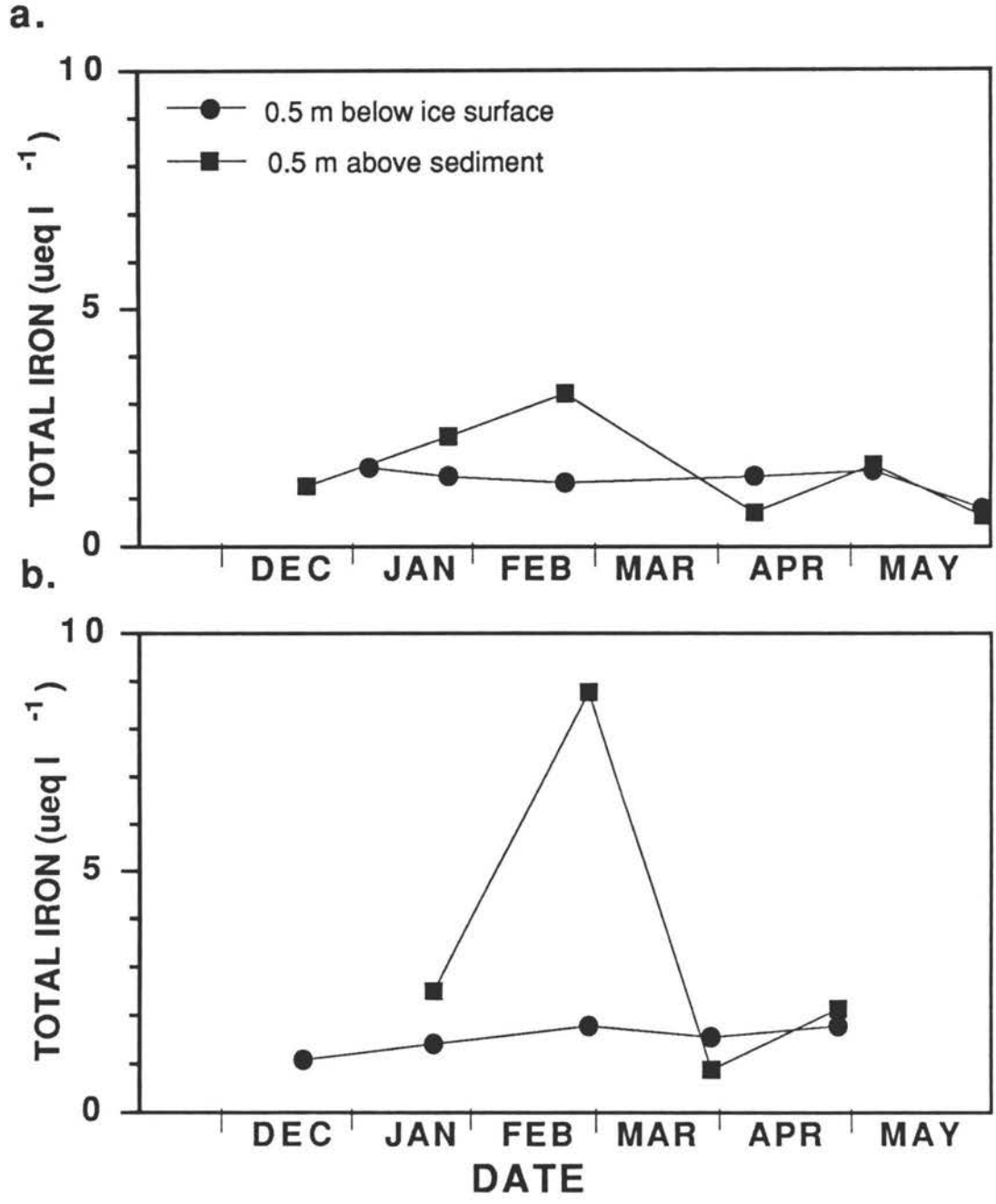


Figure 18. Iron concentrations ($\mu eq\ l^{-1}$) in The Loch at two sample depths for a) 1987-88 and b) 1988-89.

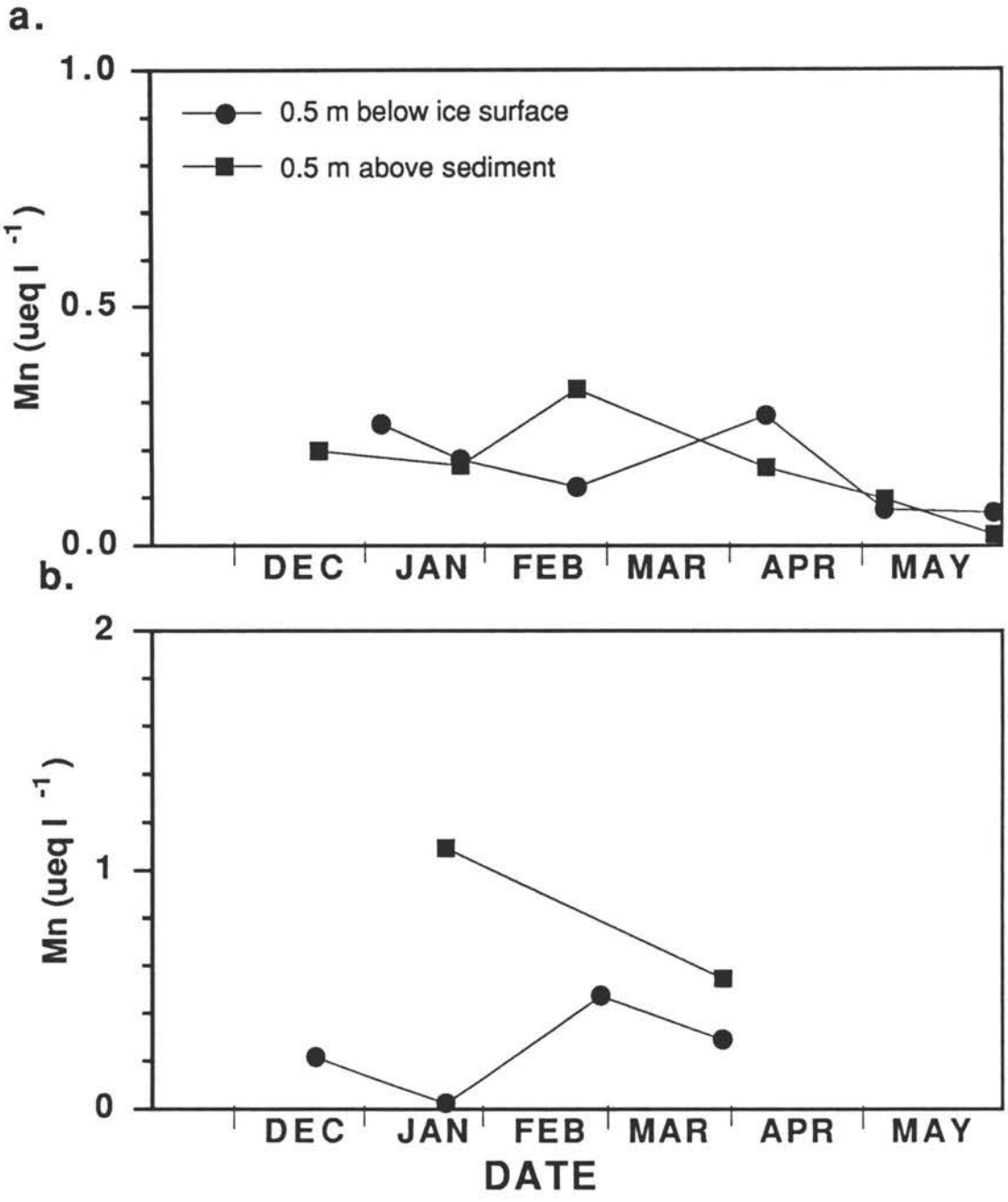


Figure 19. Manganese concentrations (μeq l^{-1}) in The Loch at two sample depths for a) 1987-88 and b) 1988-89.

the bottom waters at times. In the second year, when oxygen was at a minimum, manganese in the bottom waters reached maximum values.

If redox potentials decline below 100 mv, sulfate is reduced to hydrogen sulfide. Although there was evidence of hydrogen sulfide in Sky Pond in some winters, it was not evident in The Loch (personal observation). If redox potentials are such that H_2S is formed, there will also be abundant Fe^{2+} when sulfide is formed. The formation of FeS can cause a significant reduction in iron concentrations. In contrast, manganous sulfide is much more soluble and has little effect on Mn^{2+} concentration (Wetzel, 1983).

Iron and manganese are essential micronutrients of the algae, although manganese may be essential to only a few species (reviewed in Lund, 1965). Iron is important as a potential limiting nutrient of freshwater phytoplankton (Schelske, 1962; Reynolds, 1984). The supply of metals to algae is regulated by organic chelators. Chelators have a high affinity for metal ions so that their activity is reduced, but maintain metals in solution so that they are available for algal uptake.

Nutrients

Phosphorus, nitrogen, and carbon are critically important to algal growth, periodicity, and community composition (Lund, 1965; Reynolds, 1984). Phosphorus, considered to be the principal limiting nutrient to algae, is available only from phosphate minerals, primarily apatite. In The Loch, orthophosphate was below detection limits (ranged from 3-6 $\mu g\ l^{-1}$) at nearly all times. However, measurements of phosphorus in water rarely give an accurate measure of the nutrient that is directly available to algae (Schindler, 1971). Phosphorus is known to be accumulated in excess of immediate needs in cells during the times that it is available (Reynolds, 1984). Such consumption is termed "luxury uptake". It is difficult to estimate the total phosphorus that is required by algae in situ. Although the amount of phosphorus present during spring turnover is the single factor that best predicts annual lake productivity, the degree to which phosphorus concentrations affect the species composition of phytoplankton communities

is not known (Lund, 1965). However, in a broad sense, lakes with high concentrations of phosphorus differ in species composition from those with low concentrations.

Nitrogen may limit phytoplankton productivity at times, usually when phosphate concentration is relatively high. Morris and Lewis (1988) found that in several Colorado high elevation lakes nutrient limitation fluctuated between phosphorus only, nitrogen only, both phosphorus and nitrogen, and no phosphorus or nitrogen limitation. Freshwater algae take up nitrogen primarily in the form of nitrate. However, low nitrate concentrations do not necessarily imply nitrogen limitation. Some algae can use nitrogen in the form of ammonium or gaseous nitrogen. Sources of nitrogen include deposition from precipitation, nitrogen fixation in water and sediments, and surface water input (Wetzel, 1983). Losses of nitrogen are due to outflow from the basin, bacterial denitrification, and sedimentation losses.

Nitrate concentrations in The Loch varied from 0.044 to 1.240 mg l^{-1} (Figure 20). These values are considerably higher than concentrations reported in other Colorado mountain lakes (1-~50 $\mu g\ l^{-1}$ DIN (dissolved inorganic nitrogen), (Toetz and Windell, 1984), 3 -270 $\mu g\ l^{-1}$ DIN, (Morris and Lewis, 1988)). Nitrate was consistently lower in the bottom water samples than the surface, if only by a small amount. From December until late February there was a decline in nitrate that occurred in both years. In the second year the decline continued for the remainder of the season. However, in the first year there was a substantial increase in nitrate in early April and only a slight decline until ice out. Ammonium concentrations reached a maximum value of 0.070 mg l^{-1}, although most samples were equal to ammonium concentrations in sample blanks.

Algae can deplete carbon dioxide from the water if it is taken up faster than the rate that it dissolves from the atmosphere. Carbon limitation has been found to occur in eutrophic lakes on a diel basis and lakes at high pH (above pH 10) (Schindler, 1971; Schindler and Fee, 1973). Even though The Loch was sealed from gas exchange with

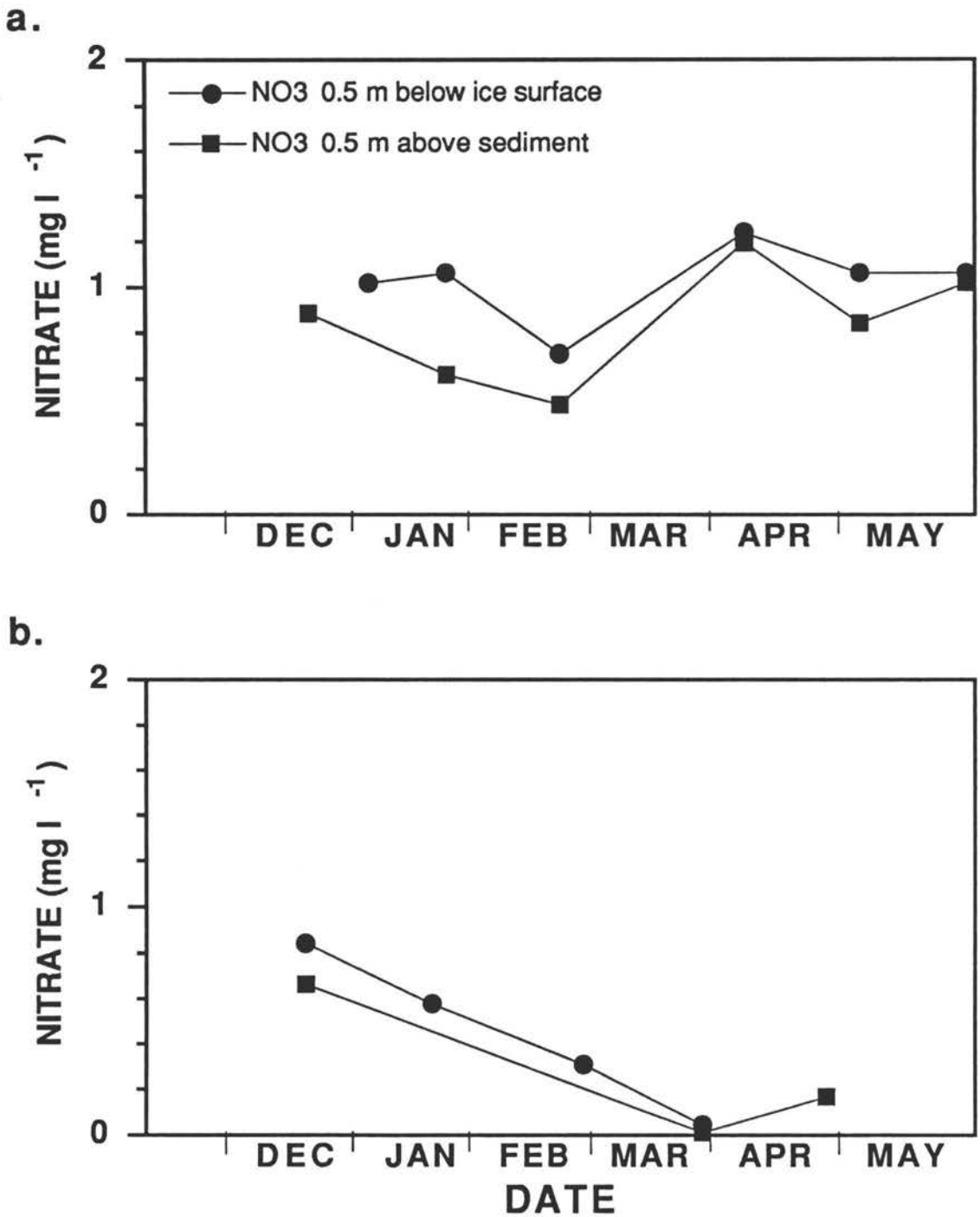


Figure 20. Nitrate concentrations (mg l^{-1}) in The Loch at two sample depths during a) 1987-88 and b) 1988-89.

the atmosphere during the study, it is unlikely that primary productivity proceeded at a rate high enough to deplete dissolved carbon dioxide.

Silica (SiO_2) concentrations ranged from 1.3 to 3.6 mg l^{-1} (Figure 21). There was no clear differentiation of silica by depth. In the first year concentrations were higher during the first part of the winter season and then declined in April followed by a slight increase, The second year concentrations were slightly lower but also reached a minimum in April followed by an increase. The dynamics of silica are driven by the weathering of aluminosilicate minerals, uptake by diatoms, and dissolution of biogenic silica. All algae require small amounts of silicon (Si) for protein and carbohydrate synthesis, but chrysophytes and diatoms obligatorily strengthen their cell walls with silica polymers (Reynolds, 1984). Several investigators have determined that silica availability controls the growth of diatoms, and consequently the species composition of the phytoplankton (Schelske and Stoermer, 1971).

Zooplankton

As integrated members of the aquatic food web, zooplankton have the capacity to influence, and are influenced themselves by the phytoplankton. Phytoplankton are primary producers and the energy source for the heterotrophic zooplankton. By selective feeding, zooplankton control size distribution, and ultimately, species composition of the phytoplankton (Porter, 1977; Vanni, 1987). Zooplankton also regenerate nutrients through excretion, which act to stimulate phytoplankton growth.

Zooplankton assemblages in The Loch were composed almost exclusively of cyclopoid copepods and rotifers. Rotifers comprised the greatest numbers of the winter zooplankton. Cladocerans, common in many Rocky Mountain lakes during the summer (Brinley, 1950; Reed, 1970; Ellsworth, 1983) were extremely rare under ice cover (Appendix II). Similarly, Pennak (1968) found winter populations of cladocerans to be negligible in Colorado mountain lakes. Adult copepods and copepodids were identified as *Eucyclops agilis* (Koch) and *Acanthocyclops* sp.. Taxonomic keys are based on

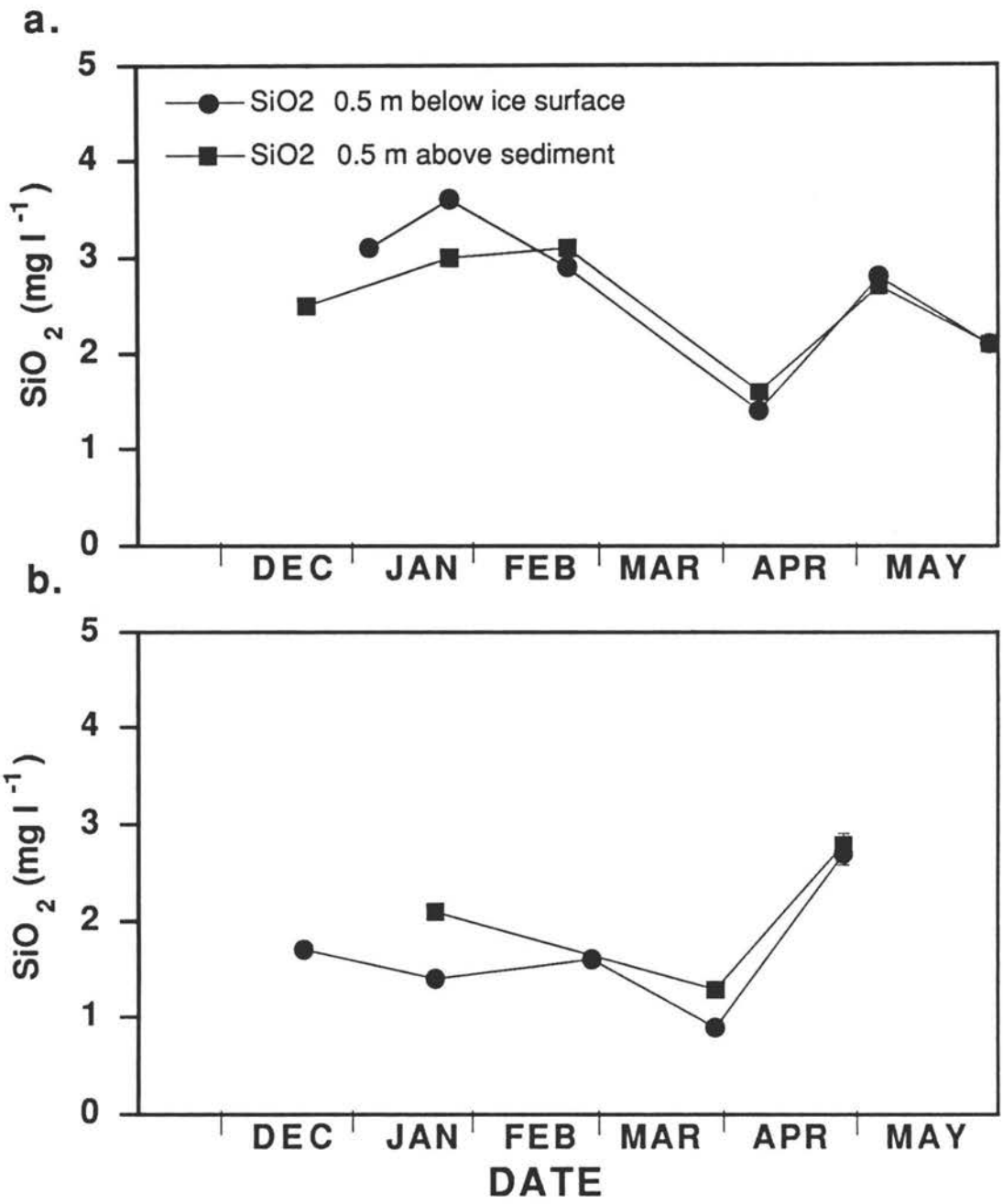


Figure 21. Silica concentrations (mg l^{-1}) in The Loch at two sample depths during a) 1987-88 and b) 1988-89.

male characteristics, but all *Acanthocyclops* found in The Loch were female, so that a species determination could not be made. *Eucyclops agilis* is herbivorous, feeding primarily on filamentous algae and diatoms (Hutchinson, 1967). Some *Acanthocyclops* are predatory and consume their own, and other, copepod species as well as rotifers and other planktonic invertebrates (reviewed in Jamieson, 1980). Copepods were present in low abundance in The Loch (Figure 22). The first year abundances of adult copepods and copepodids were consistently low, while the second year maxima occurred at various times and at various depths. Nauplius larval stages were always low except for a peak in November of the second year (up to 380 individuals $(20\ l)^{-1}$). In this peak the greatest numbers of nauplii were found in the bottom waters, with fewest at the surface (Figure 22).

Unlike the phytoplankton, copepods have relatively long life spans and are much more motile. Although males have shorter life spans, female cyclopoid copepods may live up to a year (E.R. Reed, personal communication). Many of the cyclopoid copepods are known to undergo vertical migration (Hutchinson, 1967). As a result, changes in abundance between sampling times are strongly influenced by the movements of the zooplankton.

Both genera were found in a nearby high elevation pond, also in low abundance (Ellsworth, 1983). Reed (personal communication) found that copepods in The Loch were particularly sparse compared to other Rocky Mountain National Park lakes, probably a function of water retention time. At such low abundance, the cyclopoid copepods probably do not exert a strong grazing pressure on the phytoplankton.

Rotifer abundances during the winter were greater than summer values (5 individuals l^{-1}) reported by McKnight et al. (1988). Historically, Brinley (1950) reported few or no rotifers in summer sampling of three Loch Vale lakes. Reed (1970) found low numbers of rotifers in nearby Rocky Mountain National Park lakes. Similarly, Pennak (1968) found rotifer abundance to be at a minimum in summer. In

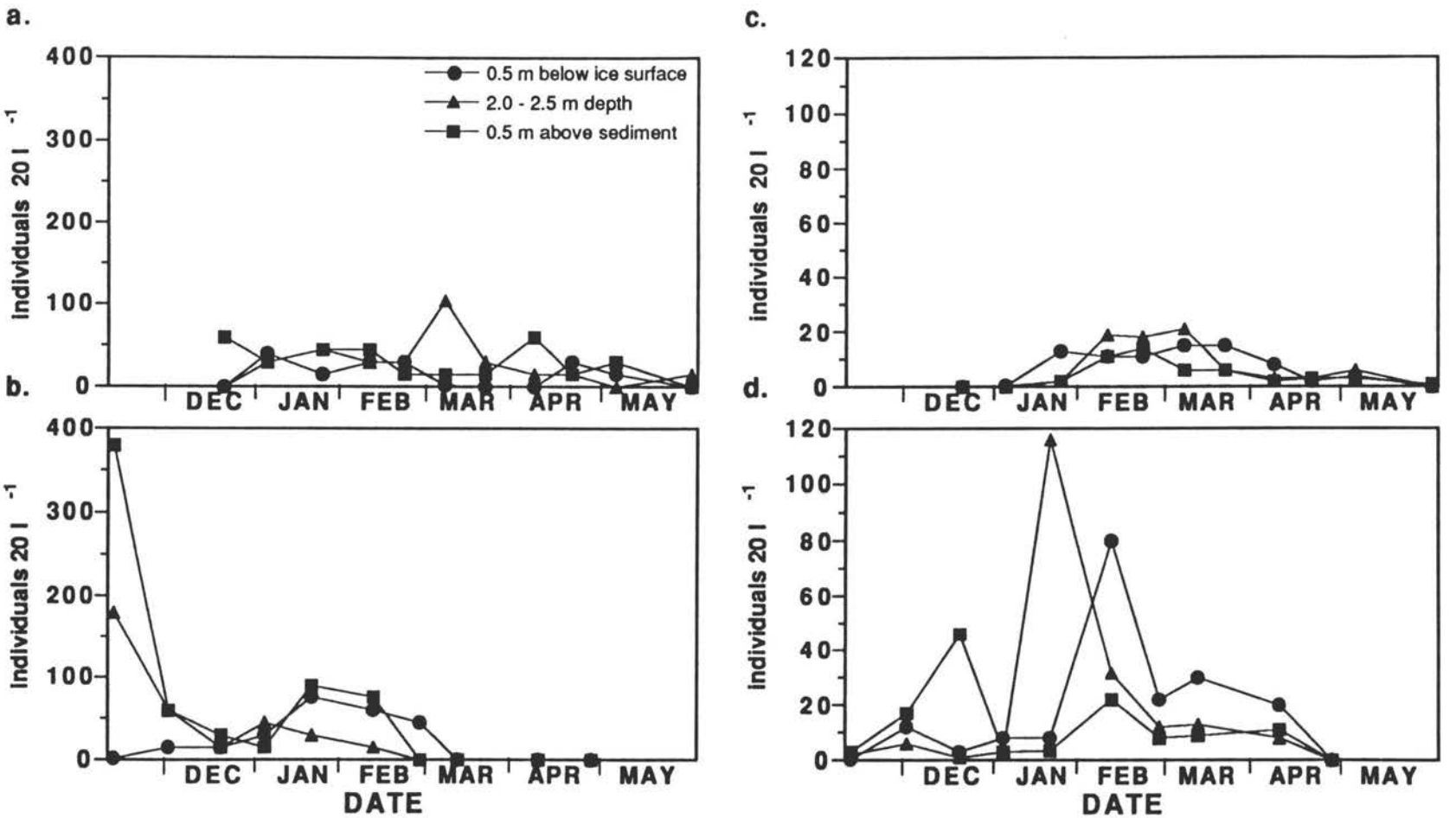


Figure 22. Abundance of copepod nauplii in The Loch during a) 1987-88 and b) 1988-89; abundance of adult and copepodid *Eucyclops agilis* and *Acanthocyclops* sp. (adult and copepodid stages of both species combined) during c) 1987-88 and d) 1988-89. Note different vertical scales.

contrast, during the winter rotifers were commonly found at abundances of several hundred individuals l^{-1} (Pennak, 1968; Ellsworth, 1983). High rotifer densities were found in the current study (Figure 23 and Figure 24), the most common species being *Keratella hiemalis* (Carlin), *Notholca squamula* (O.F. Müller), and *Polyarthra* sp.. *Keratella cochlearis* (Gosse), *Brachionus* sp. and bdelloid rotifers were found occasionally (Appendix II).

Keratella hiemalis exhibited one distinct peak in January of both years. *Keratella hiemalis* is considered to be a cold-water form (Hutchinson, 1967). The first year, the rotifer was strongly differentiated with depth. The maximum occurred while algal abundances were at a minimum. The peak in *K. hiemalis* followed the early bloom of algae. However, it did not start to increase until the phytoplankton biomass had already declined. Consequently, it is not likely that *K.hiemalis* caused a decrease in algal numbers.

Notholca squamula never reached high abundances (Figure 23). May (1980) reported that *N. squamula* was found only in low temperatures (below 10 °C) and grazed almost exclusively on *A. formosa* by breaking the frustule and ingesting the cell contents. However, broken frustules characteristic of the rotifer's feeding habits were not observed. *Asterionella formosa* was present throughout the winter but *N. squamula* was not. *Asterionella formosa* may have had an influence on its abundance, but there were probably other conditions more important to its presence.

Polyarthra sp. was the most abundant rotifer with peak values of over 700 individuals l^{-1} (Figure 24). Ellsworth (1983) also found *Polyarthra* at peak abundance in winter, but at a lesser value of 300 individuals l^{-1}. A single, sharp maximum was characteristic of all the rotifers in The Loch. In the first year, *Polyarthra* reached a maximum in February at the same time algal biomass reached a peak. Cells of the dinoflagellate *Peridinium cinctum* were visible in the gut of *Polyarthra*. The second year

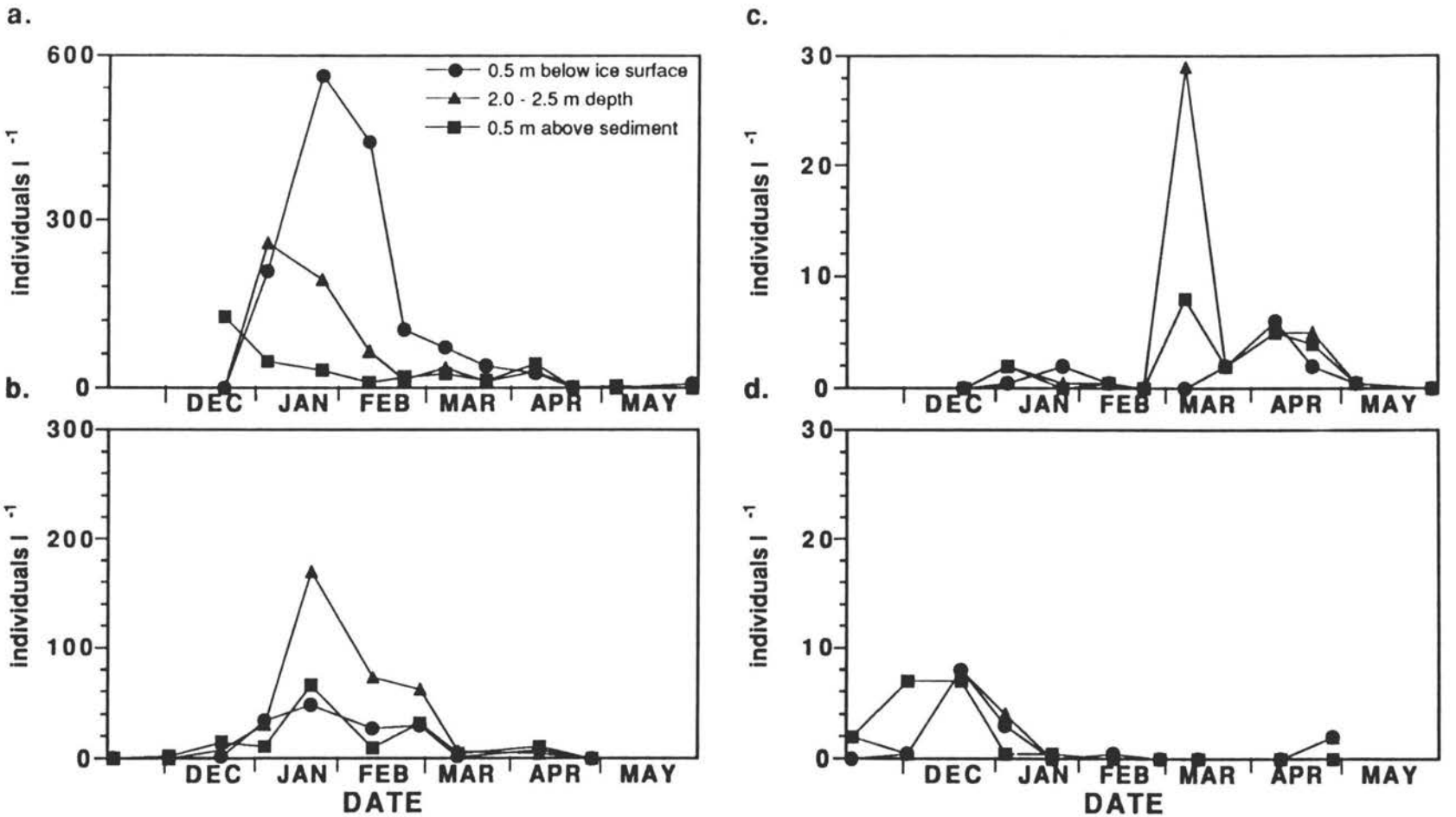


Figure 23. Abundance of *Keratella hiemalis* in The Loch during a) 1987-88 and b) 1988-89; *Notholca squamula* during c) 1987-88 and d) 1988-89. Note different vertical scales.

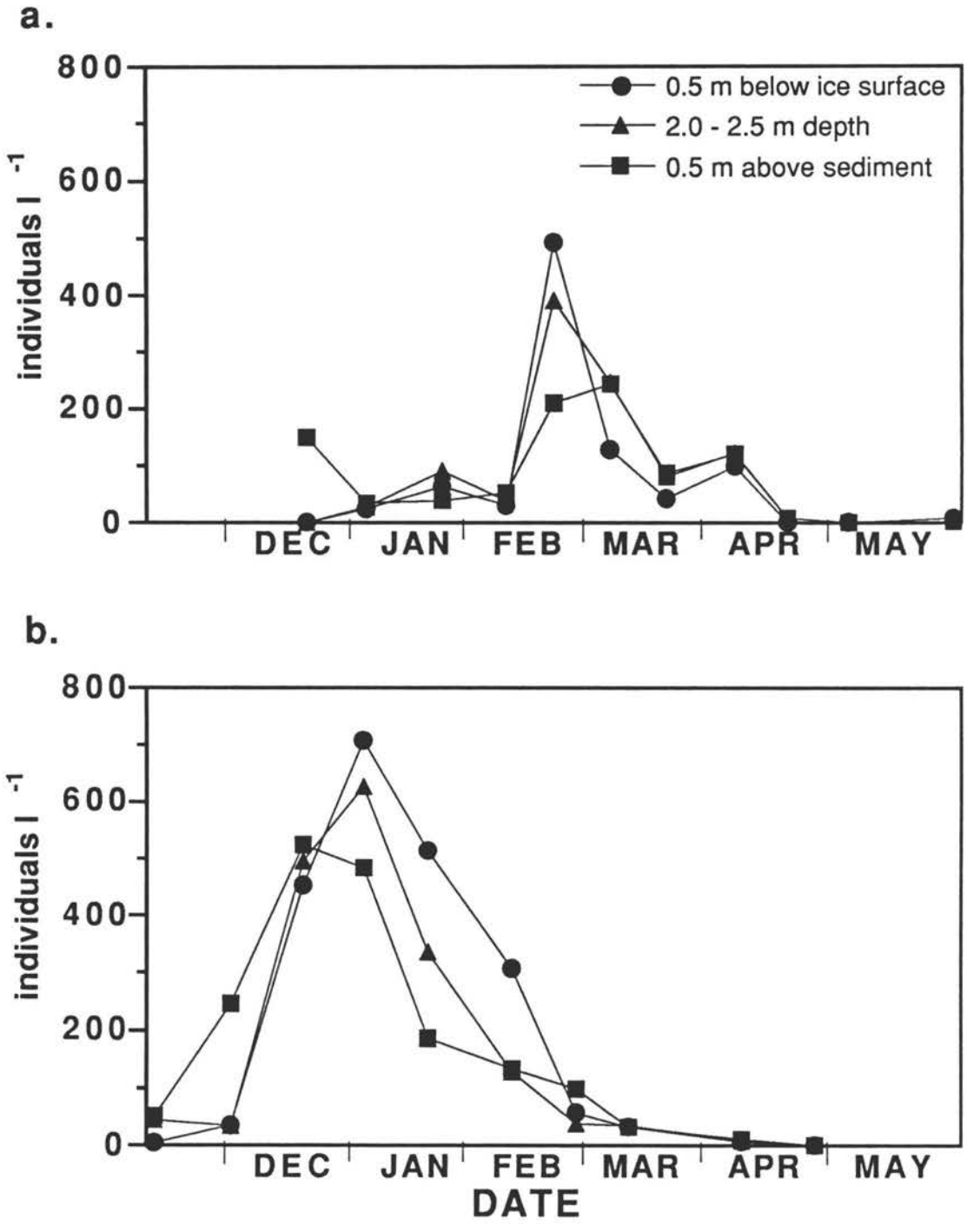


Figure 24. Abundance of *Polyarthra* sp. in The Loch during a) 1987-88 and b) 1988-89.

Polyarthra were most abundant in early January. The increase occurred before the algal bloom had reached a minimum.

Pennak (1968) commented on the remarkable winter populations of rotifers in Colorado lakes. He also observed similar short-term fluctuations in abundance. In contrast, however, Pennak found that rotifer species composition differed greatly from year to year within the same lake. The species composition of The Loch was quite similar between the two years that this study took place. Despite the high winter populations there was no apparent effect on phytoplankton species. One might expect a peak in zooplankton abundance following an algal bloom as in a general predator-prey model. Such temporal sequencing of phytoplankton and zooplankton occurred, but not consistently. At times phytoplankton and zooplankton maxima appeared simultaneously. These observations suggest that the zooplankton diet is variable, and does not lead to the demise of a given algal species. In addition, observations suggest that zooplankton populations are of a small size in relation to the algal food supply, so that their impact is negligible. The present study cannot address these hypotheses and they would require further examination.

Phytoplankton

The phytoplankton are a heterogeneous group of taxa (Reynolds, 1984). Planktonic algae are the most conspicuous members of the phytoplankton (bacteria are important as well, mediating many of the chemical processes which characterize aquatic habitats). Planktonic algae are primarily, but not always, photo-autotrophic. They are important as primary producers and form the base of limnetic food webs. Therefore, changes in species composition and abundance of the phytoplankton are of inherent interest because of their impact on higher trophic levels. Furthermore, phytoplankton are sensitive to fluctuations in the aquatic habitat. The seasonal succession of phytoplankton is a striking example of how changes in physical, chemical, and biological factors produce changes in algal species composition.

Biomass

Two methods, chlorophyll *a* and cell volume, were used to estimate phytoplankton biomass. Chlorophyll *a* under ice ranged from 0.2 to 21.4 $\mu g\ l^{-1}$ (Figure 25). These values are comparable to those found in the open water period (McKnight, et al., 1986; 1988). In 1987-88, chlorophyll values were low until February when they began to increase. Chlorophyll values in the surface waters reached a maximum of 21.4 $\mu g\ l^{-1}$ in early February. The values in the middle and bottom depths attained maxima in March, but did not reach such high values. February and March were the only times when chlorophyll was greater in the surface sample. At all other times, there was no differentiation by depth. There was no differentiation by depth in 1988-89. Chlorophyll values were at their maximum in early winter. They subsequently decreased and remained low for the duration of ice cover.

Biomass was also measured by estimation of cell volumes. Cell volumes were reported as biovolume rather than reported as biomass. (The conversion requires assuming algal specific density is equal to that of water, and making appropriate calculations). Total mean phytoplankton biovolume ranged from $3.0 * 10^4$ to $3.7 * 10^6$ $\mu m^3\ ml^{-1}$ (Figure 26).

The pattern of algal biomass was similar between the two years, consisting of an initial peak, a minimum, a second peak, and decreasing biomass until ice-out (Figure 26). The changes in algal biomass reflect the net result of growth and loss processes. Loss processes include death, sedimentation of live cells, and zooplankton grazing. Simulation models of phytoplankton populations have indicated that loss rates are essential driving variables of species succession (Kalff and Knoechel, 1978). Something can be learned about loss processes from the amplitude and duration of biomass peaks because they are directly related to the growth and loss functions that produce them. A sharp biomass peak, such as that in February of 1988, can be thought of as a temporary imbalance of growth and loss. In contrast, a broader, more enduring

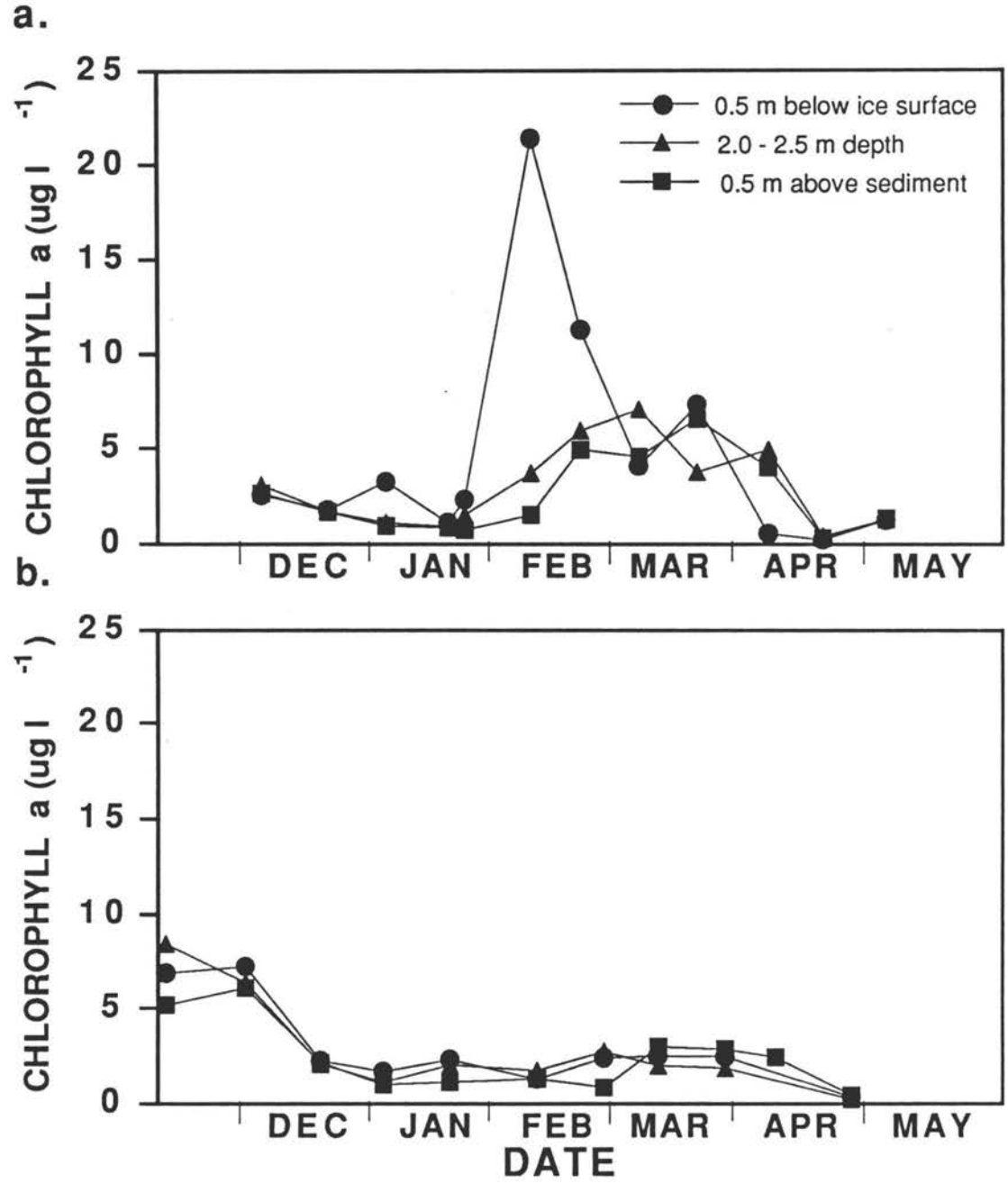


Figure 25. Chlorophyll *a* concentrations in The Loch at three sample depths during a) 1987-88 and b) 1988-89. Each point represents the mean value of two samples.

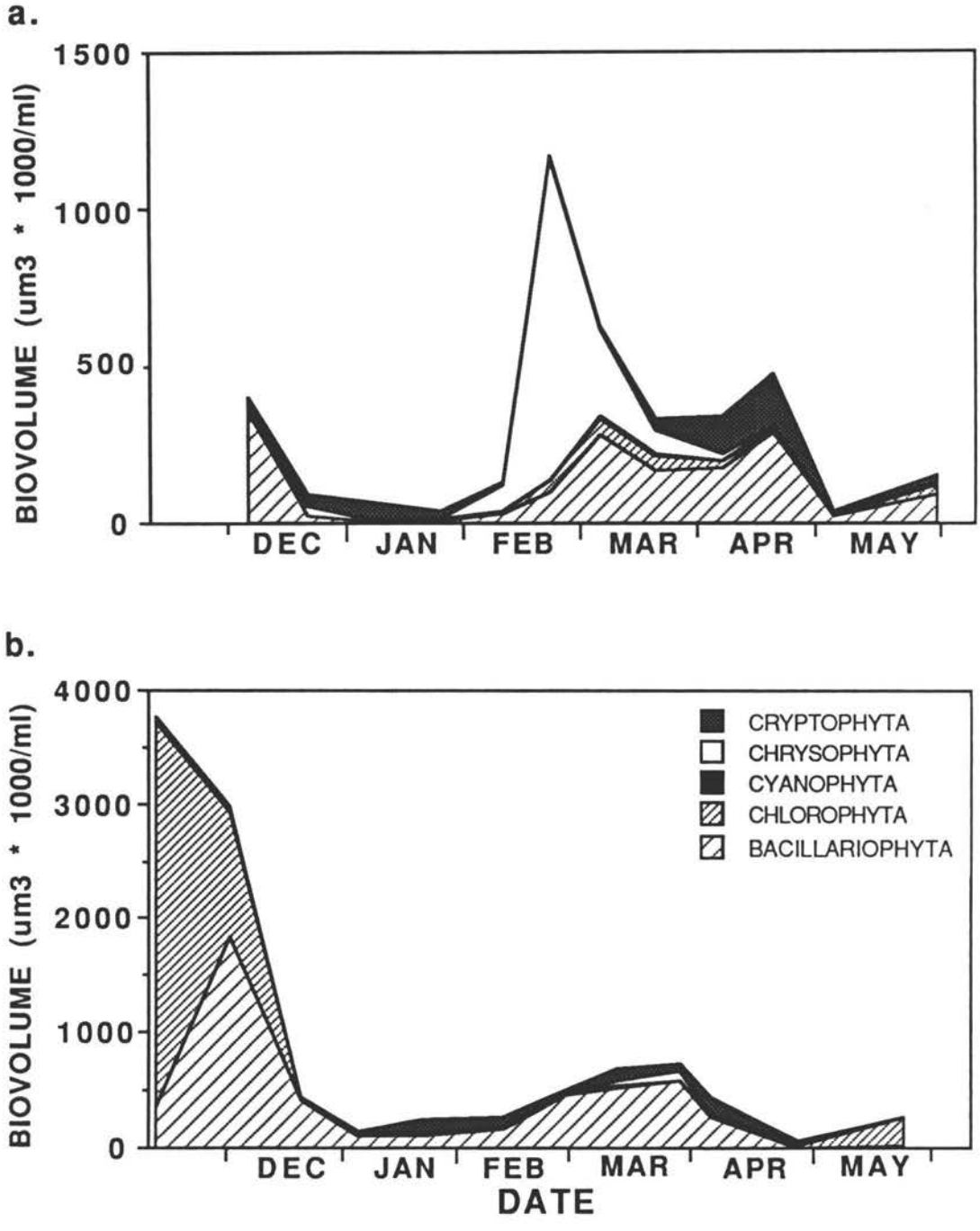


Figure 26. Total phytoplankton biovolume in The Loch as the mean of three sample depths, separated to show the contribution of the algal divisions, for a) 1987-88 and b) 1988-89.

peak requires that growth and loss processes remain in close balance for a period of time. Low biomass can persist with either high or low growth rate provided that growth is balanced by equivalent losses.

Although percent composition by taxonomic division varied between years, the pattern of biomass remained the same (Figure 26). The pattern of change in biovolume was caused by several factors. In this type of study it is impossible to determine conclusively the contribution of each variable. I will suggest some possible explanations.

The process of ice formation and concurrent changes in biomass may be important to the control of algal biomass. Based on the phenomenon of freeze concentration, one would predict an increase in nutrients with the formation of ice cover on The Loch. Phosphorus (as orthophosphate) concentrations were below detection limits in this study (3 - 6 $\mu g\ l^{-1}$), so its dynamics are unknown. Nitrate concentration increased with the formation of ice cover, but the increase was not statistically significant (Table 6). A nutrient pulse with the formation of ice cover might explain the early winter bloom of phytoplankton which occurred the second year, and may have also occurred the first year. However, such an increase would occur if nutrients were in excess of algal requirements. If nutrients were limiting, they would be assimilated by phytoplankton as soon as the nutrients were released from the forming ice. No change in water chemistry would be detectable, but algal growth would increase. Ice formation is a gradual process and algal uptake could keep pace with nutrient release. Morris and Lewis (1988) determined that phytoplankton in lakes in the Colorado mountains were alternately limited by nitrogen or phosphorus, by both, or by neither. Dissolved inorganic nitrogen (primarily NO_3, NO_2, NH_4) concentrations were much greater in The Loch (Figure 20) than in the lakes examined by Morris and Lewis (~3 - 270 $\mu g\ l^{-1}$). Based on their measurements of nitrogen limitation, it is not likely that nitrogen is limiting to phytoplankton in The Loch.

Alternatively, nutrient concentrations enriched by the formation of ice cover could be predicted to be depleted during the winter season. A depletion of nutrients would lead to a decline in algal productivity. (Productivity was not measured, but for the purpose of argument it will be assumed to be correlated to biomass.) There was a decrease in phytoplankton biomass in late winter (Figure 26). Although nitrate concentrations declined throughout the season of the second year, there was no such pattern in the first year (Figure 20). This is but one possible explanation, and it may be misleading to make conclusions on such correlative results and without phosphorus data.

The changes in biomass could also be attributed to light. During the algal minimum the sun was at its lowest aspect. Total daily incident radiation was at a minimum (Figure 9). The lake is shaded by the ridge of Thatchtop Mountain (Figure 2). Beginning in early February The Loch is no longer shaded for the majority of the day. The increase in algal biomass in February may be at least partially related to the changing light regime. However, the increase in light as the winter progresses is not associated with a concomitant increase in algae, indicating the operation of additional factors.

In many studies, chlorophyll *a* is used as an estimate of biomass. Values of chlorophyll *a* were compared to estimates of biovolume (biomass) to determine the relationship of chlorophyll *a* to biomass in this study. When samples from both years were considered, chlorophyll *a* showed a poor relationship to biomass ($r^2 = 0.37$). However, when each sampling season was examined independently, the relationship was much closer (Figure 27). The first year, a linear regression of chlorophyll *a* and biovolume produced an r^2 value of 0.53, while the second year the r^2 value was equal to 0.74. Interestingly, the first year biovolume values appear to track the pattern of chlorophyll *a* (Figure 25 and Figure 26), but linear regression produced a lower r^2 value in the first year as compared to the second. This result suggests that seasonally

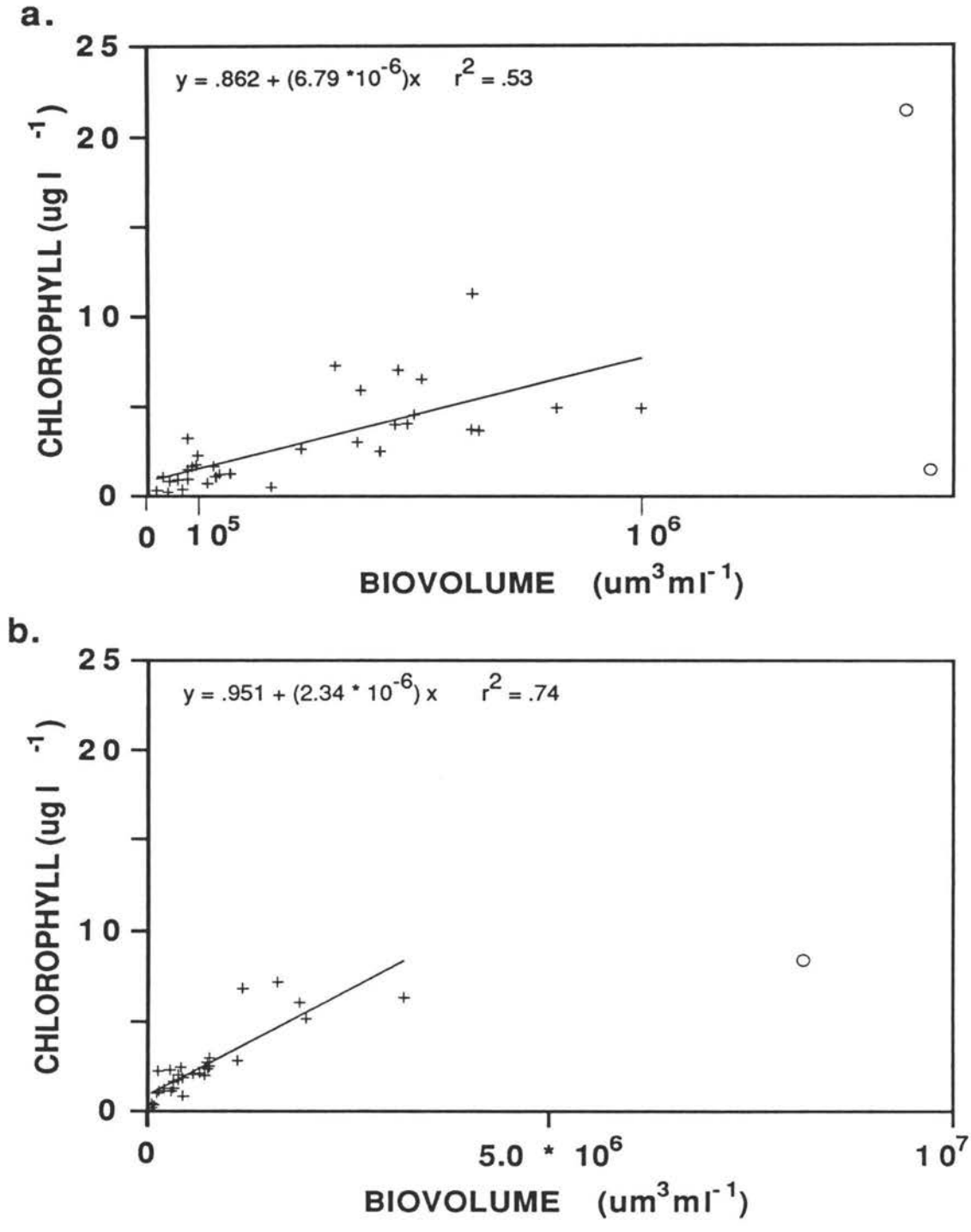


Figure 27. Mean phytoplankton biovolume of three depths vs. chlorophyll *a* concentrations for a) 1987-88 ($r^2 = 0.53$, n = 33) and b) 1988-89 ($r^2 = 0.74$, n = 30). Circles mark outliers not included in the regression.

chlorophyll *a* is not a dependable indicator of biomass, and between years there are quantitative changes in the ratio of chlorophyll *a* to biomass.

Although all photosynthetic algae, including cyanobacteria, contain chlorophyll *a*, the chlorophyll *a* content varies between different algal groups (Reynolds, 1984). Among chlorophytes, chlorophyll *a* is the major photosynthetic pigment and the ratio of chlorophyll *a* to ash-free dry weight is relatively high. Diatoms have a higher content of accessory pigments such as carotenoids and xanthophylls. In addition, diatoms have a large vacuole within the cell. Hence, the proportion of chlorophyll *a* is generally lower than in chlorophytes. The chlorophyll *a* component of cyanobacteria is comparable to that of diatoms. As a result, succession of algal taxa may produce changes in total chlorophyll *a*, even under conditions of constant algal biomass. Furthermore, within a given species algae are known to physiologically adapt to ambient light intensities (Kalff et al., 1972; Tilzer and Schwarz, 1976; Reynolds, 1988). In low light intensity algae can increase light absorption by increasing the size of chloroplasts or the numbers of chloroplasts within cells. In addition, other factors such as nutrient levels affect the percentage of chlorophyll in algal cells.

In The Loch, the patterns of biomass were similar between the two years, although the absolute biovolume was greater the second year. Moreover, the dominant algal divisions varied between the two years. Chrysophytes made up a significant portion of the biomass the first year, while during the second year chlorophytes and diatoms were more prevalent. The timing of algal peaks by taxonomic group differed between the two years. Based on taxonomic group alone, it is not surprising that there are differences in the correlation between chlorophyll *a* and biovolume between the two years. Light intensity also changed within a season and algae adjusted to light levels. These factors are masked within the sweeping measurement of chlorophyll *a* and the correlation with biomass.

In order to calculate total algal biomass, estimates of individual cell volume must be made. Individual cell volumes can be obtained from microscopic measurement or published accounts. However, cell volumes may differ from one location to another. Cell volumes of a given alga may even differ temporally. Several species volumes were calculated on different dates in 1987 (Table 8). The volumes differed substantially from published values (Reynolds, 1984; Willén, 1976) and showed appreciable variation throughout the winter season (Figures 28 and 29). *Chlorella vulgaris* Beyer. showed a significant increase in volume throughout the winter ($P < 0.05$). Temporal changes in the size of *Asterionella formosa* , based on chloroplast dimensions were not significant. Chloroplasts, rather than frustule dimensions were measured (except Dec. 6) because of the large vacuole of diatoms. Diatom frustules are slightly reduced in size with each asexual cell division. Size of individuals gradually declines in volume until sexual reproduction restores cells to their maximum dimensions (von Stosch, 1965 as cited in Sommer, 1988). The decrease in size is small and may not be visible in a single season. In the case of *Peridinum cinctum* (Müll) Ehrenb., a significant decrease in volume was found for over the winter period ($P < 0.05$). Pollingher (1988) found that *P. cinctum* varied not only in size but in shape as a bloom developed. Cell size also varied annually as a function of phosphorus availability. The small blue-green alga, *Chroococcus dispersus* (Keissl.) Lemm. was variable in volume from one date to the next. *Chlamydomonas* sp. decreased slightly throughout the winter. *Coccomyxa dispar* Schmidle, a small blue-green alga, did not change in size. Conversely, *Dinobryon sertularia* Ehrenb. volumes decreased until the final date, when the ice had melted. *Dinobryon* cells are considerably distorted with fixation, so that measurements may not reflect the true volumes. There was no change in size in the green alga, *Ankistrodesmus falcatus* var. *acicularis* (A.Brown) G.S. West.

Phytoplankton in lakes under ice have been reported to be small, with a greatest dimension of 2-8 μm (Jordan et al., 1988). Similarly, The Loch algal community was

Table 8. List of common species with the formulas used to calcuate cell volumes and the mean volume and 95% confidence interval for dates in 1987-88. Number of cells counted equal to 20, unless marked by (*), then n = 100. (l = length, d = diameter, h = height, $\pi = 3.14$)

Taxon	Formula	12/6/87	2/21/88	3/6/88	3/20/88	4/6/88	5/4/88	5/30/88
Ankistrodesmus falcatus	$(\pi d^2 l)/12$			15 ± .9*	15 ± 2.8	17 ± 1.9		
Asterionella formosa	l b h	401± 40*		182 ± 15	137 ± 29	150 ± 45	97 ± 26	126 ± 52
Chlamydomonas sp.	$(\pi d^3)/6$			46 ± 2.4*	40 ± 2.0	37 ± 4.6		
Chlorella vulgaris	$(\pi d^3)/6$	5.4 ± .8	7.2 ± .7*		7.8 ± 1.2	12 ± 2.7		
Chlorococcum sp.	$(\pi d^3)/6$	54 ± 5						
Chlorogonium sp.	$(\pi d^2 l)/12$							176 ± 34
Chroococcus dispersus	$(\pi d^3)/6$		2.2 ± .2	5.6 ± 1.1	3.5 ± .4	7.8 ± 1.5	3.5 ± .7	7.2 ± 1.9
Coccomyxa dispar	$(\pi d^2 l)/6$			1.4 ± .1*	1.8 ± .3	1.6 ± .3		
Cryptomonas sp. 1	$(\pi d^2 l)/6$					1794±146		
Cryptomonas sp. 2	$(\pi d^2 l)/6$					149 ± 15		
Dinobryon sertularia	$(\pi d^2 l)/6$		217 ± 13*	200 ± 30	162 ± 27	119 ± 18	247 ± 37	
Peridinium cinctum	$(\pi d^3)/6$		7795±31	6740±46		5376±372		
Phormidium sp.	$(\pi d^2 h)/4$				3.1 ± .2			
Rhodomonas sp. 1	$(\pi d^2 l)/6$						21 ± 2.7	
Rhodomonas sp. 2	$(\pi d^2 l)/6$							85 ± 7
Scenedesmus sp.	$(\pi d^2 l)/6$	36 ± 7		37 ± 8				
indeterminate protozoan 1	$(\pi d^2 l)/6$			527				
indeterminate protozoan 2	$(\pi d^2 l)/6$					509		
fungal chytrid	$(\pi d^3)/6$	40 ± 5*		24 ± 5				

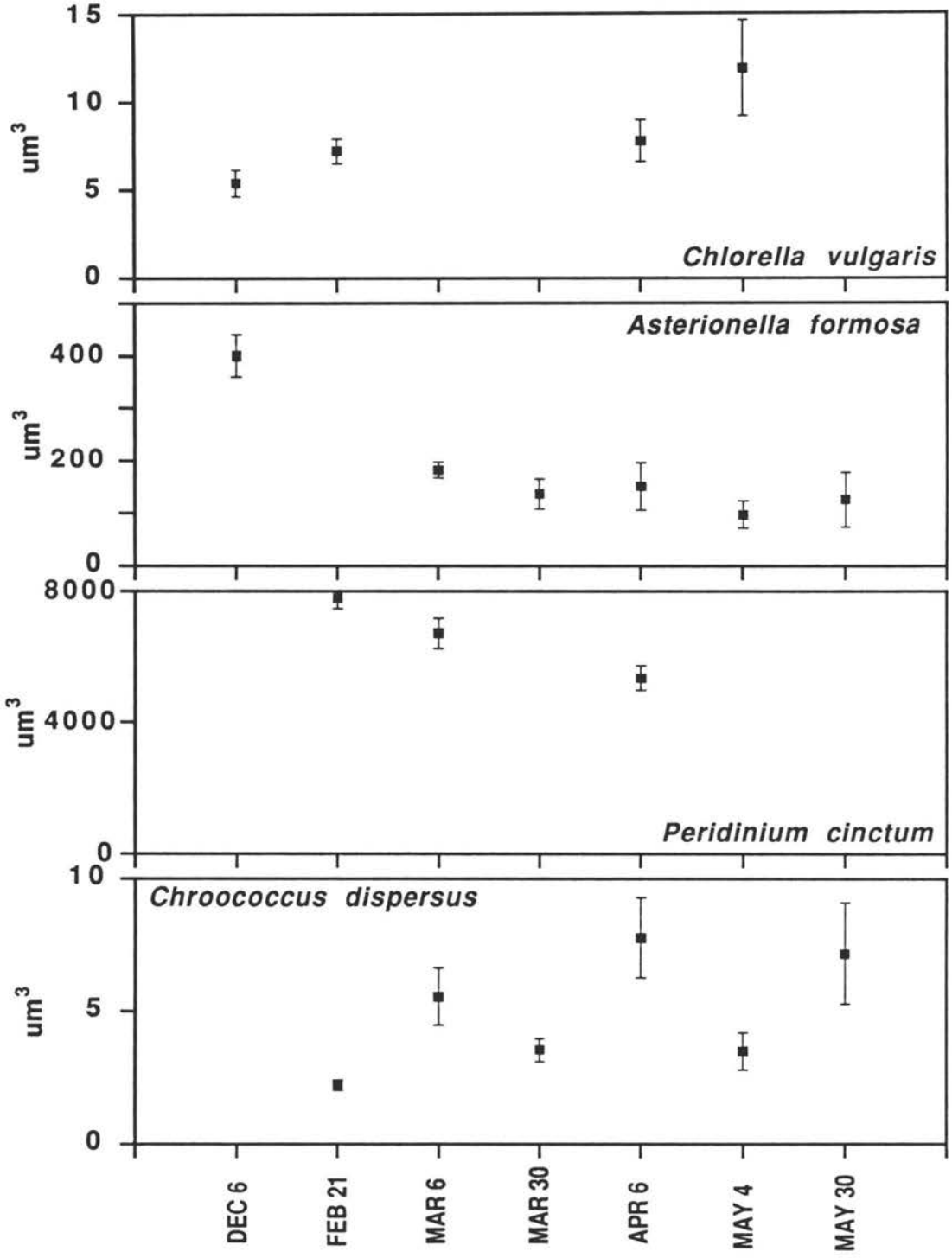


Figure 28. Algal cell volume and 95% confidence interval measured on dates during 1987 in The Loch. (Chloroplast dimensions were measured on *Asterionella formosa* except December 6 when the entire frustules were measured.)

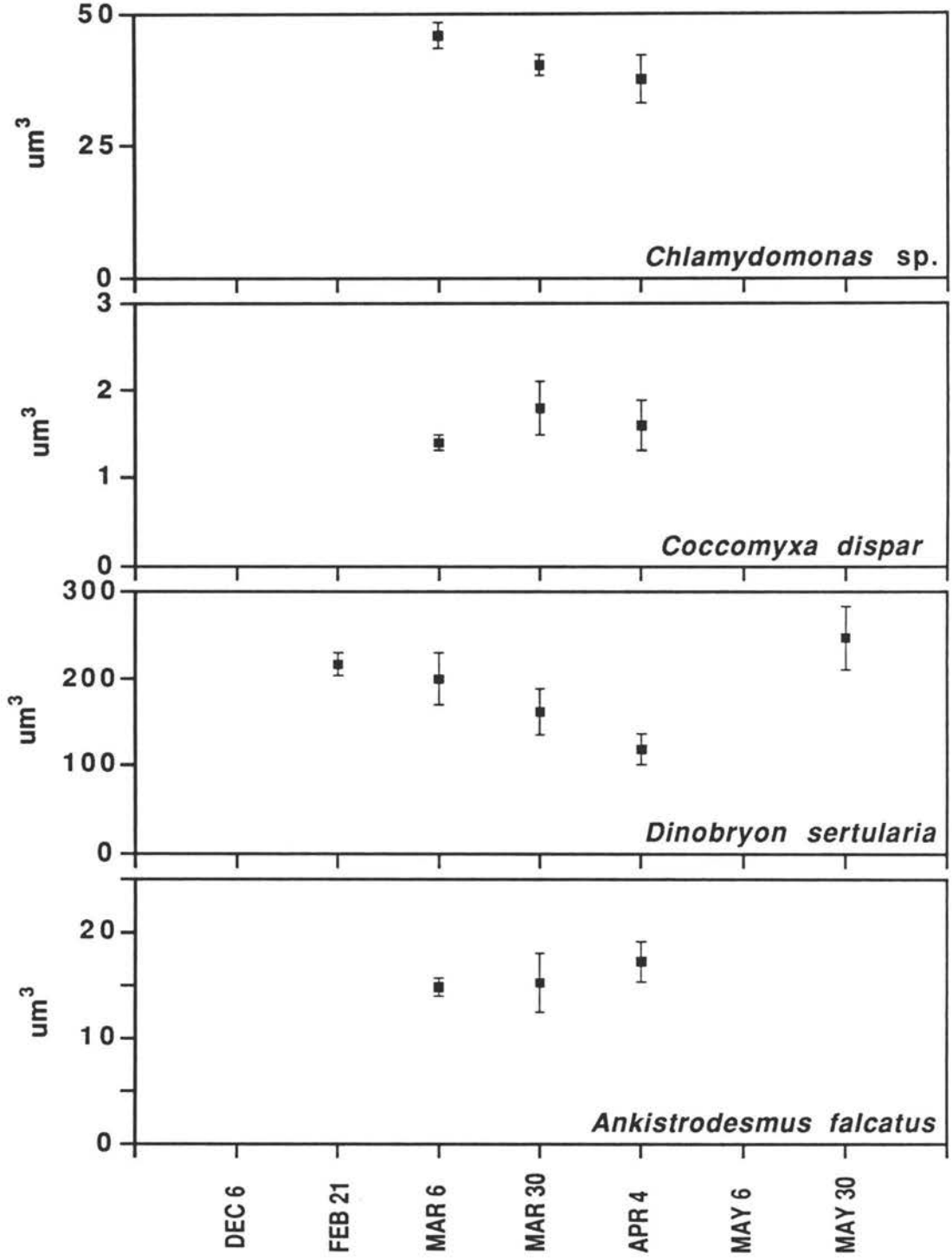


Figure 29. Algal cell volume and 95% confidence interval measured on dates during 1987 in The Loch.

often numerically dominated by small algae (Appendix I). However, the larger species made up much more of the total biovolume. Nanoplankton, algae less than 35 µm, have been found to consistently have high production rates (Kalff and Knoechel, 1978). Their rates of productivity may far exceed their representation in the total biomass. The small algae rarely produce blooms, suggesting that they suffer from high loss rates from zooplankton grazing.

Species Composition

Phytoplankton species composition changed continually throughout the winter (Appendix I). The change in composition at the division level is summarized in Figure 30. The percent composition of the community by volume was initially dominated by diatoms, followed by cryptophytes in the first year. Chrysophytes dominated in mid-winter followed by diatoms (almost exclusively *Asterionella formosa*). The pyrrophytes (dinoflagellates), chlorophytes, and cyanobacteria also fluctuated in their numbers but never dominated the plankton by volume. The second year, chlorophytes were initially over 80% of the community. Following their decline, *A. formosa* again contributed to the majority of the algal biomass. In the late spring *A. formosa* declined and chlorophytes, for a second time, were a large percentage of the community. Cryptophytes had a bimodal peak in both years, but it was less pronounced in the second year. Chysophytes were present in the second year, but did not form the large peak that they did in the first.

The community composition can also be examined by species dominance patterns (Table 9 and Figure 31). In the first year the numerically dominant species contributed about 10 to 50% of the total. The second most dominant species was always a lower percentage of the community, followed by the third. The remaining taxa varied in their contribution to the total. "Remaining" species made up the largest percentage of the total in January and February when biomass was at a minimum. The second year showed a

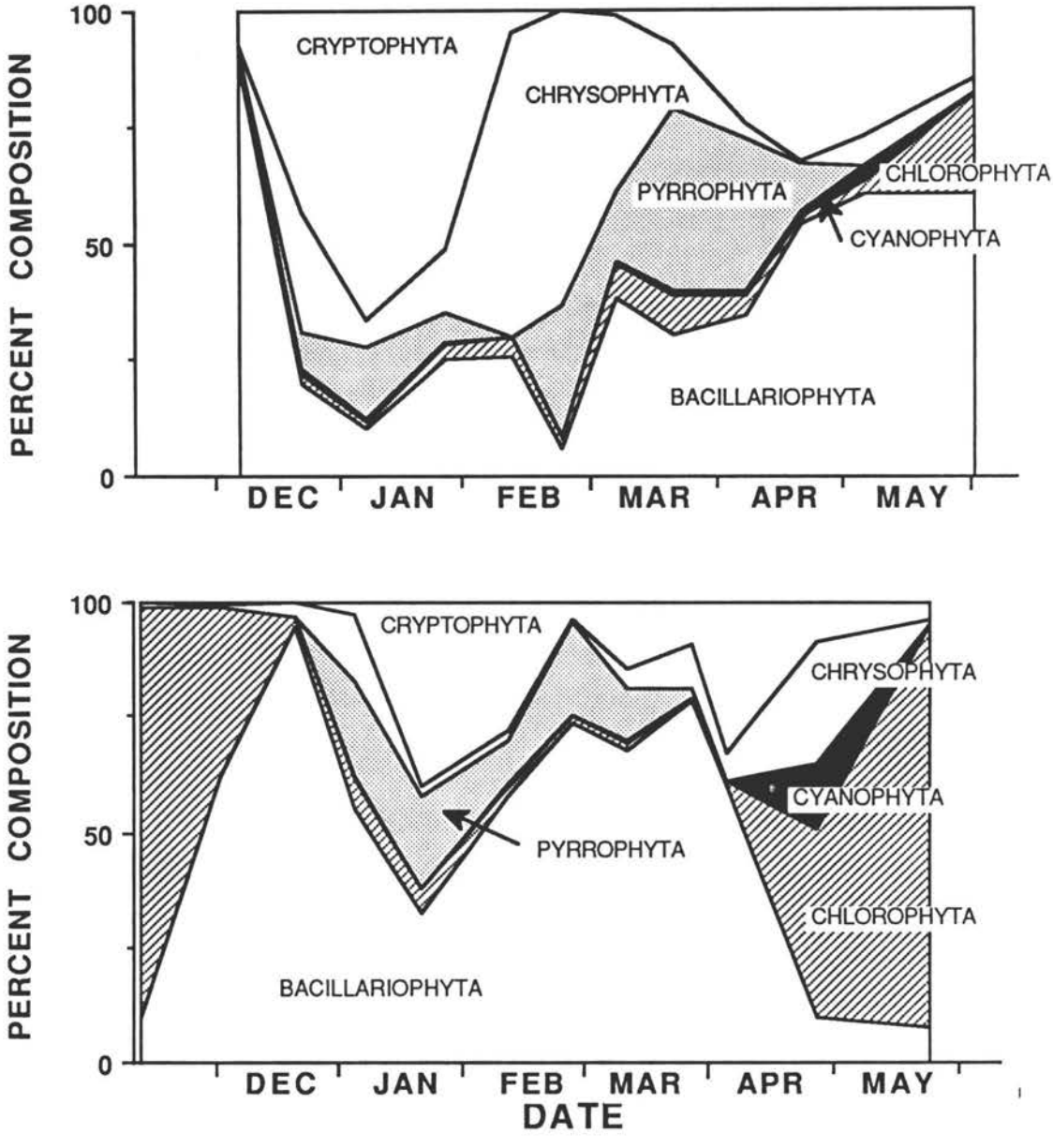


Figure 30. Volume percent composition of the phytoplankton community by taxonomic division in The Loch for the mean of three depths during a) 1987-88 and b) 1988-89.

Table 9. Listing by numerical abundance the three most dominant and the total number of taxa in The Loch during 1987-88 and 1988-89.

Date	1st most abundant taxa	2nd most abundant taxa	3rd most abundant taxa	Total
6 Dec 87	*Oscillatoria* sp.	*Asterionella formosa*	*Chroococcus dispersus*	30
21 Dec 87	*Chroococcus* spp.	*Chlorella vulgaris*	*Coccomyxa dispar*	27
5 Jan 88	*Chroococcus dispersus*	indeterm. flagellate	Cryptomonas ovata	22
24 Jan 88	*Chroococcus dispersus*	indeterm. chrysophyte	indeterm. flagellate	28
9 Feb 88	*Chlorella vulgaris*	*Dinobryon sertularia*	*Chroococcus dispersus*	23
21 Feb 88	*Chlorella* sp.	*Chroococcus dispersus*	*Coccomyxa dispar*	23
6 Mar 88	*Coccomyxa dispar*	*Dinobryon sertularia*	*Chroococcus dispersus*	26
20 Mar 88	*Coccomyxa dispar*	*Chroococcus dispersus*	*Ankistrodesmus falca.*	26
6 Apr 88	*Chroococcus dispersus*	*Asterionella formosa*	*Coccomyxa dispar*	29
19 Apr 88	*Asterionella formosa*	*Chroococcus dispersus*	*Ankistrodesmus falca.*	41
4 May 88	*Chroococcus dispersus*	*Rhodomonas* sp.	*Oscillatoria* sp.	35
30 May 88	*Chlamydomonas* sp.	*Asterionella formosa*	*Selenastrum* sp.	39
13 Nov 88	*Chlamydomonas* sp.	*Asterionella formosa*	*Chroococcus dispersus*	23
2 Dec 88	*Chlamydomonas* sp.	*Asterionella formosa*	*Oscillatoria* sp.	24
20 Dec 88	*Asterionella formosa*	*Chlamydomonas* sp.	*Chlamydomonas* sp.	23
4 Jan 89	*Chlorella vulgaris*	*Asterionella formosa*	*Chroococcus dispersus*	28
20 Jan 89	*Chlorella vulgaris*	*Asterionella formosa*	*Chroococcus dispersus*	23
10 Feb 89	*Chlorella vulgaris*	*Asterionella formosa*	*Coccomyxa dispar*	23
26 Feb 89	*Asterionella formosa*	*Chlorella vulgaris*	*Chroococcus dispersus*	18
11 Mar 89	*Asterionella formosa*	*Coccomyxa dispar*	*Chroococcus dispersus*	32
27 Mar 89	*Asterionella formosa*	*Dinobryon* sp.	*Chroococcus dispersus*	30
8 Apr 89	*Asterionella formosa*	*Chroococcus dispersus*	*Dinobryon* sp.	24
26 Apr 89	*Chlamydomonas* sp.	*Oscillatoria* sp.	*Chroococcus dispersus*	31
23 May 89	*Chlamydomonas* sp.	*Chroococcus dispersus*	*Asterionella formosa*	19

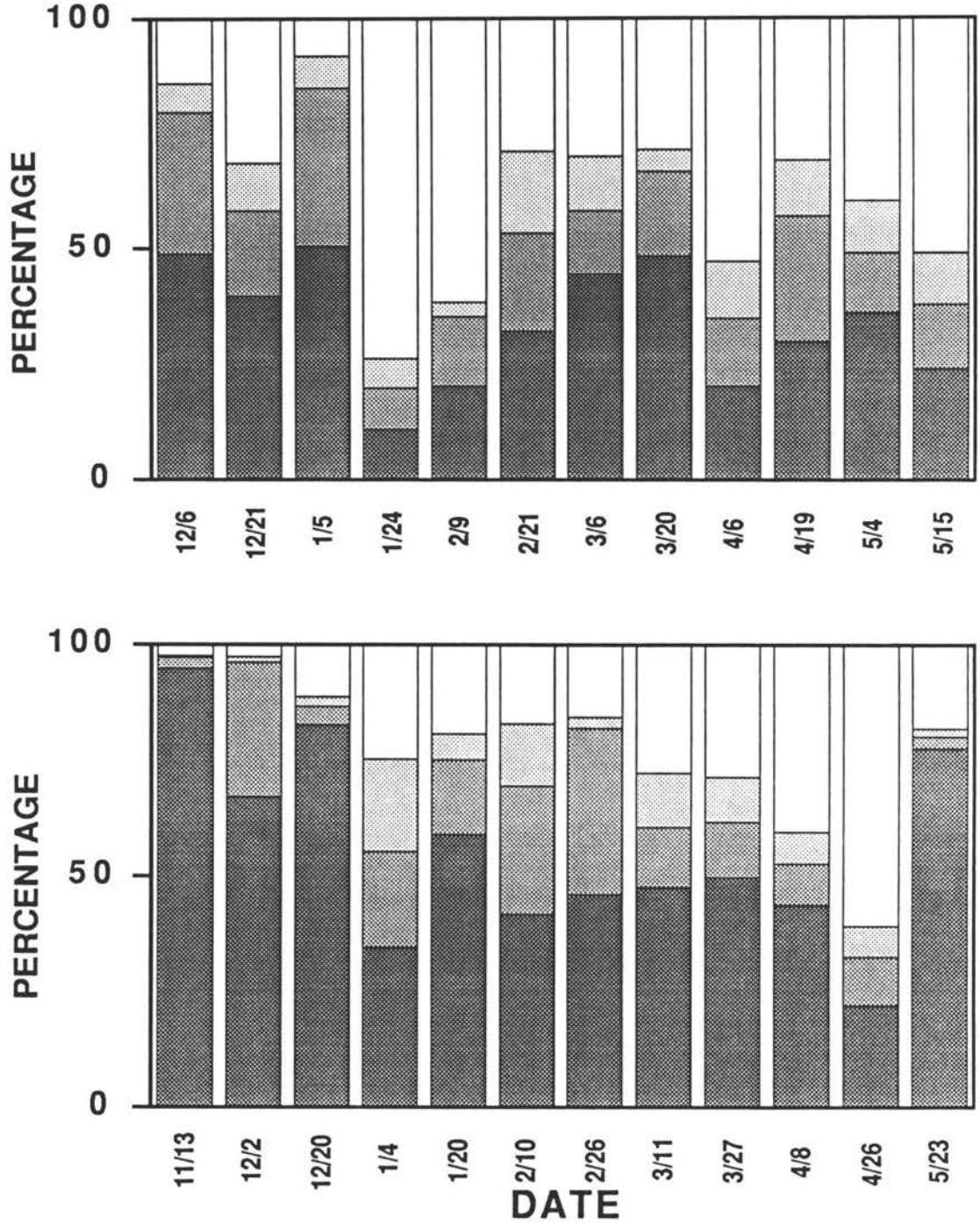


Figure 31. Numerical percent composition of the phytoplankton community in The Loch during a) 1987-88 and b) 1988-89. The darkest shading is the numerical percentage of the most abundant species. The lighter shading represents the second, the lightest shading is the third, and the white encompasses the remaining species.

very different pattern. The most numerically dominant species was over 90% of the total on one date. Overall, it was a larger contribution than the first year. The second and third most numerous species again made up a smaller percentage of the total.

To this point, species have been grouped into their respective divisions in order to summarize the overall trends. In addition, values for depth have been averaged values of the three discrete sample depths. However, data in summarized form does not show the dynamics of each species and their distribution by depth. The spatio-temporal dynamics of the most common species are described below for each taxonomic division.

Bacillariophyta

Asterionella formosa was found to be the single most dominant species. It was present in nearly all samples and contributed a substantial proportion of the total biomass (Figure 32). *Synedra* sp. was the only other diatom that was consistently present, but it occurred in low numbers. In the second year both *A. formosa* and *Synedra* sp. had a greater biomass. In both years a bimodal pattern of *A. formosa* abundance occurred, with the first peak in early December and second peak in March and April. During the first peak, *A. formosa* was differentially distributed by depth. Cells were most numerous at the surface and decrease in abundance with depth. In contrast, later in the season there was either no differentiation by depth, or cells were least numerous at the surface.

Diatoms have siliceous cell walls, which makes them particularly dense. They sink rapidly in the absence of turbulence in the water column. Empty *A. formosa* frustules were observed lower in the water column following the initial winter peak in early December (Figure 33). On the sample date two weeks later, peaks in empty frustules were found. At the next sample date, the number of empty frustules was at a minimum. *Asterionella formosa* reached a maximum and then settled from the water column. Live, healthy cells have slower sinking rates than dead or senescent cells (Tilman and Kilham, 1976; Sommer, 1987). Nevertheless, the pattern of

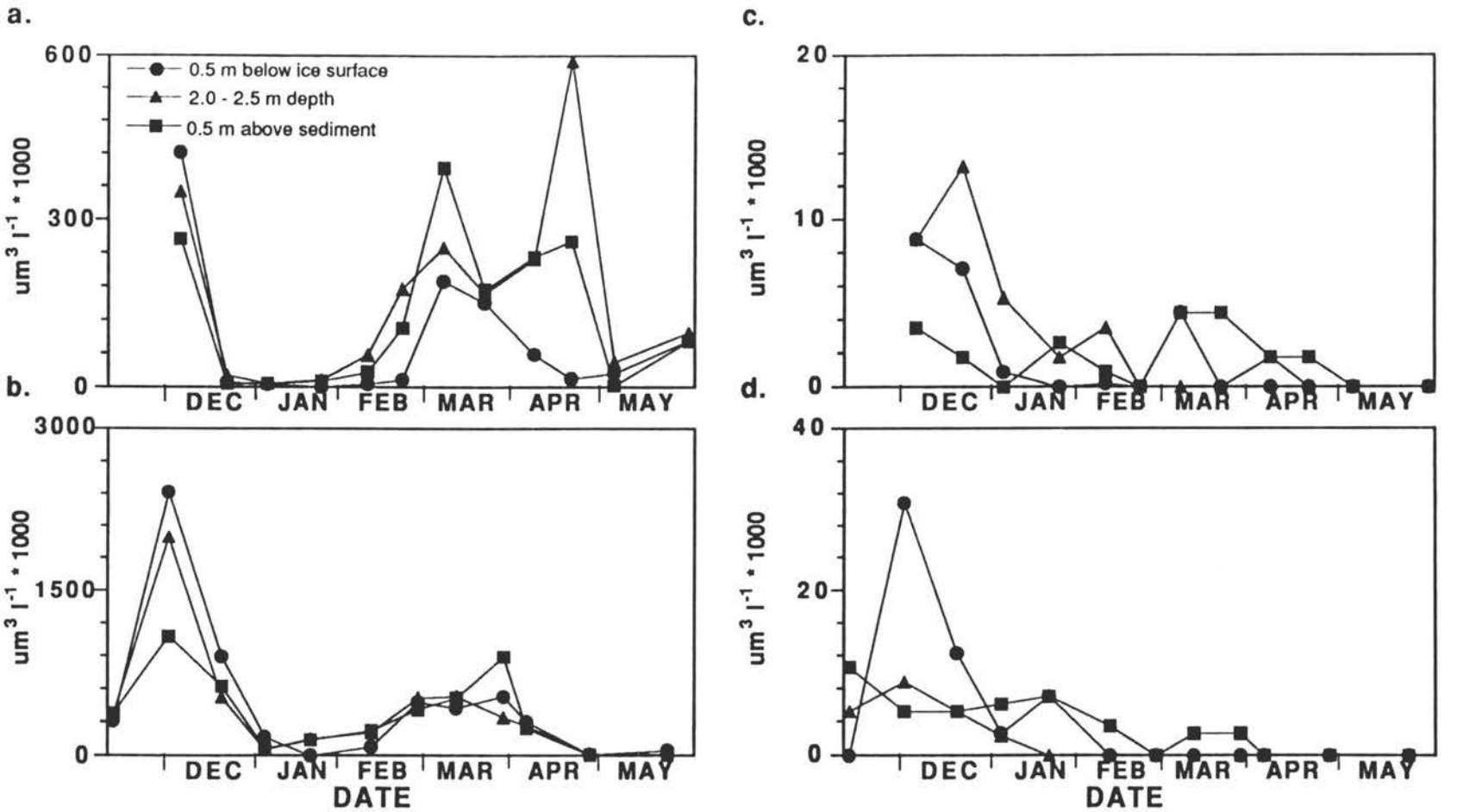


Figure 32. Biovolume of *Asterionella formosa* in The Loch during a) 1987-88 and b) 1988-89; *Synedra* sp. during c) 1987-88 and d) 1988-89. Note different vertical scales.

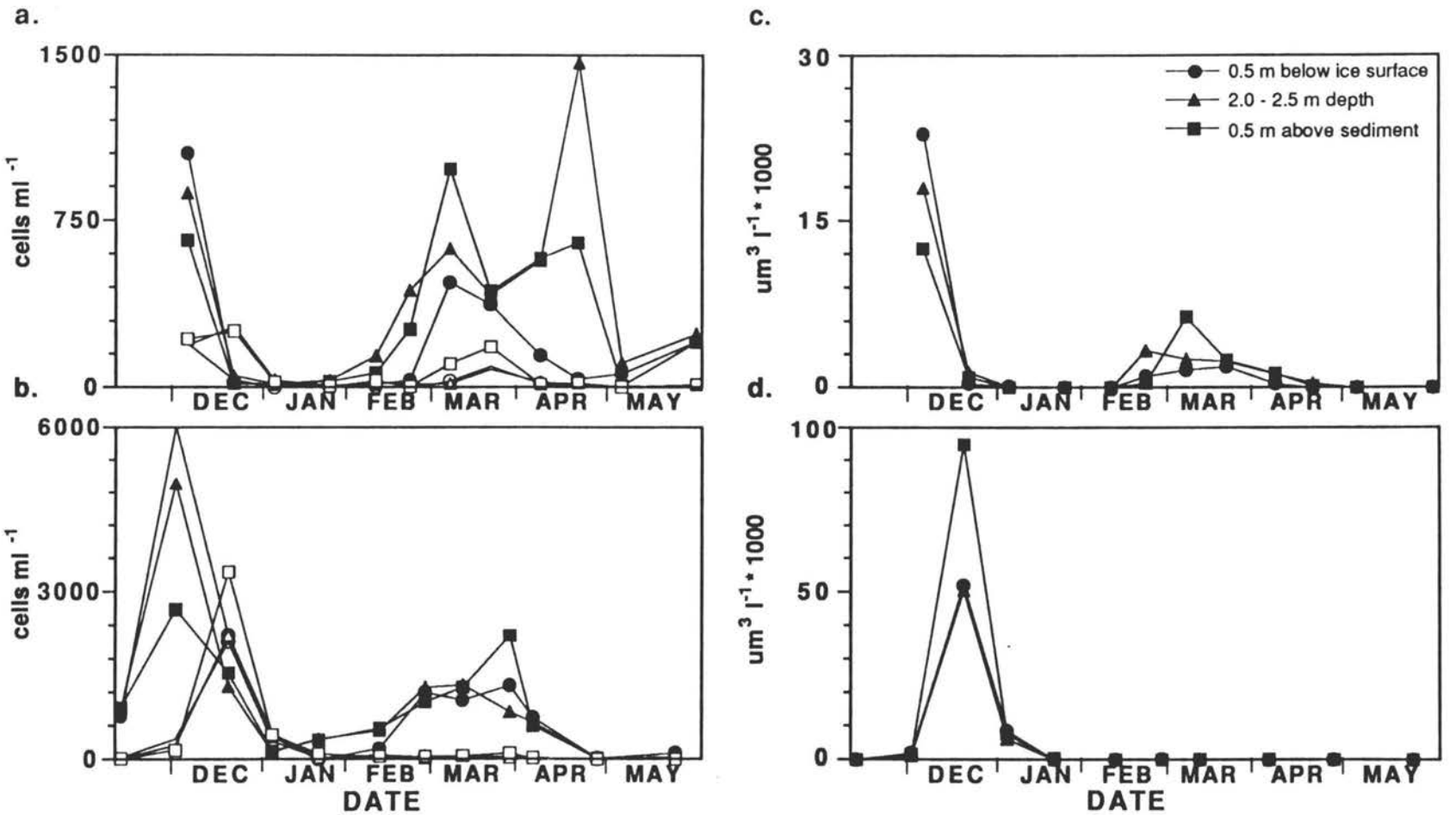


Figure 33. Abundance of live and dead cells of *Asterionella formosa* in The Loch during a) 1987-88 and b) 1988-89; biovolume of fungal chytrid parasites on *A. formosa* and *Ankistrodesmus falcatus* var. *acicularis* during c) 1987-88 and d)1988-89. Note different vertical scales.

A. formosa growth and decline may give some indication of water movement beneath the ice cover.

Concentrations of silica are often limiting to diatoms. Talling (1966) found that an increase in a population of *A. formosa* ended when dissolved silica declined below 0.5 mg l^{-1}. Concentrations of dissolved silica were not measured to be below that level in The Loch (Figure 21). However, there were changes in concentration in silica throughout the winter in both seasons. Without stream inflow and outflow, The Loch can be considered to be a closed system. Changes in concentration of silica can be attributed to uptake by diatoms (assuming constant mineralization rates). A depression in silica concentrations to 1.5 mg l^{-1} occurred in March /April, which was potentially limiting to *A. formosa* growth.

Diatoms were abundant in the early winter. Gaining position in the water column is vital in order for a population to develop. In amictic Antarctic lakes, diatoms are found in benthic littoral regions but not in the stable, stratified pelagic zone (Vincent, 1981; Parker et al., 1982). Without turbulence diatoms are not maintained in suspension for populations to increase in number. There is a question of how much turbulence is necessary for *A. formosa* to remain in suspension. Winter populations of *A. formosa* in a eutrophic Midwest lake were found to be host to epiphytic choanoflagellates that were phototaxic (E.F. Stoermer, personal communication). The flagellates kept the cells in the upper regions of the water column. No such flagellates were found attached to individuals of the *A. formosa* population in The Loch. The midwinter occurrence of diatoms may be tied to turbulence. This is not to say that the minimum in January is indicative of lack of turbulence. Several other processes may alternatively explain the decline. Light is at a minimum in January. Grazing may play a role. Kudoh and Takahashi (1989) determined that *A. formosa* ceased growth as a result of low temperatures in winter under ice cover. Since temperatures in The Loch did not change, temperature was not thought to be a factor. *Asteronella formosa* may have slower

growth rates in winter, but temperature cannot explain the early decline. In addition, fungal chytrid parasites may affect the health of the population.

Chytrids were found to correspond to the first peak in *A. formosa* in both years (Figure 33). The second peak of *A. formosa* did not result in an increase in chytrids. Koob (1966) investigated parasitism of *A. formosa* by a chytrid in Colorado lakes, but found that the diatom population had declined before any evidence of parasitism was found. Three chytrid species were found on *A. formosa* in the English Lake District (Canter and Jaworski, 1978). In culture experiments, chytrids caused the diatom populations to decline to low levels but not become extirpated. In natural communities, fungal epidemics have at times represented a significant factor in the decline of *A. formosa* populations (Canter and Lund, 1968; Sommer, 1987). Canter (1979) reported a wide range of algal groups affected by parasites and revealed the impact on the growth and wane of the phytoplankton.

Chlorophyta

The dynamics of the motile versus the non-motile algae may give some indication of the preferred depths and the ability of species to overcome water currents. Within the division Chlorophyta (green algae) species developed maxima at different times of the season.

Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West was common in the phytoplankton. Although it reached high numerical abundances of over 500 cells ml^{-1} (Appendix I), it is small in volume and did not make up a corresponding percentage of the total biomass (Figure 34). *Ankistrodesmus falcatus* is a narrow, needle-like alga that lacks flagella. It occasionally harbored a parasite, which I believe to be the same chytrid found on *A. formosa*. In 1987-88, *A. falcatus* low in biomass until February. *Ankistrodesmus falcatus* biomass rapidly increased in in December of 1988-89, when light was minimum. The only other alga to increase at this time was the chlorophyte, *Chlorella* spp..

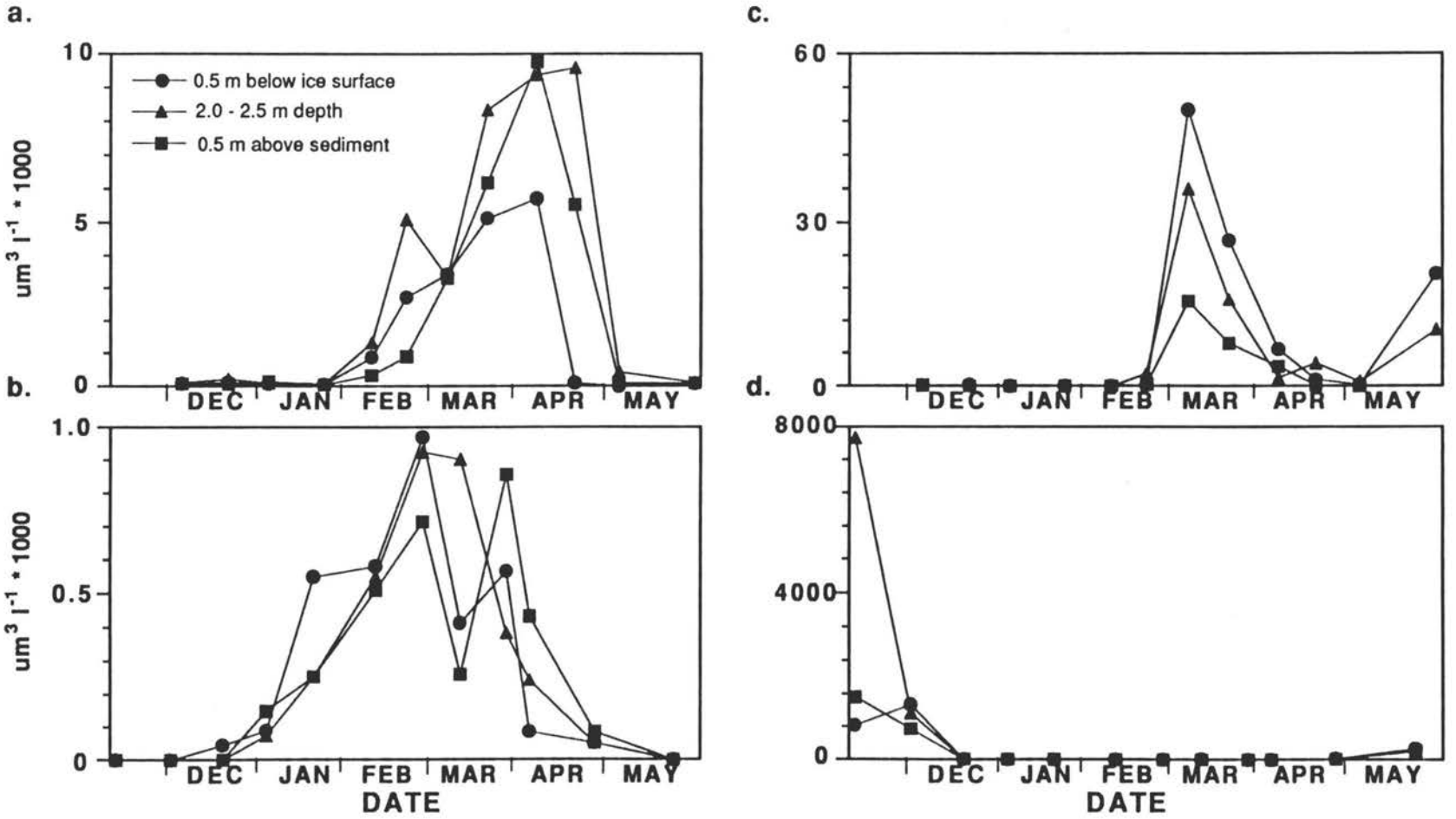


Figure 34. Biovolume of *Ankistrodesmus falcatus* var. *acicularis* in The Loch during a) 1987-88 and b) 1988-89; *Chlamydomonas* sp. during c) 1987-88 and d) 1988-89. Note different vertical scales.

In the first year, *Chlamydomonas* sp. populations peaked in March and increased again after the ice melted (Figure 34). *Chlamydomonas* sp. is a flagellate and has the ability to move vertically within the water column. The peak in March showed a strong differentiation by depth, with cells most abundant at the surface and least abundant in the bottom waters. Such a distribution suggests preference for light, since light is the only resource that decreases with depth. Zooplankton are not likely to have caused such a distribution, because they were also distributed with most organisms at the surface and fewer with increasing depth (Figures 23 and 24). Maximum biomass occurred in November of the 1988-89 season. There were no additional peaks. The population at mid-depth was most numerous. Light may have not been as limiting early in the winter before ice reached maximum thickness and total solar irradiance declined.

Chlorococcum sp. was often distributed by depth despite its lack of motility (Figure 35). It had bimodal peaks in both years, and these occurred at different times of the winter between years. The smaller, spherical *Chlorella* sp. was also distributed by depth. Some algae must be able to overcome water motions and grow at a given depth. Turbulence can be assumed to distribute cells equally within the water column. Water currents are the only way that non-motile algae can reach upper waters from inoculum in the sediments. In order for organisms to become differentially distributed by depth, they must have differential growth or loss rates with depth. Furthermore, these growth or loss rates must be such that they are not obscured by further turbulence. It seems likely that cells in the upper waters had greater growth rates with increased light. Loss may occur due to zooplankton grazing. However, zooplankton were also greatest in the surface waters.

Two other non-motile chlorophytes, *Scenedesmus* sp. and *Coccomyxa dispar* Schmidle did not follow the pattern of differential distribution (Figure 36). *Scenedesmus* sp. had a single maximum in the first year. Furthermore, the organisms were most abundant in the bottom waters. In contrast, in the second year there were low

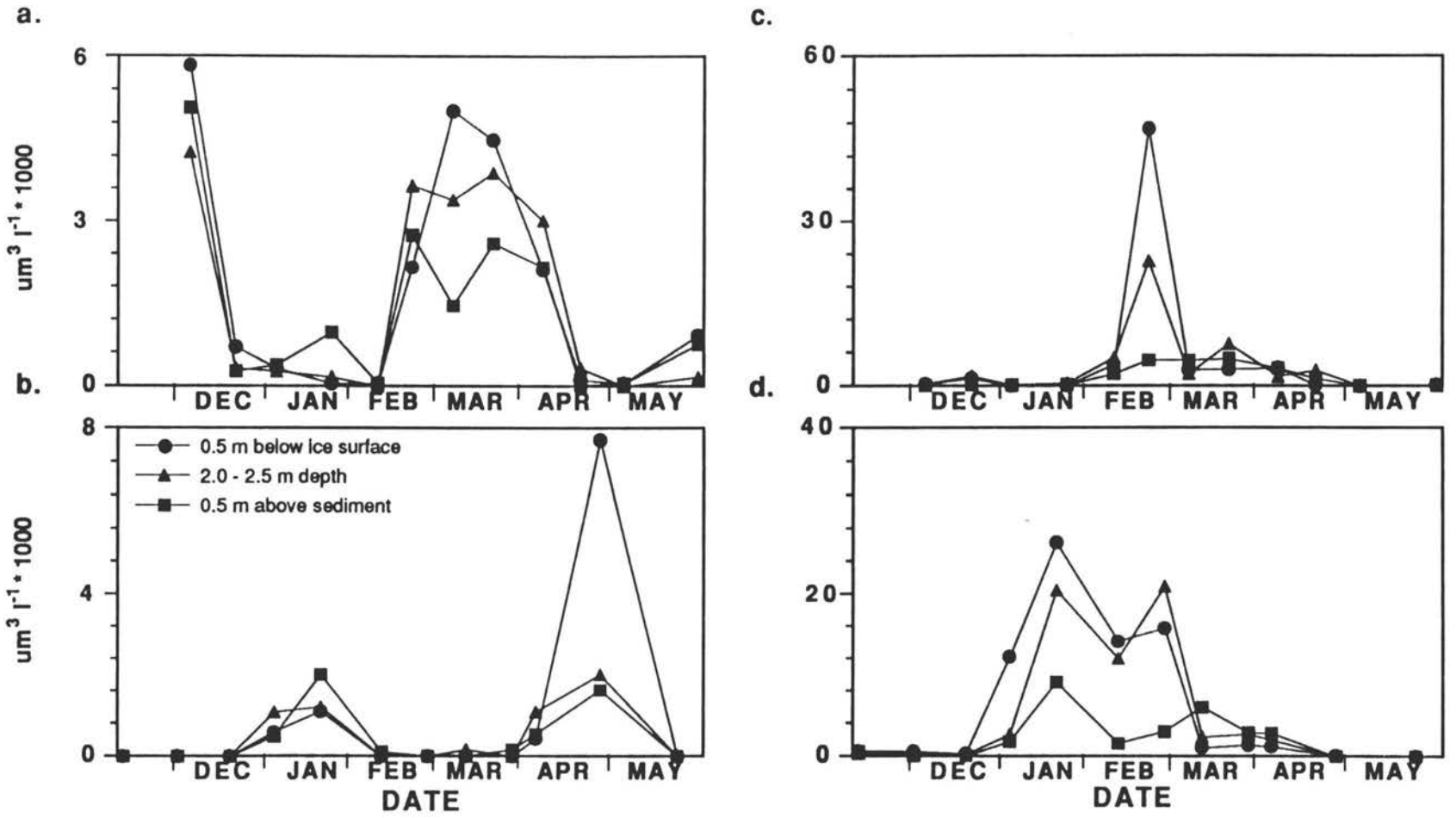


Figure 35. Biovolume of *Chloroccum* sp. in The Loch during a) 1987-88 and b) 1988-89; *Chorella* spp. during c) 1987-88 and d) 1988-89. Note different vertical scales.

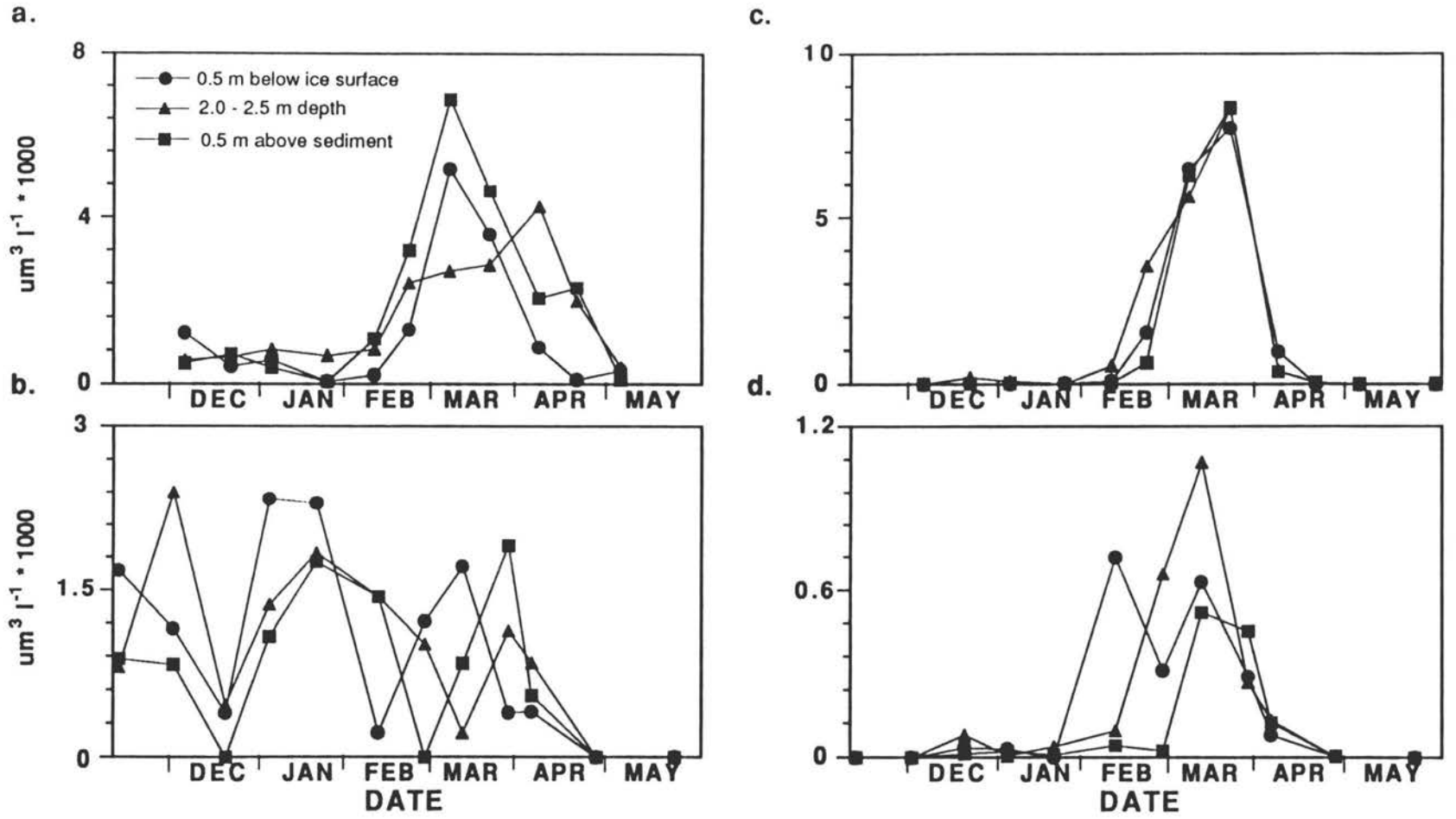


Figure 36. Biovolume of *Scenedesmus* sp. in The Loch during a) 1987-88 and b) 1988-89; *Coccomyxa dispar* during c) 1987-88 and d) 1988-89. Note different vertical scales.

abundances throughout the water column. *Coccomyxa dispar* peaked in mid-March in both years. In the first year, the organisms were distributed homogeneously. Such a pattern did not occur the second year.

Cyanobacteria

Cyanobacteria (blue-green) species are grouped together in Figure 37. The cyanobacteria were primarily composed of spherical and filamentous species (Appendix I). No large colonies were present. Maximum cyanobacteria biomass occurred in February, March, and April of the first year. In the initial stages of the peak, the cells were distributed by depth. Maximum abundance occurred later in the season of the second year and cells were distributed homogeneously in the water column.

Pyrrophyta

The phyrrophytes, or dinoflagellates, were almost exclusively *Peridinium cinctum* (Müll.) Ehrenb. (Figure 37). *P. cinctum* is a large flagellated alga that was an important contributor to the total biomass. *Peridinium cinctum* populations experienced unimodal, sharp maxima in biomass in both years. *P. cinctum* was thought to be nearly inedible by zooplankton (Sommer, 1987). However, in the first year it was often present in the gut of the rotifer *Polyarthra* sp.. Because of its large size and rigid cell walls *P. cinctum* may have simply been more obvious within *Polyarthra.* Other algae may have been unrecognizable because of their more collapsible cell coverings and smaller size.

Chrysophyta

The chrysophytes (golden-brown algae) were composed of the flagellates *Dinobryon* spp., *Mallomonas* spp., and several indeterminate small species. *Dinobryon* made up the majority of the biomass and occurred in sharp maxima in both years (Figure 38). In each of these peaks the cells were strongly stratified by depth. Chrysophytes have been reported to migrate on a diel basis over distances of 0.5 to 2 m (reviewed in Sangren, 1988). Sangren suggested that the phototaxic behavior of

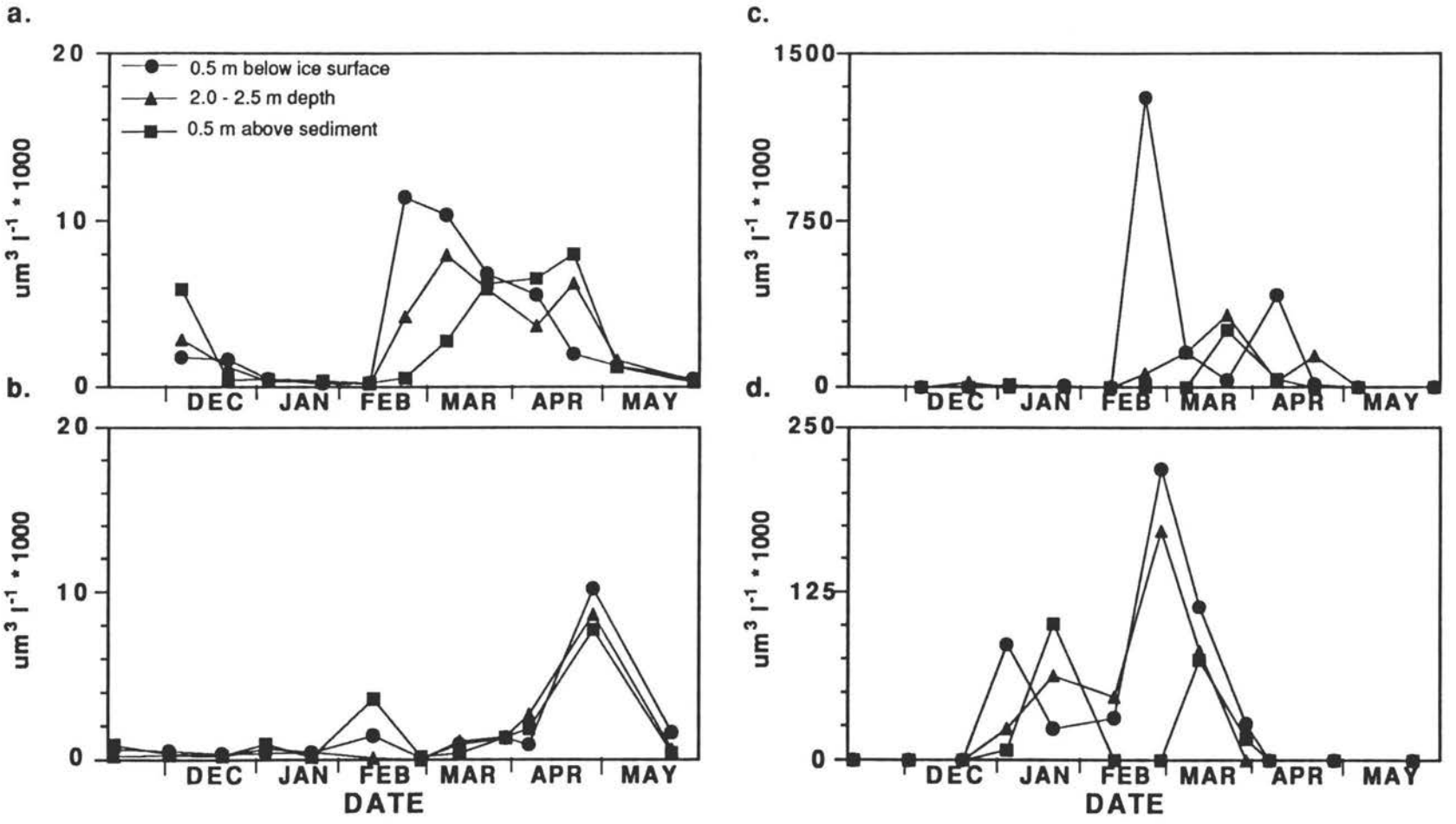


Figure 37. Biovolume of Cyanophyta in The Loch during a) 1987-88 and b) 1988-89; Pyrrophyta during c) 1987-88 and d) 1988-89. Note different vertical scales.

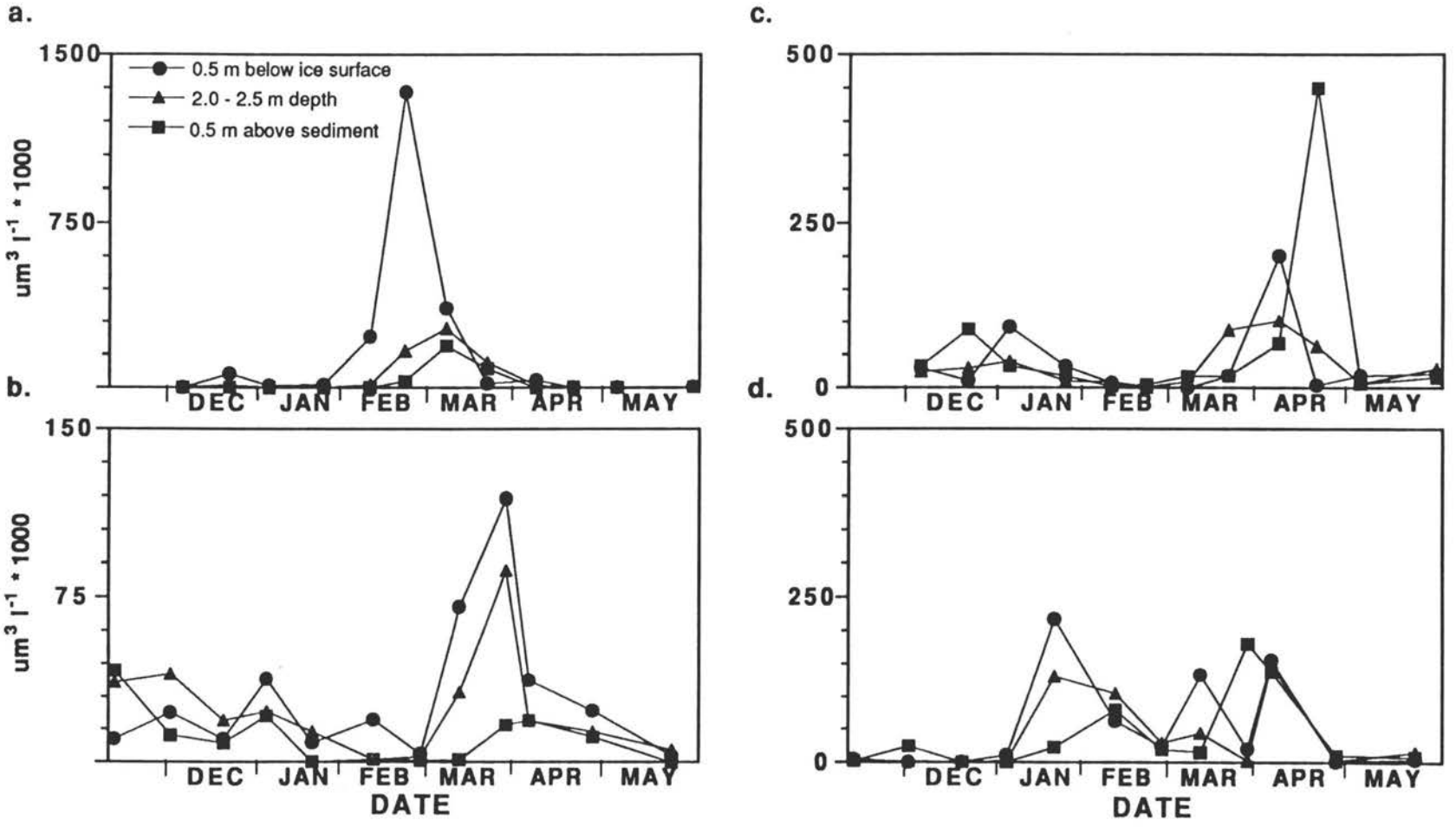


Figure 38. Biovolume of Chrysophyta in The Loch during a) 1987-88 and b) 1988-89; Cryptophyta during c) 1987-88 and d) 1988-89. Note different vertical scales.

chrysophytes is likely to be important to survival. Phototaxic movement (the ability to move toward, or away, from light) allows the organisms maintain themselves in favorable light conditions.

Almost every genus of chrysophyte examined has been found capable of ingesting bacteria, treated beads, or other algae (Sanders and Porter, 1987). Bird and Kalff (1987) showed the magnitude to which *Dinobryon* grazing influenced food webs. *Dinobryon* was found to consume bacteria at rates greater than zooplankton and protozoans. Chrysophytes are considered facultative autotrophs. Temperature, light, DOC, and particle concentration influence the relative importance of phagotrophic versus autotrophic nutrition. Phosphorus concentration shows a remarkable correlation to chrysophyte biogeographical distribution (reviewed in Sangren, 1988). An inverse relation exists between chrysophyte occurrence and nutrient availability. Lehman (1976) investigated this relationship and found that phosphate is not toxic to *Dinobryon*, as some studies suggested. *Dinobryon* was not inhibited by high phosphate concentrations. Rather, *Dinobryon* is efficient at extracting nutrients at low ambient concentrations. Furthermore, increases in temperature were found to cause declines in the populations. *Dinobryon sertularia* was found to be physiologically limited to water temperatures below 20° C.

Cryptophyta

Cryptophytes were often present, but had less distinct patterns of biomass (Figure 38). There was no consistent differentiation by depth and abundances were low. Wright (1964) found that several cryptophyte species were present under ice cover. Two of the *Cryptomonas* species tested in culture grew heterotrophically on acetate at low temperatures. Phagotrophy has been reported in the cryptophytes (reviewed in Klaveness, 1988). Cryptophytes have been found to be one of the more favorable food items to zooplankton (Klaveness, 1988; Sommer, 1987). Other loss processes may be minor compared to grazing in cryptophytes.

Summary

The aquatic habitat under ice cover is not static in The Loch. Rather, the winter season is dynamic in respect to physico-chemical parameters, and the abundance and composition or zooplankton and phytoplankton. Because of The Loch's large surface area to volume ratio, between 40 and 80% of the lake volume becomes frozen. The process of freeze concentration leads to dissolved constituents increasing in concentration in the remaining lakewater. Although not all ions increased significantly, pH, Ca, Na, K, SO_4, and alkalinity showed a significant increase in the water below the ice. Such increases may have an enriching effect on algal growth. The light regime also changes throughout the course of the winter. The fluctuations in light transmitted through the ice surface were attributed more to the changing aspect of the sun rather than ice thickness or sparse snow accumulation. Oxygen concentrations were at a maximum in early winter. A midwinter depression occurred in both years followed by an increase until the ice melted. Oxygen concentrations increased despite a waning algal biomass. The cause for the late winter increase in oxygen was not determined, but may have been due to unmeasured benthic algal growth or inflow of oxygen-rich surface waters. After the ice-cover attained maximum thickness, the concentration of conservative ions remained relatively constant. However, nutrient concentrations varied. Although the pattern of increase and decrease were not consistent between years, there were changes in nitrate concentration. Nitrate values were high in The Loch, as compared to other Colorado high elevation lakes. Although phosphorus may have been limiting to algal growth, it is not likely that nitrate was limiting. Silica concentrations were at minimal in late March/April and then increased in May. The uptake by diatoms, almost exclusively *A. formosa,* is most likely responsible for the decrease. Concentrations of silica did not, however, decline to a level that are likely to be limiting to diatom growth. The increase in May may be due to inflow of melt water, which contained higher concentrations of silica after contact with watershed soils.

Winter zooplankton populations were made up almost exclusively of cyclopoid copepods and rotifers. The abundance of copepods was low, but punctuated by unimodal peaks in the second year of the study. Rotifer abundance was high, and greater than densities reported during the open water period. The patterns of rotifer abundance showed similar sharp unimodal peaks. Maxima of *K. hiemalis* occurred during the algal minimum in January. The increase began after the algal populations had declined, so *K. hiemalis* probably did not cause the algal minimum. *Polyarthra* sp. were the most abundant rotifers and were more closely associated with peaks in algal biomass early in winter. However, a recurrent late winter decline in phytoplankton could not be explained by zooplankton grazing.

The phytoplankton community was dynamic under ice-cover, both in terms of biomass and species composition. The pattern of phytoplankton biomass was consistent between the two years. The pattern can be characterized by an early winter peak, followed by a minimum in January. A second maximum occurred in February / March, followed by a decrease until late May / April, and then a slight increase in May, when the ice melted. The pattern of algal biomass was repeated both years, and it resulted principally from the dynamics of the diatom, *A. formosa* , the most abundant phytoplankter.

Although the same dominant (and most of the rare) taxa were present both years, they varied in time of occurrence and abundance. Chlorophytes, cryptophytes, and cyanobacteria were all important components of the phytoplankton, but they did not occur at the same time in both seasons. An exception is the chrysophyte, *Dinobryon* spp., which was present only in February/March of both seasons. However, *Dinobryon* spp. did vary substantially in abundance between the two years.

The dynamics of the phytoplankton can tentatively be attributed to several factors and their interactions. Each factor probably varied in importance to phytoplankton dynamics throughout the season. Freeze concentration may have caused nutrient

enrichment leading to the algal bloom in early winter. In January, minimum incident light corresponded to an algal minimum. Grazing by the rotifer *Polyarthra* sp. may have played a role in the algal minimum. In addition, *A. formosa* individuals were infected with a large number of fungal chytrids, which may have played a role in the decline of the diatom. In February, biomass increased substantially as the sun was at a higher aspect which decreased surface reflectance on the ice as well as decreased shading by nearby mountain ridges. Total daily radiation increased as daylength increased. Nutrients still available from freeze concentration and more favorable light conditions could have caused the second increase in phytoplankton biomass. Later, light continued to increase, but the planktonic algae declined, possibly indicating a depletion of nutrients in late winter. Alternatively, algae may have been inhibited by light, leading to their decline. Populations were at their lowest abundance in late April / early May. An increase in nutrients may have been brought in by stream inflow causing an increase in biomass as the ice melted.

CONCLUSIONS

The presence of ice-cover creates conditions which differ in several important respects from those prevailing during the open water period. Ice-cover seals the lake from the exchange of atmospheric gases and the mixing action of wind. The stability of the water column is favorable to planktonic algae that are able to maintain position because cells can adapt physiologically to low ambient light conditions. The phytoplankton do not experience a rapidly changing light regime, as occurs in wind mixed lakes. The resulting stability of the water column, however, does not result in stability of phytoplankton and zooplankton populations.

The changes in species composition, or succession, of the phytoplankton is considered to be the result of alternating physical and biologic controls (Sommer, 1987). Light, temperature, and the balance of sinking and resuspension are examples of physical controls. The abiotic environment defines the algal community based on physiological limits. Within these limits, biologic interactions have the capacity to influence the species composition. The availability of nutrient is also considered a biotic interaction because nutrient depletion is usually a consequence of algal consumption. Within The Loch, there are numerous overlapping processes that have potential controlling influence on the phytoplankton. Concentrations of dissolved constituents vary due to freeze concentration. Light impinging on the lake surface changes during the season. Nutrient or mineral deficiencies may occur, leading to competition. Fungal chytrid parasites and zooplankton grazing may influence algal species composition and abundance. It is certain that the importance of these factors alternate with one another and act in a

synergistic manner. There is probably also a stochastic component of the seasonal succession.

The results of this study show that the winter is not a season to be neglected in terms of phytoplankton and zooplankton dynamics. The period of ice-cover encompasses more than half the year in many Colorado high elevation lakes. The Loch is not unusual in its shallow depth and rapid flushing rates in summer, but many subalpine and alpine lakes are considerably deeper and have longer water residence times. Two of the other lakes in the Loch Vale watershed (Glass Lake and Sky Pond) are deeper and have longer residence times. These lakes contain up to ten times the algal abundance of The Loch in summer (McKnight et al., 1988). It is likely that their winter phytoplankton populations are substantial as well.

This study also provides a baseline of dynamics of an algal assemblage in an unacidified lake. If acidification were to occur, it would most likely be detected during the early spring, when the first fraction of melt occurs (Hultberg, 1977; Johanessen and Henriksen, 1978). A pH minimum occurred in The Loch in April / May with pH ranges from 5.7 to 6.1 (Baron and Bricker, 1987). The time of the pH minimum roughly corresponded to the second algal biomass minimum. However, neither biomass nor production are expected to change with acidification (Schindler, 1985). Other factors concurrent with snowmelt most likely play a role in the algal minimum observed in the present study. Increased flushing occurs with snowmelt, which may be more important to inhibiting algal growth than pH. Any future anthropogenic acidification of The Loch would more likely engender changes in phytoplankton species richness, composition, and dominant species (Geelen and Leuven, 1986).

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APPENDIX I

Appendix I. Species list of planktonic algal taxa, protozoans, and chytrid fungi in The Loch. Each value is the number of cells ml^{-1} (some filaments are reported as length, in $\mu m\ ml^{-1}$) found from the mean of three replicate samples and with the standard deviation of the mean in parentheses. (S = 0.5 m below ice surface, M = 2.0 - 2.5 m depth, B = 0.5 m above sediment).

DATE: December 6, 1987

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	201 (83)	193 (1)	221 (67)
Asterionella formosa Hass. (live)	1051 (138)	873 (128)	662 (68)
indeterminate Pennales	-	-	2
Synedra sp.	10	10 (2)	4
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	6 (2)	8 (3)	6
Chlamydomonas sp.	3 (3)	2	4 (1)
Chlorella ellipsoidea Gerneck	51 (50)	23 (10)	-
Chlorella vulgaris Beyerinck	-	33 (33)	-
Chlorella sp.	-	-	13 (12)
Chlorococcum sp.	108 (47)	79 (30)	94 (54)
Coccomyxa dispar Schmidle	1	15 (20)	4
Scenedesmus sp.	34 (11)	16 (9)	14 (3)
indeterminate flagellates	-	3	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	3	2	1
Kephryion sp.	-	1	-
Mallomonas sp.	-	1	-
indeterminate flagellates	5	10	4
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	9	8 (7)	14 (7)
Rhodomonas sp. 1	58 (20)	33 (24)	21 (15)
Rhodomonas sp. 2	16	26(14)	26 (22)
Rhodomonas sp. 3	4	3	-
indeterminate flagellates	139	89 (65)	55 (49)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	260 (96)	138 (76)	125 (51)
Chroococcus minimus (Keissel.)Lemm.	31	26 (37)	7
Chroococcus sp.	55 (48)	20 (34)	11
Merismopedia sp.	3	-	5
Oscillatoria sp.	1119 (497)	2355 (870)	634 (61)

Appendix I. continued

DATE: December 6, 1987 continued

TAXA	S	M	B
CYANOBACTERIA			
Phormidium sp.	-	49 (42)	72 (66)
Rhabdoderma sp.	-	3	-
Synechoccus sp.	-	-	5
indeterminate cyanobacteria	-	2	-
PYRROPHYTA			
cyst	3	-	-
PROTOZOA			
indeterminate ciliates	3	9 (3)	6
CHYTRID FUNGI	570 (278)	449 (57)	312 (176)

Appendix I. continued

DATE: December 22, 1987

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	36 (15)	275	256 (35)
Asterionella formosa Hass. (live)	22 (7)	53	19 (20)
Navicula sp.	-	-	1
Synedra sp.	8 (3)	15	2
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	8 (7)	15	5 (2)
Chlamydomonas sp.	4	-	-
Chlorella ellipsoidea Gerneck	-	9	2
Chlorella vulgaris Beyerinck	-	228	30 (21)
Chlorella sp.	180 (144)	-	-
Chlorococcum sp.	13 (8)	6	5 (6)
Coccomyxa dispar Schmidle	23 (34)	201	25 (31)
Scenedesmus sp.	12	18	20 (14)
Selenastrum sp.	-	3	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	291 (58)	62	6 (3)
Kephryion sp.	2	-	-
Mallomonas sp.	1	-	-
indeterminate flagellates	43 (16)	9	-
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	2	12	39 (17)
Rhodomonas sp. 1	51 (44)	-	-
Rhodomonas sp. 2	1	3	-
Rhodomonas sp. 3	1	-	-
indeterminate flagellates	36	299	227 (114)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	184 (112)	-	-
Chroococcus minimus (Keissel.)Lemm.	7	-	8 (9)
Chroococcus sp.	84 (83)	461	187 (53)
Dactylococcopsis sp.	2	12	1
Oscillatoria sp.	54 (94)	-	-
Rhabdoderma sp.	-	21	-
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	-	3	-
PROTOZOA			
indeterminate ciliates	2	-	-
CHYTRID FUNGI	9 (8)	35	25 (14)

Appendix I. continued

DATE: January 5, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	-	35 (17)	25 (13)
Asterionella formosa Hass. (live)	14	17	18 (13)
Navicula sp.	-	-	1
Synedra sp.	1	6 (7)	-
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	6	7 (8)	10 (9)
Chlamydomonas sp.	-	1	-
Chlorella sp.	6	33 (11)	20 (8)
Chlorococcum sp.	6	5 (6)	7 (4)
Coccomyxa dispar Schmidle	15	67 (58)	28 (22)
Scenedesmus sp.	16	23 (5)	11 (11)
Selenastrum sp.	-	1	1
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	49	13 (6)	3
indeterminate flagellates	-	-	3
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	50	19 (5)	13 (11)
Rhodomonas sp.	24	7 (7)	6
indeterminate flagellates	15	156 (92)	261 (110)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	228	152 (73)	217 (30)
Dactylococcopsis sp.	-	27 (47)	1
Phormidium sp. ?	7	2	8
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	5	-	-
CHYTRID FUNGI	3	2	-

Appendix I. continued

DATE: January 24, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	1	11 (7)	6 (6)
Asterionella formosa Hass. (live)	1	34 (10)	29 (11)
Melosira sp.	-	-	5
Synedra sp.	-	2	3
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	4 (5)	6 (2)	3
Chlorella ellipsoidea Gerneck	-	1	1
Chlorella vulgaris Beyerinck	17 (5)	71 (45)	-
Chlorococcum sp.	1	3	18 (31)
Coccomyxa dispar Schmidle	20 (10)	10 (3)	11 (7)
Scenedesmus sp. 1	2	19 (6)	10 (8)
Scenedesmus sp. 2	-	-	2
Selenastrum sp.	-	2	1
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	26 (3)	5 (2)	-
indeterminate flagellates	212 (144)	18 (13)	16 (13)
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	18 (3)	3	9 (4)
Rhodomonas sp.	9 (13)	-	4 (2)
indeterminate flagellates	2	122 (30)	59 (27)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	79 (22)	107 (17)	114 (47)
Chroococcus minimus (Keissel.)Lemm.	24 (12)	27 (18)	59 (22)
Chroococcus sp.	4	-	1
Phormidium sp.	-	23 (9)	24 (15)
Rhabdoderma sp.	12 (21)	-	-
Synechoccus sp.	-	-	4
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	1	-	-

Appendix I. continued

DATE: February 2, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	3 (3)	23 (19)	32
Asterionella formosa Hass. (live)	16 (6)	144 (14)	68
Melosira sp.	8	-	4
Navicula sp.	2	5	4
Synedra sp.	-	4	1
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	59 (3)	90 (30)	23 (12)
Chlorella vulgaris Beyerinck	-	698 (350)	297 (94)
Chlorococcum sp.	1	-	1
Coccomyxa dispar Schmidle	71	42 (55)	37 (12)
Scenedesmus sp.	6	23 (14)	30 (6)
Selenastrum sp.	2	-	-
indeterminate flagellates	1	-	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	1078 (73)	70 (52)	3
Mallomonas sp.	1	-	-
indeterminate flagellates	8 (2)	1	2
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	4	5	1
Rhodomonas sp.	4	1	1
indeterminate flagellates	5 (5)	7 (10)	16 (6)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	116 (20)	56 (11)	68 (26)
Chroococcus minimus (Keissel.)Lemm.	4	-	-
Lyngbya sp. ?	-	31 (27)	40 (27)
Phormidium sp.	4	-	-
Synechoccus sp.	2	-	1
PROTOZOA			
indeterminate ciliates	-	6 (6)	4
CHYTRID FUNGI	-	3	-

Appendix I. continued

DATE: February 21, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	-	17 (29)	4
Asterionella formosa Hass. (live)	35 (21)	437 (138)	264 (136)
indeterminate Pennales	-	18 (31)	-
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	183 (33)	343 (73)	61 (26)
Chlamydomonas sp. 1	7	25	6
Chlamydomonas sp. 2	-	25	-
Chlorella sp.	6497 (2311)	3131 (651)	649 (124)
Chlorococcum sp.	40 (24)	68 (52)	51 (20)
Coccomyxa dispar Schmidle	1538 (294)	3538 (606)	648 (166)
Crucigenia quadrata Morren	-	-	2
Scenedesmus sp.	36 (31)	67 (58)	89 (15)
Staurastrum sp.	-	-	2
Ulothrix sp.	-	42 (73)	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	6007 (2169)	231 (63)	34 (32)
indeterminate flagellates	62 (17)	237 (321)	47 (14)
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	4	9 (16)	34 (7)
Rhodomonas sp.	36 (34)	-	-
indeterminate flagellates	-	-	4
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	5083 (1244)	1732 (761)	143 (71)
Chroococcus minimus (Keissel.)Lemm.	44 (41)	237 (321)	247 (77)
Chroococcus sp.	86	76 (132)	8
Gloeothece sp.	7	-	-
Synechoccus sp.	-	68	2
indeterminate	4	34 (59)	-
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	169 (43)	8	4
CHYTRID FUNGI	26 (26)	85 (14)	10

Appendix I. continued

DATE: March 6, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	29 (39)	19	110 (83)
Asterionella formosa Hass. (live)	472 (105)	624 (184)	984 (258)
Navicula sp.	-	-	5
Synedra sp.	5	-	5
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	231 (61)	224 (31)	221 (81)
Chlamydomonas sp.	1079 (206)	775 (266)	339 (195)
Chlorella ellipsoidea Gerneck	5	-	15 (25)
Chlorella sp.	397 (317)	297 (22)	622 (209)
Chlorococcum sp.	93 (81)	63 (59)	27 (21)
Coccomyxa dispar Schmidle	4622 (2026)	4025 (886)	4473 (1135)
Scenedesmus sp.	144 (56)	63 (55)	191 (26)
Selenastrum sp.	105 (49)	54 (31)	5
Ulothrix sp.	-	11	278 (480)
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	1813 (557)	1350 (395)	957 (361)
indeterminate flagellates	61	33	49
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	-	5	10
indeterminate flagellates	-	9 (8)	10
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	1526 (956)	989 (370)	973 (408)
Chroococcus limneticus Lemm.	-	-	9
Chroococcus minimus (Keissel.)Lemm.	176 (128)	29 (29)	108
Chroococcus sp.	47 (44)	5	44 (54)
Oscillatoria sp.	-	50µm	161µm
Synechoccus sp.	134 (114)	44 (15)	124 (167)
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	24 (22)	24 (9)	-
PROTOZOA			
indeterminate ciliates	43 (53)	19 (17)	15
CHYTRID FUNGI	66 (32)	107 (31)	262

Appendix I. continued

DATE: March 20, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	97 (46)	83 (33)	185
Asterionella formosa Hass. (live)	375 (126)	419 (136)	434
Synedra sp.	-	-	5
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	336 (172)	546 (161)	405 (17)
Chlamydomonas sp. 1	599 (88)	395 (59)	195 (112)
Chlamydomonas sp. 2	68 (66)	-	-
Chlorogonium sp.	-	5	-
Chlorella ellipsoidea Gerneck	10	-	-
Chlorella sp.	375 (163)	975 (279)	634 (286)
Chlorococcum sp.	83 (45)	73 (64)	49 (51)
Coccomyxa dispar Schmidle	4294 (1154)	4620 (804)	4645 (705)
Scenedesmus sp.	98 (17)	78 (17)	127 (17)
Selenastrum sp.	24 (22)	20 (8)	49 (22)
Ulothrix sp.	-	10	-
indeterminate flagellates	-	-	59 (51)
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	98 (17)	706 (132)	541 (53)
indeterminate flagellates	102	40	35
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	10	49 (34)	10
Rhodomonas sp.	5	-	5
indeterminate flagellates	15 (16)	-	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	1866 (220)	1613 (142)	1745 (491)
Chroococcus minimus (Keissel.)Lemm.	180 (138)	170 (195)	68 (66)
Lyngbya sp. ?	-	5	-
Synechoccus sp.	49 (37)	93 (66)	25 (17)
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	5	49 (22)	39 (22)
PROTOZOA			
indeterminate ciliates	5	20 (8)	20
CHYTRID FUNGI	78 (52)	98 (47)	102 (39)

Appendix I. continued

DATE: April 6, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	19 (33)	25 (20)	15 (4)
Asterionella formosa Hass. (live)	146 (125)	571 (99)	580 (94)
Synedra sp.	-	2	2
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	331 (95)	542 (149)	565 (11)
Chlamydomonas sp. 1	180 (139)	38 (14)	16
Chlamydomonas sp. 2	-	2	81 (53)
Chlorella vulgaris Beyerinck	-	-	272 (72)
Chlorella sp.	268 (55)	148 (41)	-
Chlorococcum sp.	39 (22)	56 (4)	40 (7)
Coccomyxa dispar Schmidle	609 (348)	252 (175)	238 (17)
Scenedesmus sp.	24 (42)	117 (61)	56 (46)
Selenastrum sp.	19 (29)	29 (22)	9 (7)
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	297 (175)	101 (24)	-
indeterminate flagellates	15 (25)	6	2
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	107	56 (53)	36 (4)
Rhodomonas sp. 1	53	20 (18)	11 (3)
Rhodomonas sp. 2	5	-	2
Rhodomonas sp. 3	10	-	-
indeterminate flagellates	10	7	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	522 (266)	427 (112)	810 (133)
Chroococcus minimus (Keissel.)Lemm.	-	36 (21)	99 (56)
Chroococcus sp.	153 (74)	47 (51)	11
Merismopedia sp.	88	-	67
Oscillatoria sp.	112	-	-
Phormidium sp.	34	-	-
Rhabdoderma sp.	5	5 (4)	-
Synechoccus sp.	29	7	5
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	78 (78)	5 (4)	7
PROTOZOA			
indeterminate ciliates	10	13 (7)	11 (8)
indeterminate flagellates	507 (185)	70 (63)	182
CHYTRID FUNGI	15	50 (43)	52 (20)

Appendix I. continued

DATE: April 19, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	1	13 (7)	20 (18)
Asterionella formosa Hass. (live)	38 (16)	1466 (196)	650 (96)
Navicula sp.	1	-	-
Synedra sp.	-	-	2
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	6 (4)	556 (232)	321 (85)
Chlamydomonas spp.	31	90	5
Chlorella sp.	16 (10)	238 (61)	108 (18)
Chlorococcum sp.	4 (1)	27 (24)	2
Coccomyxa dispar Schmidle	4 (1)	40 (14)	45 (20)
Scenedesmus sp.	3 (3)	54 (24)	63 (34)
Selenastrum sp.	2	7	2
Stichococcus sp.	4	9	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	12 (8)	40 (47)	29 (10)
indeterminate flagellates	11	15	42
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	1	33 (17)	243 (81)
Rhodomonas sp. 1	10 (5)	61 (18)	227 (107)
indeterminate flagellates	30	70	125
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	240 (68)	774 (260)	1002 (362)
Chroococcus minimus (Keissel.)Lemm.	-	58 (28)	144 (121)
Merismopedia sp.	3	9	13
Oscillatoria sp.	4	-	52
Phormidium sp.	7	67 (82)	12 (36)
Rhabdoderma sp.	77 (35)	-	-
Synechoccus sp.	17	-	15 (12)
indeterminate filaments	13	-	-
indeterminate coccoid cells	-	2	-
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	3	27	-
PROTOZOA			
indeterminate ciliates	46 (3)	259 (167)	479 (48)
indeterminate flagellates	-	49 (62)	27 (35)
CHYTRID FUNGI	-	17 (14)	7

Appendix I. continued

DATE: May 4, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	8 (10)	1	1
Asterionella formosa Hass. (live)	62 (3)	112 (43)	7
indeterminate Pennales	-	-	1
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	-	25 (2)	6 (3)
Chlamydomonas sp. 1	8 (3)	3	1
Chlamydomonas sp. 2	-	20 (16)	-
Chlorella sp.	1	3	4
Chlorococcum sp.	1	-	1
Chlorogonium sp.	-	1	-
Coccomyxa dispar Schmidle	-	1	2
Scenedesmus sp.	9 (3)	11 (6)	3
Selenastrum sp.	4	1	-
Stichococcus sp.	4	3	-
Ulothrix sp.	-	46 (70)	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	1	7	3
Mallomonas sp.	4	12	4
indeterminate flagellates	15	19	26
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	5	-	1
Rhodomonas sp. 1	107 (18)	165 (37)	72 (27)
Rhodomonas sp. 2	4 (1)	1	4 (1)
indeterminate flagellates	86	41 (14)	36 (5)
CYANOBACTERIA			
Anabaena sp.	2	-	-
Arthrospira gomontiana Setchell	-	1	-
Chroococcus dispersus (Keissel.)Lemm.	289 (50)	349 (35)	295 (91)
Chroococcus minimus (Keissel.)Lemm.	5 (6)	1	-
Dactylococcopsis sp.	2	1	-
Merismopedia sp.	4	-	-
Oscillatoria sp.	132 (27)	124 (121)	45
Phormidium sp.	-	84 (104)	48
Rhabdoderma sp.	101 (64)	58 (101)	18 (18)
Synechoccus sp.	25 (25)	9 (9)	6 (9)
indeterminate coccoid cells	1	-	-
PROTOZOA			
indeterminate ciliates	74 (44)	130 (23)	42 (14)

Appendix I. continued

DATE: May 30, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	-	13 (8)	13
Asterionella formosa Hass. (live)	208 (38)	243 (33)	205
Cocconeis sp.	2	-	-
Eunotia sp.	-	-	1
Fragilaria sp.	-	4	-
Meridion sp.	2	1	5
indeterminate Pennales	2	1	4
Synedra sp.	1	2	-
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	5 (3)	7 (2)	6
Chlamydomonas sp.	527 (76)	319 (74)	275
Chlamydomonas nivalis (Bav.) Wille	4	-	-
Chlorella sp.	21	10 (12)	12
Chlorococcum sp.	17 (16)	3 (5)	14
Chlorogonium sp.	55 (20)	70 (14)	116
Netrium sp.	11 (9)	5	1
Scenedesmus sp.	27 (14)	36 (18)	18
Selenastrum sp.	199 (63)	215 (21)	122
Stichococcus sp.	27 (5)	30 (11)	26
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	19 (6)	13	18
Mallomonas sp. 1	3	-	-
Mallomonas sp. 2	-	1	-
indeterminate flagellates	25	21	20
CRYPTOPHYTA			
Rhodomonas sp. 1	108 (46)	89 (17)	62
Rhodomonas sp. 2	23 (10)	34 (7)	51
Rhodomonas sp. 3	60 (11)	57 (14)	29
indeterminate flagellates	236	386	208
CYANOBACTERIA			
Arthrospira gomontiana Setchell	21	4	-
Chroococcus dispersus (Keissel.)Lemm.	114 (20)	96 (26)	75
Merismopedia sp.	1	-	-
Oscillatoria sp.	21	-	22
Phormidium sp.	1	7	-
Rhabdoderma sp.	31 (29)	46 (79)	-
Synechoccus sp.	7 (5)	1	10
PROTOZOA			
indeterminate ciliates	9 (8)	5	1

Appendix I. continued

DATE: November 13, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass.	774 (692)	922 (577)	938 (200)
Synedra sp.	-	6 (10)	12 (20)
CHLOROPHYTA			
Chlamydomonas sp. 1	8310 (2792)	76100 (30000)	15104 (12000)
Chlamydomonas sp. 2	-	98 (50)	-
Chlamydomonas sp. 3	-	6 (9)	-
Chlorella vulgaris Beyerinck	24 (40)	16 (9)	24
Gonium sp.	92 (160)	46	-
Scenedesmus sp.	46 (40)	22 (20)	24
indeterminate flagellates	-	-	34
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	-	108 (49)	34
Dinobryon sp.	-	-	12 (10)
Kephryion sp.	-	-	92 (40)
indeterminate flagellates	266 (72)	334	174 (31)
CRYPTOPHYTA			
Rhodomonas sp. 1	-	6	12 (10)
Rhodomonas sp. 2	-	12 (20)	-
indeterminate flagellates	128 (40)	132 (29)	46 (20)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	24 (40)	70	92 (44)
Chroococcus sp.	58 (100)	-	-
Oscillatoria limnetica Lemm.	-	-	590 (335)
indeterminate filament	116 (200)	-	-
PROTOZOA			
indeterminate ciliates	-	-	70 (35)

Appendix I. continued

DATE: December 2, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	6019 (711)	4964 (784)	2691 (1233)
Synedra sp.	35 (35)	10	6
CHLOROPHYTA			
Chlamydomonas sp. 1	13200 (400)	11214 (1453)	7511 (2527)
Chlamydomonas sp. 2	-	68 (64)	52 (18)
Chlorella vulgaris Beyerinck	40 (20)	28 (21)	6
Chlorococcales	-	6	-
Coccomyxa dispar Schmidle	11	-	-
Gonium sp.	6	10	-
Scenedesmus sp.	32	67 (35)	23 (20)
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	-	64 (82)	11 (10)
Dinobryon sertularia Ehrenb.	69 (18)	50 (35)	6
Dinobryon sp.	35 (18)	65 (39)	40 (27)
statospores	6	47	-
Mallomonas sp.	-	6	-
indeterminate flagellates	6	27 (32)	-
CRYPTOPHYTA			
Cryptomonas sp.	-	6	-
Rhodomonas sp.	-	11	-
indeterminate flagellates	11	22	29 (20)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	162 (118)	28 (26)	40 (56)
Chroococcus sp.	11	-	-
Oscillatoria sp.	162	177	301
indeterminate filaments	-	58	-
PROTOZOA			
indeterminate ciliates	23 (27)	17	52 (17)
indeterminate flagellate sp. 1	689 (315)	91 (30)	92 (40)
indeterminate flagellate sp. 2	6	-	46 (36)
CHYTRID FUNGI	87 (30)	51 (19)	69 (60)

Appendix I. continued

DATE: December 20, 1988

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	2230 (330)	1313 (302)	1551 (437)
Synedra sp.	14 (13)	6	6
CHLOROPHYTA			
Actinotaenium sp.	3	-	-
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	3	-	-
Chlamydomonas sp. 1	127 (80)	79 (70)	41 (10)
Chlamydomonas sp. 2	45 (18)	39 (27)	46 (20)
Chlorella vulgaris Beyerinck	23 (26)	17 (16)	6
Coccomyxa dispar Schmidle	25 (26)	57 (71)	10 (9)
Scenedesmus sp.	11	13	-
indeterminate flagellates	-	-	6
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	3	13	-
Dinobryon sertularia Ehrenb.	3	-	6
Dinobryon sp.	3	9 (2)	6
Mallomonas sp.	-	8	-
statospores	-	-	6
indeterminate flagellates	3	-	-
CRYPTOPHYTA			
Cryptomonas sp.	8 (9)	3	-
indeterminate flagellates	3	4	11
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	28 (10)	59 (34)	46
Chroococcus minimus (Keissel.)Lemm.	-	8	-
Chroococcus sp.	40 (35)	42 (47)	29
Phormidium sp. ?	70	69	-
PROTOZOA			
indeterminate ciliates	14 (13)	10 (9)	46
indeterminate flagellates	14 (10)	26 (9)	12
CHYTRID FUNGI	2131 (677)	2069 (852)	3889 (321)

Appendix I. continued

DATE: January 4, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	411 (114)	129 (26)	157 (71)
Melosira sp.	-	-	4
indeterminate Pennales	-	1	-
Synedra sp.	3	27	7 (7)
CHLOROPHYTA			
Actinotaenium sp.	3	1	-
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	6	5	10 (5)
Chlamydomonas sp. 1	25 (17)	3	7
Chlamydomonas sp. 2	34 (9)	159 (43)	153 (35)
Chlorella vulgaris Beyerinck	844 (312)	182 (59)	125 (38)
Chlorococcum sp.	11	20 (13)	9
Coccomyxa dispar Schmidle	23 (10)	5 (5)	10 (3)
Scenedesmus sp.	65 (69)	38 (11)	30 (5)
indeterminate flagellates	-	7	1
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	3	-	3
Dinobryon sertularia Ehrenb.	17	13 (5)	3
Dinobryon sp.	5	3	-
indeterminate flagellates	-	-	1
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	6	13	3
Rhodomonas sp.	11	4	1
indeterminate flagellates	-	4	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	138 (100)	232 (66)	297 (106)
Chroococcus minimus (Keissel.)Lemm.	-	-	3
Chroococcus sp.	48	44 (16)	30 (5)
Lyngbya limnetica Lemm.	-	24 (28)	63 (63)
Oscillatoria sp.	-	-	3
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	11	3	1
PROTOZOA			
indeterminate ciliates	11 (5)	11 (11)	7
indeterminate flagellates	62 (13)	38 (11)	38 (22)
CHYTRID FUNGI	217 (26)	158 (94)	193 (85)

Appendix I. continued

DATE: January 20, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	-	372 (103)	353 (71)
Synedra sp.	8 (8)	-	8
CHLOROPHYTA			
Actinotaenium sp.	-	3	-
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	37 (21)	17	17 (6)
Chlamydomonas sp.	-	45 (44)	130 (41)
Chlorella vulgaris Beyerinck	1819 (554)	1416 (137)	629 (134)
Chlorococcum sp.	20 (5)	22 (21)	37 (32)
Coccomyxa dispar Schmidle	-	28 (10)	7
Scenedesmus sp.	64 (50)	51 (61)	49
indeterminate flagellates	-	3	-
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	3	-	-
Dinobryon sp.	20	22 (5)	-
Kephryion sp.	8 (9)	3	-
indeterminate flagellates	79 (25)	-	6
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	121 (124)	73 (56)	13 (9)
Rhodomonas sp.	11	6	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	191 (25)	166 (140)	7
Chroococcus sp.	-	51 (61)	23
Lyngbya sp.	11	-	11
Oscillatoria sp.	8	-	53
Rhabdoderma sp.	-	11	4
indeterminate filament	-	-	6
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	3	8	13
PROTOZOA			
indeterminate ciliates	17 (9)	14	9
CHYTRID FUNGI	-	-	10

Appendix I. continued

DATE: February 10, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	192 (106)	523 (155)	561 (251)
Synedra sp.	-	-	4
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	39	37 (5)	34 (12)
Chlamydomonas sp. 1	4	-	-
Chlamydomonas sp. 2	4	19 (10)	-
Chlorella vulgaris Beyerinck	977 (350)	828 (214)	110 (251)
Chlorococcales	3	-	-
Chlorococcum sp.	-	-	2
Coccomyxa dispar Schmidle	511 (280)	68 (26)	31
Scenedesmus sp.	6	40 (35)	17 (25)
indeterminate flagellates	4	3	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	43	6	50
Kephryion sp.	24 (12)	-	-
Mallomonas sp.	4	-	2
indeterminate flagellates	15 (18)	-	-
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	35 (30)	59 (30)	45 (11)
indeterminate flagellates	6	5	8
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	103 (53)	56 (18)	-
Chroococcus turgidus (Kütz.) Naeg.	6	-	-
Dactylococcoposis sp.	12	-	6
Phormidium sp. ?	-	-	69
indeterminate filament	-	-	17
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	4	6	-
PROTOZOA			
indeterminate ciliates	7	3	-

Appendix I. continued

DATE: February 26, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	1194 (139)	1286 (286)	1030 (519)
CHLOROPHYTA			
Actinotaenium sp.	-	3	-
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	65 (43)	62 (6)	48 (34)
Chlorella vulgaris Beyerinck	1087 (208)	1449 (373)	209 (91)
Coccomyxa dispar Schmidle	222	469 (362)	17 (18)
Scenedesmus sp.	34 (29)	28 (10)	-
Sphondylosium sp.	6	-	-
indeterminate flagellates	-	3	-
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	11	-	-
Kephryion sp.	14 (5)	11	-
Mallomonas sp.	-	-	8
indeterminate flagellates	-	-	3
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	14 (5)	17 (9)	11
indeterminate flagellates	6	-	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	42 (45)	-	17
Dactylococcoposis sp.	14 (5)	3	-
Phormidium sp. ?	-	-	52
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	28 (26)	22	-
CHYTRID FUNGI	6	3	-

Appendix I. continued

DATE: March 11, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	1057 (86)	1326 (182)	1289 (383)
indeterminate Pennales	3	-	-
Synedra sp.	-	-	3
CHLOROPHYTA			
Actinotaenium sp.	2	-	-
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	27 (6)	59 (55)	17 (15)
Chlamydomonas sp. 1	131 (69)	42 (34)	11
Chlamydomonas sp. 2	13 (6)	11 (5)	8
Chlorella ellipsoidea Gerneck	57 (92)	-	-
Chlorella vulgaris Beyerinck	11	152 (51)	389 (128)
Chlorococcales	19	20 (21)	-
Chlorococcum sp.	-	3	-
Coccomyxa dispar Schmidle	287 (199)	487 (148)	236 (128)
Scenedesmus sp.	47 (27)	6	23 (10)
Selenastrum *sp.*	-	-	3
Ulothrix sp.	-	3	-
indeterminate flagellates	-	83	-
indeterminate filament	11µm	-	14 µm
CHRYSOPHYTA			
Dinobryon bavaricum ? Imhof	4	-	-
Dinobryon sertularia Ehrenb.	242 (68)	129 (61)	3
Kephryion sp.	19 (9)	31 (18)	-
Mallomonas sp.	-	-	3
indeterminate flagellates	5	17 (17)	5
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	74 (31)	25 (14)	90 (27)
indeterminate flagellates	28 (27)	8 (9)	3
CYANOBACTERIA			
Anacystis sp.	-	14 (13)	11 (5)
Chroococcus dispersus (Keissel.)Lemm.	299 (5)	455 (108)	147 (64)
Chroococcus minimus (Keissel.)Lemm.	-	14	-
Dactylococcoposis sp.	-	20 (5)	3
Gleothece sp.	34	-	-
Lyngbya sp. ?	59	6	11
Synechoccus sp.	-	-	3
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	16 (10)	12	11 (5)
Peridinium sp.	2	-	-
PROTOZOA			
indeterminate ciliates	27 (6)	3	3
CHYTRID FUNGI	-	-	5

Appendix I. continued

DATE: March 27, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	1317 (157)	853 (47)	2216 (248)
indeterminate Centrales	3	-	-
Navicula sp.	-	-	3
Synedra sp.	-	-	3
CHLOROPHYTA			
Actinotaenium sp.	-	-	3
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	37 (27)	25 (9)	56 (40)
Chlamydomonas sp. 1	3	3	-
Chlamydomonas sp. 2	3	11	11
Chlorella vulgaris Beyerinck	87 (78)	172 (34)	188 (129)
Chlorococcum sp.	-	-	3
Coccomyxa dispar Schmidle	160 (14)	149 (54)	251 (77)
Pandorina sp.	11	-	-
Scenedesmus sp.	11	28	53 (27)
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	749 (202)	256 (55)	65 (13)
Dinobryon sociale Ehrenb.	11	-	-
Dinobryon sertularia Ehrenb.	59 (69)	180 (27)	7
Dinobryon sp.	31	293 (40)	59 (59)
statospores	115 (56)	-	-
Kephryion sp.	17 (9)	3	-
Mallomonas sp.	-	-	14 (13)
indeterminate flagellates	-	3	3
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	11	20 (13)	101 (44)
Cryptomonas sp.	3	-	-
indeterminate flagellates	8	-	-
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	301 (144)	315 (48)	220 (29)
Chroococcus minimus (Keissel.)Lemm.	-	17	-
Chroococcus sp.	23	65	42 (22)
Dactylococcoposis sp.	8	11	-
Lyngbya limnetica Lemm.	-	-	124 (107)
Oscillatoria sp.	17	6	-
Rhabdoderma sp.	-	-	14
indeterminate filament	-	-	8
PYRROPHYTA			
Peridinium cinctum (Müll.) Ehrenb.	5	-	3
PROTOZOA			
indeterminate ciliates	14	5	5

Appendix I. continued

DATE: April 8, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (dead)	-	~20	25
Asterionella formosa Hass. (live)	749 (39)	662 (118)	607 (108)
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	5	14 (5)	25 (9)
Chlamydomonas sp. 1	-	-	2
Chlamydomonas sp. 2	20 (13)	28 (20)	15
Chlorella vulgaris Beyerinck	50 (39)	87 (32)	118 (29)
Chlorococcum sp.	8	20 (21)	10
Coccomyxa dispar Schmidle	50 (59)	84	78 (21)
Scenedesmus sp.	11	23 (10)	15
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	169 (55)	84 (58)	64 (19)
Dinobryon sertularia Ehrenb.	53 (39)	17 (17)	28 (35)
Dinobryon sp.	53	31 (22)	35 (27)
statospores	-	6	-
Kephryion sp.	6	3	-
Mallomonas sp.	3	-	8
indeterminate flagellates	100 (34)	-	84
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	79 (13)	76 (17)	70 (13)
indeterminate flagellates	8	8	10 (12)
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	79 (13)	180 (49)	164 (80)
Chroococcus sp. 1	39 (39)	42 (9)	12 (14)
Chroococcus sp. 2	59	110 (52)	23 (21)
Dactylococcoposis sp.	-	6	-
Lyngbya limnetica Lemm.	-	-	61 (64)
Lyngbya sp. ?	-	17	-
Oscillatoria sp.	25	6	28
Rhabdoderma sp.	3	-	28 (10)
Synechoccus sp.	-	-	6
PROTOZOA			
indeterminate ciliates	14 (5)	8	-
CHYTRID FUNGI	-	-	3

Appendix I. continued

DATE: April 26, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	22 (18)	8	14 (13)
Navicula sp.	3	-	-
CHLOROPHYTA			
Ankistrodesmus falcatus var. *acicularis* (A. Brown) G.S. West	3	3	5
Carteria sp. ?	3	-	-
Chlamydomonas sp. 1	256 (107)	248 (125)	28 (35)
Chlamydomonas sp. 2	14	14 (5)	82 (48)
Chlamydomonas sp. 3	3	3	73 (32)
Chlorella vulgaris Beyerinck	3	-	-
Chlorococcum sp.	143 (61)	37 (32)	3
Coccomyxa dispar Schmidle	3	3	3
indeterminate filament	-	-	6
CHRYSOPHYTA			
Dinobryon cylindricum Imhof	11 (13)	14 (10)	-
Dinobryon sertularia Ehrenb.	37 (18)	11	6
Dinobryon sp.	19 (10)	11 (5)	3
Mallomonas sp.	3	3	8
indeterminate flagellates	118	118	214
CRYPTOPHYTA			
Cryptomonas ovata Ehrenb.	-	-	3
indeterminate flagellates	45 (27)	71 (50)	144 (69)
CYANOBACTERIA			
Anacystis sp.	-	3	-
Chroococcus dispersus (Keissel.)Lemm.	90 (90)	59 (39)	14 (13)
Chroococcus varias ? A. Braun	6	-	-
Chroococcus sp.	-	17	-
Dactylococcopsis sp.	-	6	17 (9)
Lyngbya sp.	23	8000µm	7500µm
Oscillatoria sp. 1	175 (119)	45 (58)	39 (42)
Oscillatoria sp. 2	-	-	39
Rhabdoderma sp.	14	-	-
Synechoccus sp.	14	-	6
indeterminate filament	8000µm	-	-
PROTOZOA			
indeterminate ciliates	-	-	5

Appendix I. continued

DATE: May 23, 1989

TAXA	S	M	B
BACILLARIOPHYTA			
Asterionella formosa Hass. (live)	110	8	42
Navicula sp.	-	8	-
CHLOROPHYTA			
Chlamydomonas sp. 1	2736	2078	2373
Chlamydomonas sp. 2	8	8	8
Chlorococcales	17	25	-
Selenastrum sp.	34	-	17
Ulothrix subtilissima Raben.	34	-	-
indeterminate flagellates	-	16	8
CHRYSOPHYTA			
Dinobryon sertularia Ehrenb.	8	17	-
indeterminate flagellates	25	24	-
CRYPTOPHYTA			
indeterminate flagellates	34	110	59
CYANOBACTERIA			
Chroococcus dispersus (Keissel.)Lemm.	-	152	84
Oscillatoria sp. 1	76	34	68
Oscillatoria sp. 2	-	68	-
Synechoccus sp.	25	8	34
indeterminate filaments	1500 µm	-	-
PROTOZOA			
indeterminate ciliates	-	8	-

APPENDIX II

Appendix II. Species list of zooplankton taxa in The Loch. Each value is the number of cells l^{-1} found from the mean of two replicate samples. (S = 0.5 m below ice surface, M = 2.0 - 2.5 m depth, B = 0.5 m above sediment).

DATE: December 21, 1987

TAXA	S	M	B
COPEPODA			
nauplii	-	-	3
ROTIFERA			
Keratella hiemalis	-	-	127
Polyarthra sp.	-	-	150

DATE: January 5, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.025	0.025	-
nauplii	2	1.5	1.5
ROTIFERA			
Keratella cochlearis	0.75	-	-
Keratella hiemalis	208	259	48
Notholca squalma	0.75	1.5	1.5
Polyarthra sp.	24	27	34

DATE: January 24, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.67	0.075	0.1
nauplii	0.75	2.25	2.25
ROTIFERA			
Keratella hiemalis	563	194	32
Notholca squalma	1.5	0.75	-
Polyarthra sp.	63	91	39

Appendix II. continued.

DATE: February 9, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.53	0.925	0.55
nauplii	1.5	1.5	2.25
ROTIFERA			
indeterminate Bdelloida	2.25	-	-
Brachionus sp.	-	-	1.5
Keratella hiemalis	442	66	10
Notholca squalma	0.75	-	-
Polyarthra sp.	30	38	52

DATE: February 21, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.55	0.88	0.7
nauplii	1.5	1.5	0.75
ROTIFERA			
indeterminate Bdelloida	0.75	0.75	-
Brachionus sp.	0.75	-	-
Keratella hiemalis	104	15	20
Notholca squalma	0.75	-	-
Polyarthra sp.	493	391	210

DATE: March 6, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.73	1.06	0.3
nauplii	0.075	5.25	0.75
ROTIFERA			
Keratella hiemalis	72	36	26
Notholca squalma	-	29	7.5
Polyarthra sp.	128	246	243

Appendix II. continued.

DATE: March 20, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.75	0.3	0.28
nauplii	-	1.5	0.75
OSTRACODA	-	-	0.05
ROTIFERA			
indeterminate Bdelloida	-	8.5	-
Brachionus sp.	-	-	1.5
Keratella hiemalis	39	12	14
Notholca squalma	1.5	1.5	1.5
Polyarthra sp.	42	81	87

DATE: April 4, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.4	0.14	0.08
nauplii	-	0.75	3
ROTIFERA			
indeterminate Bdelloida	-	0.75	-
Brachionus sp.	0.75	-	2.25
Keratella hiemalis	27	30	44
Notholca squalma	6	5	5
Polyarthra sp.	99	122	120

DATE: April 19, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.75	0.125	0.15
nauplii	1.5	0.75	0.75
ROTIFERA			
indeterminate Bdelloida	-	-	0.75
Brachionus sp.	0.75	-	-
Keratella hiemalis	0.75	3	2.25
Notholca squalma	2.25	4.5	3.75
Polyarthra sp.	-	7.5	7.5

Appendix II. continued.

DATE: May 4, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.175	0.275	0.125
nauplii	0.75	-	1.5
ROTIFERA			
indeterminate Bdelloida	-	-	0.75
Keratella hiemalis	0.75	-	3.75
Notholca squalma	0.75	0.75	0.75
Polyarthra sp.	0.75	-	-

DATE: May 30, 1988

TAXA	S	M	B
CLADOCERA			
Bosmina sp.	0.05	-	-
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	-	-	0.05
nauplii	-	0.75	-
ROTIFERA			
Polyarthra sp.	7.5	1.5	1.5

DATE: November 13, 1988

TAXA	S	M	B
CLADOCERA			
Bosmina sp.	-	-	0.05
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.025	0.075	0.125
nauplii	0.075	9	19
ROTIFERA			
Keratella hiemalis	0.75	-	0.75
Notholca squalma	-	2.25	1.5
Polyarthra sp.	3.75	44	51

DATE: December 2, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.6	0.28	0.85
nauplii	0.75	3	5
ROTIFERA			
Keratella hiemalis	2.25	0.75	3
Notholca squalma	0.75	0.75	6.8
Polyarthra sp.	35	34	246

DATE: December 20, 1988

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.125	0.05	2.3
nauplii	0.75	0.75	1.5
ROTIFERA			
Brachionus sp.	-	0.75	-
Keratella hiemalis	1.5	8	15
Notholca squalma	8	8	7
Polyarthra sp.	453	496	524

DATE: January 4, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.4	0.125	0.2
nauplii	1.5	2.25	0.75
ROTIFERA			
indeterminate Bdelloida	-	-	0.75
Keratella hiemalis	34	31	11
Notholca squalma	3	3.8	0.75
Polyarthra sp.	708	627	484

Appendix II. continued.

DATE: January 20, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	0.4	5.8	0.175
nauplii	3.8	1.5	4.5
ROTIFERA			
indeterminate Bdelloida	-	9	-
Brachionus sp.	1.5	0.75	-
Keratella hiemalis	48	170	66
Notholca squalma	-	-	0.75
Polyarthra sp.	514	335	187

DATE: February 10, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	4	1.58	1.1
nauplii	3	0.75	3.8
ROTIFERA			
indeterminate Bdelloida	-	1.5	0.75
Brachionus sp.	3.8	1.5	-
Keratella cochlearis	3	-	-
Keratella hiemalis	27	73	10
Notholca squalma	0.75	0.75	-
Polyarthra sp.	307	129	134

DATE: February 26, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	1.1	0.65	0.38
nauplii	2.25	-	-
ROTIFERA			
indeterminate Bdelloida	2.25	-	0.75
Keratella hiemalis	30	62	32
Polyarthra sp.	57	38	99

Appendix II. continued.

DATE: March 11, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	1.5	0.63	0.45
ROTIFERA			
indeterminate Bdelloida	2.25	-	-
Brachionus sp.	-	-	0.75
Keratella hiemalis	2.25	7	5
Polyarthra sp.	32	34	32

DATE: April 26, 1989

TAXA	S	M	B
ROTIFERA			
indeterminate Bdelloida	-	1.5	-
Brachionus sp.	-	-	0.05
Notholca squalma	1.5	1.5	-

DATE: April 8, 1989

TAXA	S	M	B
COPEPODA			
Eucyclops agilis and *Acanthocyclops* sp.	1	0.4	0.55
ROTIFERA			
Brachionus sp.	0.75	0.75	-
Keratella hiemalis	8	5	11
Polyarthra sp.	6	8	11