PIGMENT ANALYSIS OF THE DISTRIBUTION, SUCCESSION, AND FATE OF PHYTOPLANKTON IN THE MCMURDO DRY VALLEY LAKES OF ANTARCTICA

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Phytoplankton populations in lakes of the McMurdo Dry Valleys have been the subject of taxonomic and ecologic study since the early 1960s. Populations in the major lakes studied (Lakes Bonney, Fryxell, Hoare, and Vanda) include various species of chlorophytes, chrysophytes, cryptophytes, and cyanobacteria. Earlier reports were based primarily on microscopic analyses of preserved water samples. We sampled suspended particulate matter from the four lakes listed above for analysis of algal pigments by high-performance liquid chromatographic (HPLC) methods. Fresh waters beneath ice cover in all lakes were dominated by cryptophyte algae, based on alloxanthin-dominated pigment signatures. Deeper, more saline waters in Lake Bonney were dominated by chrysophytes (fucoxanthin-containing algae) and chlorophytes (chlorophyll-*b*-containing algae). Comparisons with cell counts from Lake Bonney and with published reports of species composition from all the lakes imply that cryptophytes and chrysophytes may have been underestimated by previous microscopic cell counts of preserved water samples. Temporal trends in Lake Bonney showed all three chlorophyll maxima (5 m, 12 m, and 18 m) contained significant quantities of pigments at the onset of light in September and sequential development of deeper phytoplankton populations through the spring growth season. Particles collected early in spring may include significant amounts of detritus that contain pigments. These pigmented particles could include remnants from algal blooms of the previous year's growth season, which may overwinter without significant breakdown because of (1) the slow rate of photo-oxidation under dark, cold conditions, and (2) a paucity of grazing. This explanation is supported by a trend of decreasing chlorophyll breakdown products during the spring, which appear to be photo-oxidized as light intensity increases in Lake Bonney.

INTRODUCTION

The lakes located in the dry valleys near McMurdo Sound, Antarctica contain highly stratified phytoplankton populations under unique conditions. Perennial ice-cover, low advective stream inflow, and strong vertical gradients in salinity [e.g., *Spigel and Priscu*, this volume] make these lakes among the most hydrodynamically stable aquatic systems known. The plankton of these lakes are entirely microbial, primarily algae and bacteria, though protozoans and rotifers may be abundant in certain lakes [*James et al.*, this volume]. These microbial populations exhibit growth under a broad range of temperature, salinity, and nutrient conditions. Low irradiance influences the phytoplankton of these lakes, which show extreme physiological acclimation [e.g., *Lizotte and Priscu*, 1992a, 1992b, 1994; *Neale and Priscu*, 1995, this volume; *Lizotte et al.*, 1996].

Phytoplankton pigment composition was recog-

nized as a measure that could address the following objectives of our dry valley lakes studies: 1) characterize photoacclimation with depth and over the growth season; 2) distinguish whether changes in photosynthetic parameters over the season are due to shifts in cellular processes or to taxonomic changes; and 3) determine the degree of vertical separation between taxonomic groups of phytoplankton in response to physical and chemical gradients. In addition, pigment signatures allowed us to determine the relative contribution of major phytoplankton groups to total biomass being monitored as chlorophyll-*a* concentration, based on the abundance of specific accessory pigments [e.g., *Everitt et al.* 1990].

Comparisons between this chemotaxonomic approach and microscopic phytoplankton cell counts would also allow us to verify and make comparisons with past studies of phytoplankton species composition in the McMurdo Dry Valley lakes. Studies of phytoplankton composition in the dry valley lakes since the early 1960s have been based on microscopy [*Armitage and House*, 1962; *Goldman et al.*, 1967; *Koob and Leister*, 1972; *Vincent*, 1981; *Parker et al.*, 1982], but only the most recent reports have been quantitative [e.g., *Spaulding et al.*, 1994]. Herein we review the published taxonomic work, and, in the context of introducing a chemotaxonomy approach, we discuss the possibility of methodological biases. For example, different groups of phytoplankton have been reported to dominate Lake Bonney, depending on whether results were based on fresh samples [*Koob and Leister*, 1972] or on preserved water samples [e.g., *Parker et al.*, 1982]. We also determined whether some phytoplankton groups may be underestimated by microscopy due to insufficient preservation methods, as demonstrated in marine systems [*Gieskes and Kraay*, 1983; *Buma et al.*, 1990].

We proposed previously [*Lizotte and Priscu*, 1992a] that shade-adapted phytoplankton populations from perennially ice-covered lakes in the McMurdo Dry Valleys present a system analogous to multiple deep chlorophyll maxima. Herein we report on the vertical distribution, seasonal growth, and overwinter fate of distinct phytoplankton communities that make up the chlorophyll maxima in four dry valley lakes.

METHODS

Site Description

Four lakes in the McMurdo Dry Valleys were sampled: Bonney, Fryxell, Hoare, and Vanda. Ice covers of 3 to 5 m thickness are present year-round [*Adams et al.*, this volume], with some ice thinning and the melting of a moat along the shore during austral summer. Streams fed by meltwater from glaciers deliver fresh water if and when spring-summer temperatures permit [*Lyons et al.*, this volume; *Conovitz et al.*, this volume]. None of these lakes have surface drainage, but the lakes lose water at the surface due to evaporation and ice ablation. Shallow depths in these lakes are freshwater and are supersaturated in O_2 and N_2. The deepest waters of these lakes are depleted in oxygen, with H_2S present in the deepest waters of Lakes Fryxell, Hoare, and Vanda.

Lake Bonney is located at the head of the Taylor Valley (77°43'S, 162°20'E). This lake has two basins separated by a narrow sill approximately 40 m wide and 12 m deep. Maximum water column depths are about 40 m in each basin. The west lobe is 1.3 km^2 and abuts the face of the Taylor Glacier, which feeds several major streams draining into the basin. The east lobe is 3.5 km^2 and receives major stream input from glaciers east of the lake. The depth of the steepest chemocline, below which oxygen is depleted, was 18 m in the west lobe and 20 m in the east lobe at the time of this study.

Lake Hoare (77°38'S, 163°07'E) is a 1.9 km^2 freshwater reservoir that is dammed by the Canada Glacier. Maximum depth is 34 m. Temperature and sodium concentrations are relatively uniform to a depth of approximately 28 m, below which is an anaerobic layer.

Lake Fryxell is at the mouth of the Taylor Valley (77°37'S, 163°07'E) about 7 km from McMurdo Sound. Surface area is 7.1 km^2 and maximum depth is 21 m. The main chemocline and oxycline is at ca. 9 m.

Lake Vanda is located in the Wright Valley (77°32'S, 161°33'E) and has an area of 6.7 km^2. Maximum depth is about 80 m and the anaerobic hypolimnion is below a depth of approximately 60 m. Lake Vanda receives significant amounts of fresh water in some years from the Onyx River.

Sample Collection

Water samples were collected over three field seasons from 1989 to 1991 between late winter (September 9) and summer (January 9). Collections were made from stations at the center of each basin through ice holes of 0.25 to 1.0 m diameter. Most

samples of Lake Bonney were from the east lobe. Depths were measured relative to the piezometric level in ice holes (approximately 0.3 m below the top of the ice cover). Water was collected with 10-liter Niskin bottles and placed in HDPE jars stored (< 6 h) in a dark cooler for transport to the laboratory.

Water subsamples (1.5 to 7.0 liters) were passed through glass-fiber filters (Whatman GF/C) to concentrate particulate material for pigment analysis. Filters were placed in cryogenic vials and stored in liquid nitrogen. For microscopy cell counts, 100-ml subsamples were placed in glass bottles and preserved with acid-Lugol's solution [*APHA*, 1985] at 1% final concentration.

Pigment Analyses

Pigments were extracted from filtered material by maceration in 5 ml of acetone on ice. The grinding apparatus was rinsed twice with 1 ml of acetone. Macerated and rinsed materials were placed in the dark at 4°C for 2 h to 3 h. Glass fibers and particulates were then removed by filtration through a Whatman GF/F filter. The volume of acetone extract was recorded and the sample was stored in the dark on ice. Acetone extract was mixed 1:1 (v:v) with an ion-pairing agent (IPA) solution containing tetrabutylammonium acetate [*Mantoura and Llewellyn*, 1983]. Immediately after mixing with IPA, 1.0 ml of sample was injected into a Waters HPLC system consisting of a 15-cm C-8 reverse-phase column, two pumps (model 510), a gradient controller (model 680), a photodiode array detector (PDA, model 991) and a fluorometer (model 370) containing cutoff filters for detecting the fluorescence of chlorophylls. The elution gradient was linear from 60%:40% (v:v) acetone:IPA to 100% acetone in 20 min at a flow rate of 2 ml min^{-1}. Pigments were detected by absorption at either 440 nm (for carotenoids, chlorophylls, and chlorophyllides) or 410 nm (for phaeophytins and phaeophorbides).

Pigment standards were acquired from commercial sources (Sigma Chemical) or made from algal cultures or fresh spinach. Standards for chlorophyll-*a*, chlorophyll-*b*, α-carotene, β-carotene, lutein, and bacteriochlorophyll-*a* were available commercially. Phaeophytin-*a* was made from chlorophyll-*a* by acidification. Lutein, violaxanthin, and neoxanthin were isolated from spinach leaf extracts using an HPLC preparatory column. Alloxanthin, diadinoxanthin, fucoxanthin, chlorophyllides, and phaeophorbides were identified in samples based on absorption spectra measured by the PDA detector (from 380 nm to 750 nm, every 1.3 nm, at 2.3 s intervals). Peaks for chlorophylls, chlorophyllides, phaeophorbides, and phaeophytins were corroborated by detection with the fluorometer.

Pigments were quantified by applying specific extinction coefficients [E; *Rowan*, 1989] to absorbances measured by the PDA detector. For each pigment, E was weighted for the ratio between absorbance at the peak wavelength for E (A_{max}) and absorbance at the detection wavelength (A_{det} at either 440 nm or 410 nm). $A_{max} : A_{det}$ ratios were estimated from the slopes of least-square regressions of A_{max} and A_{det} values from PDA spectra collected during HPLC runs of standards and samples. Pigment concentrations (C) were calculated as:

$$C = \text{Area} * (A_{max} : A_{det}) * F * V_e / (E * V_f * V_i)$$

where Area is the integrated area of a peak on the chromatogram, F is the flow rate, V_e is the volume of extract, V_f is the volume of water filtered, and V_i is the volume of extract injected into the HPLC.

Phytoplankton Cell Counts

Water samples preserved in acid-Lugol's solution were placed in 100-ml Utermöhl settling chambers and allowed to settle for 5 days. Phytoplankton cells were counted for the entire sample using an inverted compound microscope [*Lund et al.*, 1958]. Species designations are based on the key of *Seaberg et al.* [1979]. Cell dimensions were measured for a subset of each taxonomic group and biovolumes were calculated using appropriate geometric shapes.

RESULTS

Chromatograms of samples from three depths in Lake Bonney (Figure 1) show the efficacy of the HPLC method for separating the major phytoplankton pigments present. The population immediately beneath the ice cover had a pigment signature with three major contributors, chlorophyll-*a* (chl-*a*), alloxanthin, and chl-*c* (= chl-c_1 + chl-c_2). This chromatogram indicates dominance by cryptophyte algae. The 13-m sample was more complex because of the addition of a significant fucoxanthin peak, which indicates the presence of chromophyte algae. An even greater diversity of pigments was observed at 18 m, with chl-*b*, lutein, violaxanthin, and neoxanthin indicating a substantial chlorophyte population. Microscopic examinations of

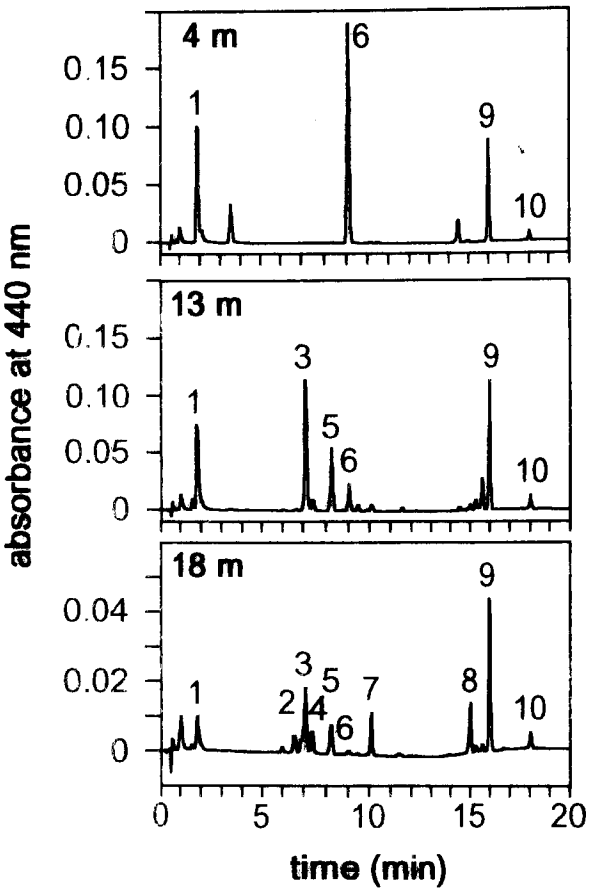

Fig. 1. Chromatograms for samples collected from the east lobe of Lake Bonney on December 5, 1991. Peaks identified by numbers: 1) chlorophyll-*c*, 2) neoxanthin, 3) fucoxanthin, 4) violaxanthin, 5) diadinoxanthin, 6) alloxanthin, 7) lutein + zeaxanthin, 8) chlorophyll-*b*, 9) chlorophyll-*a*, 10) β-carotene.

these samples showed that significant populations of corresponding algae were coincident with the accessory pigments identified as markers: the cryptophyte *Chroomonas lacustris* with alloxanthin; the chrysophyte *Ochromonas* sp. with fucoxanthin; and the chlorophyte *Chlamydomonas subcaudata* with chl-*b*.

We developed our HPLC method to be as simple as possible with the capability of separating the major pigments present in the study lakes. More complex methods can separate a greater variety of algal pigments [e.g., *Wright et al.*, 1991]. Like most general HPLC methods developed for phytoplankton pigment analysis, this method is not capable of distinguishing among chl-c_1, chl-c_2, and Mg 2,4-divinylpheaoporphyrin-a_5 monomethyl ester. Because of this limitation, and the lack of significant amounts of chlorophyll-c_3 in our samples (which can be separated by our method), a single chl-*c* pigment class was quantified. Our HPLC method was also unable to differentiate between α-carotene and β-carotene, thus the peak identified as β-carotene may include various forms of related carotenes. Though we did not test for the ability to distinguish lutein from zeaxanthin, similar protocols are unable to make that separation [e.g., *Mantoura and Llewellyn*, 1983]; current protocols are capable [e.g., *Wright et al.*, 1991]. For our samples, we identified a peak as lutein + zeaxanthin, based on 1) an absorbance spectra resembling lutein and 2) the presence of other chlorophyte accessory pigments that were co-detected (e.g., chl-*b*, violaxanthin, and neoxanthin) and our microscopy observations of much larger biovolumes of chlorophytes (which typically contain more lutein than zeaxanthin) than cyanobacteria (which contain zeaxanthin but no lutein). The method is also incapable of separating diadinoxanthin and 19'-hexanoyloxyfucoxanthin (a pigment found in some prymnesiophytes). However our cell counts showed that chrysophytes were abundant when the peak identified as diadinoxanthin was present, and we are unaware of any reports of prymnesiophyte species from these lakes. Finally our samples were not expected to show evidence for conversion of xanthophylls by de-epoxidation (e.g., violaxanthin to zeaxanthin in chlorophytes, or diadinoxanthin to diatoxanthin in chrysophytes) because of the low-light environment and the relatively long, dark periods of sample storage during transport after collection (1 to 4 h).

Vertical profiles of pigment concentrations collected over the spring-summer phytoplankton growth season in Lake Bonney showed that the three distinct populations outlined above with diagnostic pigments (alloxanthin, fucoxanthin, and chl-*b*) develop sequentially (Figure 2). From 4 m to 8 m, the cryptophyte marker alloxanthin is dominant on all dates. The 10 m and 12 m populations are alloxanthin-dominated early in the season, but a significant fucoxanthin peak was observed in December and January. Fucoxanthin is the dominant marker pigment from 13 m to 20 m as late as November, with a deep population of chl-*b* containing algae growing at 17 m to 20 m in December and January.

Ratios of pigments diagnostic for certain taxa (such as alloxanthin, fucoxanthin, and chl-*b*) to chl-*a* can be used as a relative measure of the contribution of certain taxa (cryptophytes, chrysophytes, and chlorophytes, respectively) to phytoplankton biomass. When pigment ratios measured over two field seasons are plotted

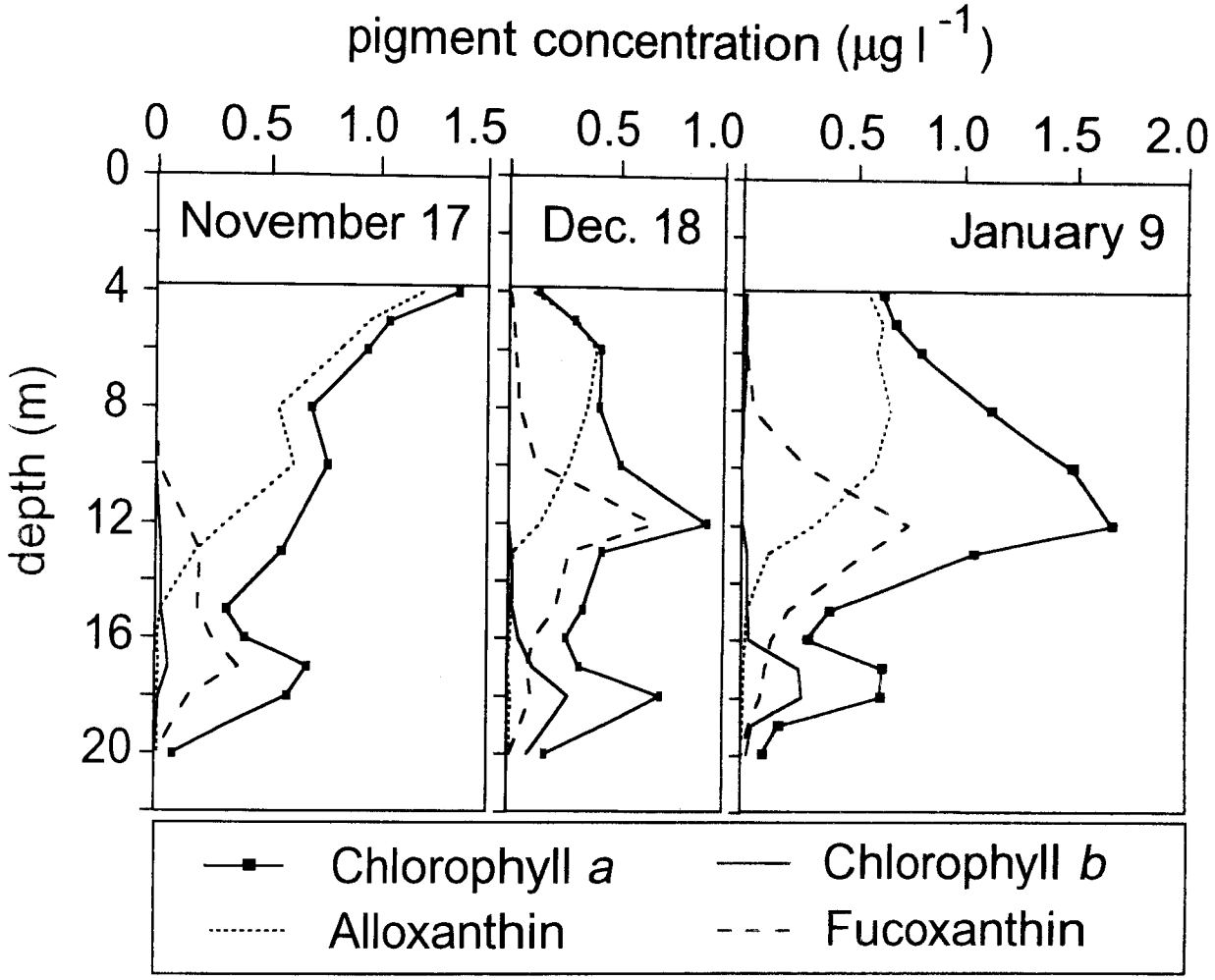

Fig. 2. Profiles of algal pigment concentrations in Lake Bonney during 1990-1991.

against date for the three chlorophyll maxima in Lake Bonney, we see a pattern of sequential blooms by different taxa at each depth (Figure 3). Early in the season, the chl-*a* signal appears to be associated with significant contributions of all three marker pigments. Later in the season, each chlorophyll maxima has a chl-*a* signal associated primarily with one marker pigment: alloxanthin beneath the ice, fucoxanthin at mid-depth, and chl-*b* in the deepest population. These shifts may represent a decrease in taxonomic diversity as dominant taxa bloom.

For Lake Bonney, we can compare pigment ratios to the biovolume of taxonomic groups (determined from cell counts on preserved water samples) for three dates in 1990-1991 (Table 1). Alloxanthin:chl-*a* molar ratios ranged from 1.2 to 1.4 for under-ice populations, with negligible ratios for fucoxanthin:chl-*a* and chl-*b*:chl-*a*. These results demonstrate the dominance of cryptophyte algae under-ice, in contrast to biovolume results showing that chlorophytes (42 to 53%) were equal to or greater than cryptophytes (37 to 40%). At the middle chlorophyll maxima (13 m), fucoxanthin:chl-*a* ratios imply dominance by chrysophytes, (0.49 to 0.87), whereas biovolume results show that chrysophytes (56 to 63%) were joined by significant contributions of chlorophytes (21 to 32%) despite low chl-*b*:chl-*a* ratios (0.03 to 0.04). Only for the late season samples from the deep chlorophyll maximum were the ratios of chl-*b*:chl-*a* high enough (0.33 to 0.40) to corroborate the substantial contribution by chlorophytes to biovolume (86 to 92%).

Overall we measured very low ratios of chl-*b*:chl-*a*

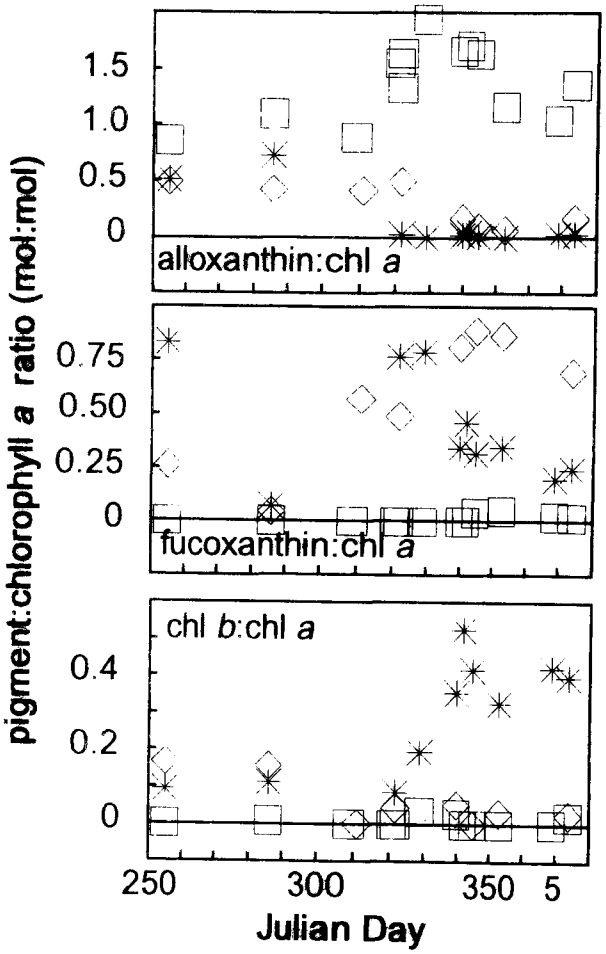

Fig. 3 Seasonal trends in the molar ratios of accessory pigments to chlorophyll-*a* in Lake Bonney. Samples were collected from 4 to 5 m (squares), 13 m (diamonds), and 17 m (stars) during field seasons in 1990–1991 and late 1991.

in samples containing <60% biovolume as chlorophytes. One possibility is that the cells counted as chlorophytes were atypical in chl-*b*:chl-*a* or in pigment per biovolume. A significant amount of the chlorophyte biovolume was represented by cells that resembled chlamydomonad zygospores [*Sharp*, 1993]. Early in the growth season, these lakes also show poor correlations between chl-*a* concentrations and photosynthetic production, implying that a large fraction of the biomass is associated with inactive cells [*Lizotte et al.*, 1996].

Pigment composition in the oxygenated epilimnia of various lakes in the dry valleys shows that alloxanthin-containing cryptophytes dominated most phytoplankton populations (Table 2). This cryptophyte signature was clearly seen in shallow populations of all the basins and throughout the epilimnia of Lakes Fryxell, Hoare, and the west lobe of Bonney. Chrysophyte algae, detected by the presence of fucoxanthin, were dominant only in the mid-depths of the epilimnion in the east lobe of Lake Bonney, and were significant at all depths in Lake Vanda. Chlorophyte algae, detected by the presence of chl-*b*, were dominant only in the bottom of the epilimnion in the east lobe of Lake Bonney, but were significant immediately beneath the ice in Lake Hoare. The only samples that showed evidence of carotenoids from cyanobacteria (tentatively identified as myxoxanthophyll, but not quantified) were from Lake Vanda. The xanthophyll typically used to detect cyanobacteria is zeaxanthin; however spectral scans of the "lutein + zeaxanthin" peak resembled lutein. The dominant pigment in the hypoliminion of Lake Fryxell (10 to 11 m) was bacteriochlorophyll-*a* (not quantified), indicating a large population of photosynthetic bacteria. The next most prevalent pigments at these depths were alloxanthin, chl-*a*, and chl-*c*, in ratios similar to the shallower phytoplankton populations of Lake Fryxell.

Pigment signatures in the east lobe of Lake Bonney become most complex near the interface between the super-oxygenated epilimnion and the oxygen-poor hypolimnion (ca. 20 m). This part of the water column, 18 m to 21 m, was always the chl-*a* minimum, and had relatively high concentrations of chlorophyll breakdown products compared to shallower or deeper waters (Table 3). The main breakdown products present were chlorophyllides and phaeophorbides. Ratios of phaeophytin-*a*:chl *a* were low at all depths (< 0.02). Above 15 m, the relative amounts of chlorophyll breakdown products were much lower.

Seasonal trends for concentrations of phaeophorbides, chlorophyllides, and chl-*a* in the oxycline waters of Lake Bonney were reconstructed from late season collections in 1990–1991 and early season collections in 1991 (Figure 4). The late season bloom of phytoplankton just above the oxycline was observed in the data from 17 m. Smaller increases in chl-*a* were noted at 20 m and 23 m late in the season. Both of the chlorophyll breakdown products showed decreasing trends from the winter-spring transition through the austral spring. A late spring sample collected from 18 m on December 5, 1991 matched the December 1990 increase in chl-*a*, as well as the decreases in phaeophorbide and chlorophyllide concentrations to negligible amounts.

In the oxygen-poor waters deeper than 21 m in Lake Bonney, the ratio of chlorophyll breakdown products to

TABLE 1. Relative Abundance of Phytoplankton Groups in Lake Bonney during 1990–1991, as Determined by Microscopy (% of algal biovolume) and by Pigment Analysis (molar ratios).

Date	Depth (m)	Cryptophytes (%)	(allox:chl-*a*)	Chrysophytes (%)	(fucox:chl-*a*)	Chlorophytes (%)	(chl-*b*:chl-*a*)
Nov. 17	4	40	1.38	n.d.	n.d.	42	n.d.
	13	15	0.52	56	0.49	29	0.04
	17	n.d.	0.03	42	0.77	58	0.09
Dec. 18	4	37	1.21	n.d.	0.05	53	n.d.
	13	11	0.07	63	0.87	21	0.03
	17	n.d.	n.d.	14	0.35	86	0.33
Jan. 9	4	39	1.41	n.d.	0.02	50	0.02
	13	6	0.18	59	0.70	32	0.03
	17	n.d.	0.03	8	0.24	92	0.40

Abbreviations: allox = alloxanthin; fucox = fucoxanthin; chl = chlorophyll; n.d. = not detected.

TABLE 2. Concentrations of chl-*a* and Molar Ratios of Accessory Pigments to Chlorophyll-*a* for Phytoplankton Maxima in the Dry Valley Lakes in 1990.

Lake	Date	Depth (m)	chl-*a* ($\mu g\ l^{-1}$)	allox:chl-*a*	fucox:chl-*a*	chl-*b*:chl
Bonney (east lobe)	Dec. 18	4	0.13	1.21	0.05	n.d.
		13	0.41	0.07	0.87	0.03
		17	0.31	n.d.	0.35	0.33
Bonney (west lobe)	Dec. 1	4	0.70	1.58	0.02	n.d.
		13	0.89	1.11	0.12	n.d.
Hoare	Dec. 8	5	0.41	0.72	n.d.	0.16
		10	2.1	0.87	n.d.	n.d.
		12.5	3.2	0.89	n.d.	n.d.
Fryxell	Dec. 7	5	2.3	0.99	0.01	0.06
		7	2.6	1.03	0.01	0.05
		8.5	4.1	0.97	0.03	0.05
Vanda	Nov. 28	3	0.09	0.46	0.41	n.d.
		20	0.14	0.49	0.41	n.d.
		57.5	0.37	0.11	0.27	n.d.

Abbreviations: allox = alloxanthin; fucox = fucoxanthin; chl = chlorophyll; n.d. = not detected.

TABLE 3. Mean (± standard deviation) of chl-*a* Concentration ($\mu g\ l^{-1}$) and the Molar ratio of Chlorophyll Degradation Products to chl-*a* in the East Lobe of Lake Bonney.

Depth (m)	n	chl-*a*	chlorophyllide:chl-*a*	phaeophorbide:chl-*a*	phaeophytin:chl-*a*
4	10	1.11 (0.58)	n.d.	0.03 (0.04)	0.001 (0.002)
5	8	0.80 (0.40)	n.d.	0.05 (0.05)	0.008 (0.015)
6	8	0.73 (0.30)	0.03 (0.06)	0.07 (0.09)	0.005 (0.004)
10	7	0.78 (0.41)	0.01 (0.02)	0.03 (0.04)	0.002 (0.002)
12	6	1.02 (0.39)	0.04 (0.04)	0.06 (0.07)	0.003 (0.006)
13	9	0.54 (0.34)	0.04 (0.06)	0.07 (0.10)	0.003 (0.007)
15	5	0.27 (0.10)	0.10 (0.13)	0.13 (0.16)	0.013 (0.026)
17	9	0.37 (0.23)	0.21 (0.39)	0.17 (0.29)	0.010 (0.029)
18	6	0.47 (0.31)	0.44 (0.60)	0.31 (0.45)	0.001 (0.002)
19	2	0.11 (0.06)	0.68 (0.64)	0.43 (0.37)	0.006 (0.006)
20	5	0.08 (0.04)	0.75 (0.55)	0.60 (0.34)	n.d.
21	2	0.08 (0.02)	0.85 (0.50)	0.67 (0.38)	n.d.
23	6	0.24 (0.05)	0.31 (0.11)	0.20 (0.11)	0.009 (0.013)
25	4	0.40 (0.06)	0.18 (0.08)	0.12 (0.06)	0.019 (0.004)
30	4	0.43 (0.06)	0.14 (0.02)	0.09 (0.04)	0.011 (0.002)
35	5	0.13 (0.03)	0.44 (0.10)	0.36 (0.10)	n.d.

Abbreviations: chl = chlorophyll; n.d. = not detected; n = sample number.

chl-*a* were lower than the peak depth (18 to 21 m), but still relatively high (Table 3). The peak concentrations for chlorophyll breakdown products were found at 23 to 25 m in conjunction with a peak in chl-*a*. Pigment signatures below 20 m most closely resembled phytoplankton from 17 to 20 m, with chl-*b* and lutein + zeaxanthin as the main accessory pigments. The hypolimnetic chl-*a* concentrations were relatively consistent on all sampling dates compared to the upper water column where the phytoplankton bloom in the spring. This consistency is demonstrated by the lower variability statistics in Table 3, and by the examples of reconstructed seasonal trends in Figure 4.

DISCUSSION

Analyses of algal pigments in suspended particulates from the dry valley lakes produced new insights to the composition of phytoplankton communities and the efficacy of the most common method for preserving phytoplankton for microscopy. For Lake Bonney, our seasonal studies also illuminated temporal trends in algal biomass, its taxonomic composition, and the fate of this algal material.

Late in spring, the chlorophyll maxima were typically dominated by a single algal group based on pigment signatures. The most common pigment signature encountered in these four lakes was for cryptophyte algae. Cryptophytes appear to dominate the entire oxygenated water column in Lakes Fryxell, Hoare, and the west lobe of Bonney, as well as the shallowest waters in the east lobe of Bonney. Chrysophytes were dominant only in the mid-depth maximum of the east lobe of Lake Bonney, but were co-dominant with cryptophytes in Lake Vanda. Chlorophytes were dominant only in the deepest

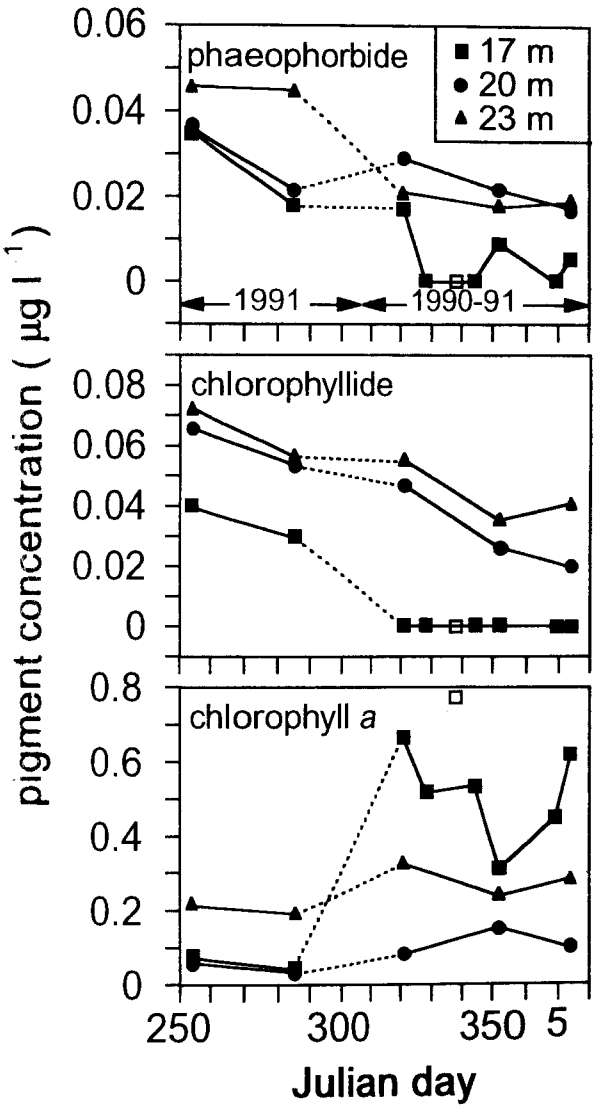

Fig. 4. Reconstructed seasonal trend of concentrations of phaeophorbides, chlorophyllides, and chlorophyll-*a* at the oxycline (20 m), 3 m above (17 m) and 3 m below (23 m) in the east lobe of Lake Bonney. Note that samples collected during the winter-spring transition are from 1991, the year after samples were collected for spring-summer. A summer 1991 sample from 18 m is shown as open squares.

maximum of the east lobe of Lake Bonney.

These results can be contrasted with published reports of phytoplankton populations in these four lakes (Table 4). If we assume our pigment analysis as a baseline, past surveys based on cell counts have overestimated the importance of chlorophytes and cyanobacteria while cryptophytes and chrysophytes were underestimated. It is important to note that most taxonomic surveys conducted in the past were not quantitative, but they did make qualitative statements about relative prevalence of species. Part of the discrepancy could be because past rankings were based on cell concentration rather than biochemical, biomass, or biovolume concentrations; the former tend to overestimate the contribution of small-celled species (i.e., for some of the species of *Oscillatoria* and *Chlorella* reported in these lakes). Our comparison between pigment analysis and cell counts supports the possibility that certain taxa are lost from water samples preserved for microscopy [*Gieskes and Kraay*, 1983; *Buma et al.*, 1990].

Another possibility is that the differences observed among studies over the past three decades (Table 4) reflect actual changes in species composition from year to year [*Spaulding et al.*, 1994]. The most obvious trend in the literature we reviewed is the increasing prominence (or recognition) of cryptophytes in these dry valley lakes. Recent studies in coastal waters off the Antarctic peninsula have observed that increases in cryptophyte populations are correlated with the timing of freshwater input from glaciers [*Moline and Prezelin*, 1996]. If cryptophyte populations are responsive to increased freshwater flux, particularly from glacier meltwaters, then they could be an important indicator organism for ecosystem-level shifts in the dry valley lakes. For the long-term ecological research projects currently underway on these lakes, it would seem prudent to use both the specific taxonomic methods of microscopy and the coarse taxonomic methods of pigment analysis to monitor phytoplankton populations until the possibility of methodological biases can be eliminated.

Phytoplankton populations in the perennially ice-covered lakes were typically separated into taxonomically distinct vertical strata. Seasonal trends in Lake Bonney show that the cryptophyte community immediately under the ice peaked during November, while deeper populations of chrysophytes, and chlorophytes continued to grow into the summer. Profiles for fucoxanthin indicate that flagellated chrysophytes, may have moved up the water column before forming a distinct peak at 12 m depth. This depth is just above the nutricline [e.g., *Priscu*, 1995], which may present a limit to further upward migration.

The peak for ratios of chlorophyll degradation products in Lake Bonney was found near the bottom of the euphotic zone, in the region of the chemocline where sinking particles may accumulate after achieving neutral buoyancy in the dense brine. The fact that the concentrations of chlorophyll breakdown products are much higher at the beginning of spring than at the end

TABLE 4. Phytoplankton Taxa (in order of abundance) Reported for McMurdo Dry Valley Lakes.

Reference (Methods*)	Bonney	Fryxell	Hoare	Vanda
Armitage and House [1962] (70 mm mesh net)	C			C
Goldman [1964] (not reported)				D
Goldman et al. [1967] (Lugol's, settled)	B C			B D C
Koob and Leister [1972] (Craf's, filtered)	C D			
Vincent [1981] (Lugol's, settled)		B C A		
Parker et al. [1982] (Lugol's, settled)	A C	A C	A C D	B D
Seaburg et al. [1983] (Lugol's, settled)	A C D	A C	A D C	B C A D
Spaulding et al. [1994] (Lugol's, settled)		A C D		
this study (Lugol's, settled)	C A B			
this study (HPLC)	A B C	A C	A C	A B

*The analysis methods reported are given in parentheses.

A = Cryptophyte; B = Chrysophyte; C = Chlorophyte; and D = Cyanobacteria.

implies that their accumulation may be based on the previous year's phytoplankton production in the upper water column. Seasonal increases in chl-*a* below 20 m were not associated with measurable primary production [*Sharp*, 1993], and the pigment signatures imply that this chl-*a* was due to cells settling from phytoplankton populations at 17 to 20 m. The seasonal trend of decreasing concentrations for degradation products in conjunction with the onset of light reaching the water column in spring implies that photooxidation may be a major loss mechanism for pigments. Another possible mechanism is bacterial degradation: there is a peak in bacterial populations at the oxycline, and an annual cycle of activity linked to primary production [e.g., *Goldman et al.*, 1964; *Ellis-Evans*, 1985; *Priscu*, 1992] may lead to increased decomposition during the spring season.

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