



Environmental Factors Associated with Deep Chlorophyll Maxima in Dry Valley Lakes, South Victoria Land, Antarctica

Authors: Burnett, Laura, Moorhead, Daryl, Hawes, Ian, and Howard-Williams, Clive

Source: Arctic, Antarctic, and Alpine Research, 38(2) : 179-189

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2006\)38\[179:EFAWDC\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2006)38[179:EFAWDC]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Environmental Factors Associated with Deep Chlorophyll Maxima in Dry Valley Lakes, South Victoria Land, Antarctica

Laura Burnett*

Daryl Moorhead*‡

Ian Hawes† and

Clive Howard-Williams†

*Department of Earth, Ecological and Environmental Sciences, University of Toledo, Toledo, Ohio, U.S.A.

†National Institute of Water and Atmospheric Research, Ltd., Christchurch, New Zealand.

‡Corresponding author.
daryl.moorhead@utoledo.edu

Abstract

Environmental factors associated with deep chlorophyll maximum (DCM) layers were examined in five lakes of the McMurdo Dry Valleys, Antarctica, to test the hypothesis that DCM are more closely associated with resource limitations than water density. Because data could not be transformed to meet the assumption of normal distribution, distance matrices were constructed from vectors of observed chlorophyll-*a* (CHL), photosynthetic active radiation intensity (PAR), soluble reactive phosphorous (SRP), dissolved inorganic nitrogen (DIN), dissolved oxygen (DO), water density (DEN), and incremental change in water density/depth (DEL). Multiple regression analyses then were based on permutation evaluations of the relationships between distance matrices (partial Mantel analyses). Results indicated that resource availability (PAR and DIN) was most frequently related to chlorophyll-*a*, although DEN and DEL often were significant within individual lakes. Hence, resource relationships were strongest across lakes and seasons whereas density relationships also were important within individual lakes. Moreover, DCM appeared sensitive to threshold levels of DEN and PAR, suggesting that controls may exist as both discrete (threshold) and continuous functions of both resource availability and water density.

Introduction

High concentrations of chlorophyll-*a* often exist at depths where radiant energy is well below ambient intensity. Such deep chlorophyll maxima (DCM) are found in aquatic and marine systems throughout much of the world but usually are restricted to times and places with limited mixing of the water column (Kiefer et al., 1972; Venrick et al., 1973; Fee, 1976; Brooks and Torke, 1977; Moll et al., 1984; Coon et al., 1987; Larson et al., 1987; Bell and Laybourn-Parry, 1999; Perez et al., 2002; Camacho et al., 2003). A DCM sometimes coincides with a major fraction of the phytoplankton standing crop and may contribute a large portion of the total primary production in the water column (Brooks and Torke, 1977; Jamart et al., 1977). Photosynthesis, plankton species composition, behavior, and grazing rates frequently change abruptly over small changes in depth near the DCM (Jamart et al., 1977; Cullen, 1982; Perez et al., 2002; Camacho et al., 2003).

Controls on the location of DCM vary with geographical region, season, and the biology of the community, but usually include currents, vertical mixing, growth, behavior, or physiology of phytoplankton (Steele and Yentsch, 1960; Venrick et al., 1973; Jamart et al., 1977; Herbrand and Voituriez, 1979; Cullen and Eppley, 1981; Kiefer and Kremer, 1981; Cullen, 1982; Coon et al., 1987; Marra et al., 1990; Revelante and Gilmartin, 1995; Deksheniaks et al., 2001). Three basic explanations of DCM formation emerge from these studies. First, spatial distributions of limiting resources define the location of the DCM as a result of localized productivity. Second, a DCM develops as a function of phytoplankton behaviors, such as rising or sinking in the water column in response to microenvironment cues. Finally, passive sinking of cells over depth generates a DCM where cells accumulate along a density gradient.

The simplest explanation is that a DCM results from the concentration of organic particles along density gradients (Jerlov, 1959). In fact, Moll and Stoermer (1982) suggested that such passive control could only be disproved if there was *in situ* production by phytoplankton, but did not suggest how to identify the role of passive

control in the presence of phytoplankton production. Cullen (1982) suggested that chlorophyll-*a* profiles at temperate latitudes often are produced by differential sinking, when sedimentation rates of phytoplankton exceed growth rates following a spring bloom. Venrick et al. (1973) found a DCM in the Pacific Ocean where a density gradient resulted from seasonal stratification of the water column that, in turn, isolated a layer of chlorophyll from wind-driven turbulence. More recently, Deksheniaks et al. (2001) found thin phytoplankton layers that were common off the coast of Washington (U.S.A.) and were strongly related to physical factors controlling stratification.

Other studies reveal more interactions between water density and biological processes (Pingree et al., 1975; Herbrand and Voituriez, 1979; Cullen, 1982). In Sproat Lake (British Columbia, Canada), Shortreed and Stockner (1990) could explain the DCM as either a function of phytoplankton migration to areas of favorable light regime or simple accumulation as a function of water density gradient. Steele and Yentsch (1960) demonstrated that a reduced sinking rate, rather than change in water density, was needed to produce the observed, seasonal pattern of chlorophyll maximum near the base of the euphotic zone in the Atlantic Ocean, near New York (U.S.A.). They found that the physiological condition of a cell was closely related to buoyancy, that buoyancy was greater during periods of high production, and that production was related to seasonal nutrient regimes controlled by mixing and density gradient. Clearly, interactions between physiological condition, sinking rates, and water density appear to be common and confound efforts to determine a single cause of a DCM.

Many of the lakes found in the dry valleys of Antarctica are amictic with strong resource and density gradients, and deep chlorophyll maximum layers. An important feature of these lakes is a permanent ice cover that provides protection from the wind, limits mixing of the water column, and ensures stable stratification (Doran et al., 1999). This stratification limits movement of nutrients from the aphotic, and sometimes anoxic, deeper waters to shallower euphotic zones, where nutrient availability limits phytoplankton production (Priscu, 1995; Lizotte et al., 1996; Dore and Priscu, 2001). The reduction in light

transmittance through permanent ice also affects primary production and plankton distribution (Wharton et al., 1989; Lizotte and Priscu, 1992). In contrast to most freshwater lakes, temperature plays only a secondary role in stabilizing the water columns of these Antarctic lakes, whereas salinity gradients exert a strong control on stratification (Spigel and Priscu, 1998). For these reasons, there is little seasonal or interannual variation in stratification of the water column. This is an interesting contrast to most other lakes and water bodies in which DCM have been examined and offers an opportunity to separate the effects of resources from density gradient under permanently stratified conditions.

The objectives of this study were to evaluate limnological factors related to the position of the DCM in lakes of the McMurdo Dry Valleys, South Victoria Land, Antarctica. More specifically, analyses were conducted to test the hypothesis that the location of DCM was more closely related to resource availability, i.e., nutrients and photosynthetic active radiation, than density gradients.

Methods

Five lakes within the McMurdo Dry Valley region of South Victoria Land, Antarctica, have deep chlorophyll maximum layers and have been studied intensively over the past 20 yr: Lakes Vanda, Fryxell, Hoare, East Bonney, and West Bonney. Considerable evidence suggests that nutrient availability limits phytoplankton production in these lakes, and that production is often enhanced near the nutricline where DCM are located (Priscu, 1995; Neal and Priscu, 1998). Our objective was to examine the relationships between DCM and both resource and density gradients in these lakes. The present study focused on data collected by the McMurdo Long-Term Ecological Research Project, U.S.A. (<http://huey.colorado.edu/LTER>), and the National Institute of Water and Atmospheric Research (NIWA), New Zealand (unpublished).

STUDY SITE

The McMurdo Dry Valleys of Southern Victoria Land comprise the largest ice-free expanse of land (ca. 4800 km²) on the continent of Antarctica. They are situated on the west side of McMurdo Sound, adjacent to the Ross Sea (ca. 77°S, 162°E) and are among the coldest and driest deserts on Earth. The climate is extremely arid with a total annual precipitation less than 10 cm yr⁻¹ and annual ablation exceeding 30 cm yr⁻¹. Air temperatures rarely exceed 0°C in the summer and drop to less than -60°C in the winter (Fountain et al., 1999). Lakes Bonney, Hoare, Fryxell, and Vanda are located in two of the McMurdo Dry Valleys (i.e., Taylor and Wright Valleys). Short descriptions of these lakes follow.

Lake Bonney occupies a glacially scoured bedrock basin in the upper Taylor Valley. The lake is approximately 25 km from the sea at an elevation of 57 m a.s.l. (Spigel and Priscu, 1998). The largest source of water to this lake is meltwater from the Taylor Glacier—which extends from the polar ice cap and terminates in the western end of the west lobe of Lake Bonney. This lake has two lobes (east and west) that are connected by a narrow, shallow channel (Torii and Yamagata, 1981). The chemical characteristics and apparent evolutionary histories of these two lobes are very different, and in the present study they were analyzed as separate bodies of water. The DCM in West Bonney is located at 12 m, whereas East Bonney has two deep chlorophyll-*a* peaks, one at 14 m and the other at 30 m. Initial analyses focused on the peak at 14 m in East Bonney, because the 30 m peak is in a biologically inactive zone of the water column and thus is unlikely to be mechanistically linked to resource availability.

Lake Hoare occupies a narrow portion of the middle Taylor Valley approximately 15 km from the sea, and is dammed to the northeast by the Canada Glacier. The lake is fed primarily by direct

runoff from the Canada and Seuss glaciers and their associated meltwater streams. Lake Hoare is the youngest lake in this study (ca. 1200 yr old) and has the weakest profile development (Doran et al., 1999). Lake Hoare shows less distinction between surface and maximum chlorophyll-*a* values due to high variances associated with observations (Fig. 1). However, peak concentrations occur at 10 m.

Lake Fryxell is formed by a moraine depression in a wider portion of the lower Taylor Valley, approximately 1 km east of Lake Hoare and closer to the valley mouth. It has a number of moraine islands and shallow areas. The primary source of water is 10 meltwater streams from the Canada and Commonwealth glaciers and alpine glaciers in the nearby Kukri Hills. Lake Fryxell has a sharp DCM at 8 m.

Lake Vanda is located in the Wright Valley adjacent to Taylor Valley, and its primary source of water is from the Onyx River, which originates from the Lower Wright Glacier (27 km east of Lake Vanda). This lake is meromictic, containing a deeper water zone (a monimolimnion below 50 m) that is permanently stable and an upper layer that circulates during the six to eight week period of water inflow (Carlson et al., 1990; Jones-Lee and Lee, 1993). Lake Vanda has a sharp peak of chlorophyll-*a* at 60 m depth, and is among the most extreme oligotrophic lakes in the world (Parker et al., 1982).

All of these lakes have permanent ice covers 3–5 m thick and a highly stratified water column with strong vertical salinity gradients and distinct profiles of chlorophyll-*a* (Fig. 1; Parker et al., 1982; Matsumoto, 1993; Spiegel and Priscu, 1998). None of these lakes have surface outflows, so the only known means of water loss is ablation. Availability of N and/or P limits primary productivity in the euphotic regions of these lakes, with upward diffusion from deeper water proposed as both a primary source of nutrients and likely factor controlling the DCM (Vincent and Vincent, 1982; Priddle et al., 1986; Priscu et al., 1987, 1989; Priscu, 1995; Lizotte et al., 1996; Spigel and Priscu, 1998). However, strong density gradients are present and may also contribute to the location of DCM (Fig. 2; James et al., 1998).

FIELD DATA

This project utilized data collected by the McMurdo Long-Term Ecological Research (LTER) project, U.S.A., and National Institute of Water and Atmospheric Research (NIWA), Ltd., New Zealand. These data include concentrations of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), dissolved oxygen (DO), and photosynthetically active radiation measured beneath the lake ice (PAR). Data from lakes in Taylor Valley were obtained from the McMurdo-LTER (<http://huey.colorado.edu/LTER>). Conductivity data and estimates of salinity for lakes in Taylor Valley were provided by Craig Wolf, Montana State University (unpublished). All data for Lake Vanda were obtained from NIWA (unpublished).

Detailed descriptions of field and laboratory methods are posted on the McMurdo LTER web site. In brief, a 30-cm-diameter hole was bored through the permanent lake ice over the deepest portion of each lake and protected with an opaque cover until sampled. Water samples were taken at several depths in each lake with Van Dorn or Niskin sampling bottles, and subdivided for subsequent analyses. Samples were returned to the Crary Laboratory, McMurdo Station, Antarctica, for chemical analysis. Similar methods were employed for Lake Vanda, with detailed descriptions available from NIWA. Sampling was performed at least twice in each lake during the austral summer; sampling schedules also are posted on the McMurdo LTER web site. Data were available between years 1993 and 1998 for lakes in Taylor Valley, and between 1993 and 1996 in Lake Vanda. Approximately 1500 unique samples (date, depth, and lake) were used in analyses.

The density of water (ρ ; kg m⁻³) at depth in each lake was calculated according to Gill (1982) as defined by the Joint Panel on Oceanographic Tables and Standards (UNESCO, 1981). This method

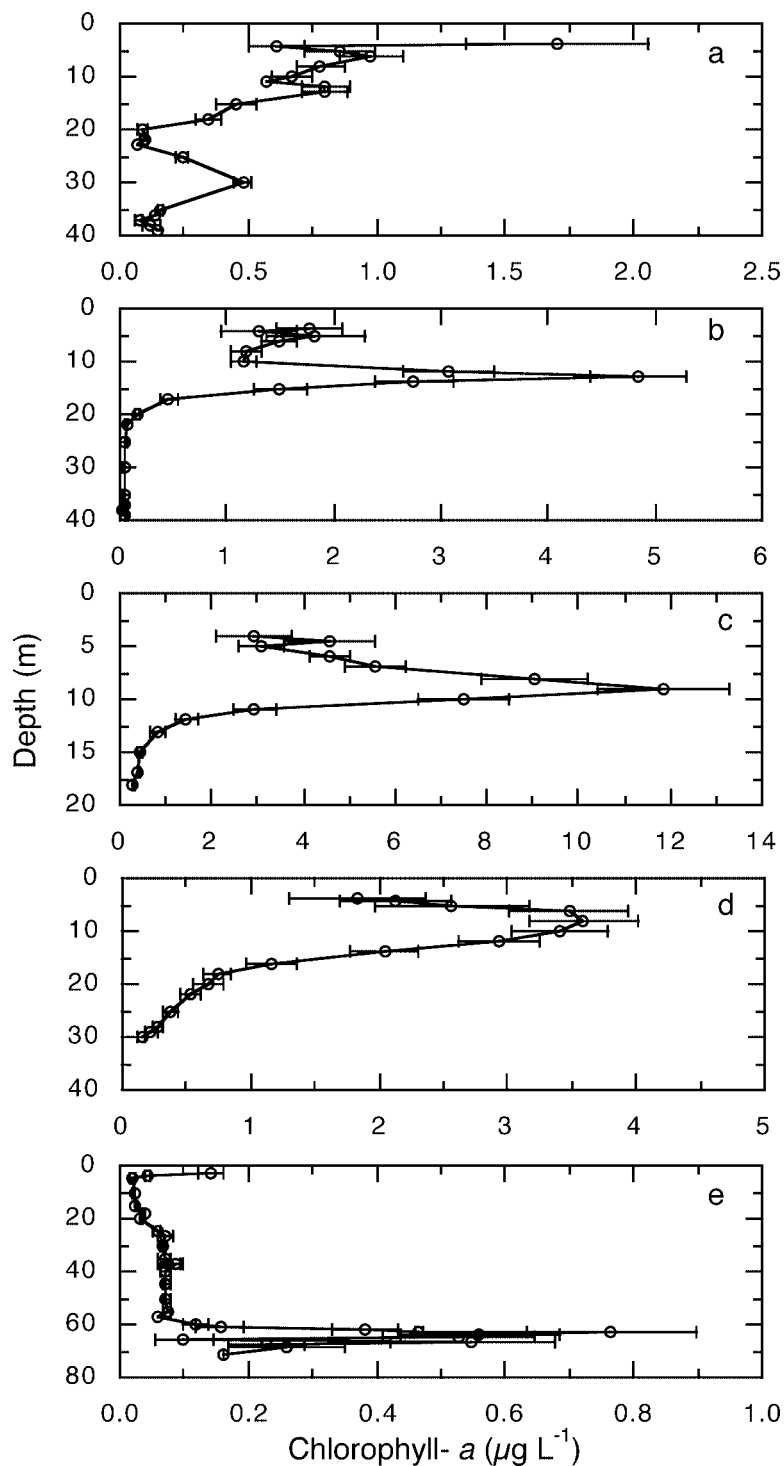


FIGURE 1. Depth profiles of chlorophyll-*a* ($\mu\text{g L}^{-1}$) concentrations (means \pm standard errors) in dry valley lakes: (a) east Lake Bonney, (b) west Lake Bonney, (c) Lake Fryxell, (d) Lake Hoare, and (e) Lake Vanda.

adjusts for the effects of temperature (t ; $^{\circ}\text{C}$), salinity (S ; practical salinity units or psu) and pressure (p ; bars), and requires several steps. First, the density of pure water (ρ_w) is calculated ($S = 0$) for a given temperature (t). Next, the density of water at one standard atmosphere ($p = 0$) is estimated, given temperature (t) and salinity (S). We assumed that water pressure increased approximately 1 bar per 10 m depth (Gill, 1982), and then calculated density at estimated pressure (p), given temperature (t) and salinity (S). Because ρ remains close to 1000 kg m^{-3} , the difference ($\sigma = \rho - 1000$; kg m^{-3}) often is used as a convenient means of expressing density in terms of departure from this benchmark (Gill, 1982). We used values of σ as representing density (DEN) in our analyses.

Variations within the density gradient in a water column might also influence the distribution of chlorophyll. For example, an abrupt increase in water density over a small change in depth could decrease the rate of settling, leading to a local accumulation of materials. We developed a measure of this incremental change in water density over depth (DEL) by dividing our metric of density (σ) at a given depth by the value at the next lower depth.

Because there were few recorded PAR measurements at depth in Lake Vanda, data used in analyses were estimated from surface observations. Intensity of PAR at depth (I_d) was calculated:

$$I_d = I_o \cdot e^{(-kd)}, \quad (1)$$

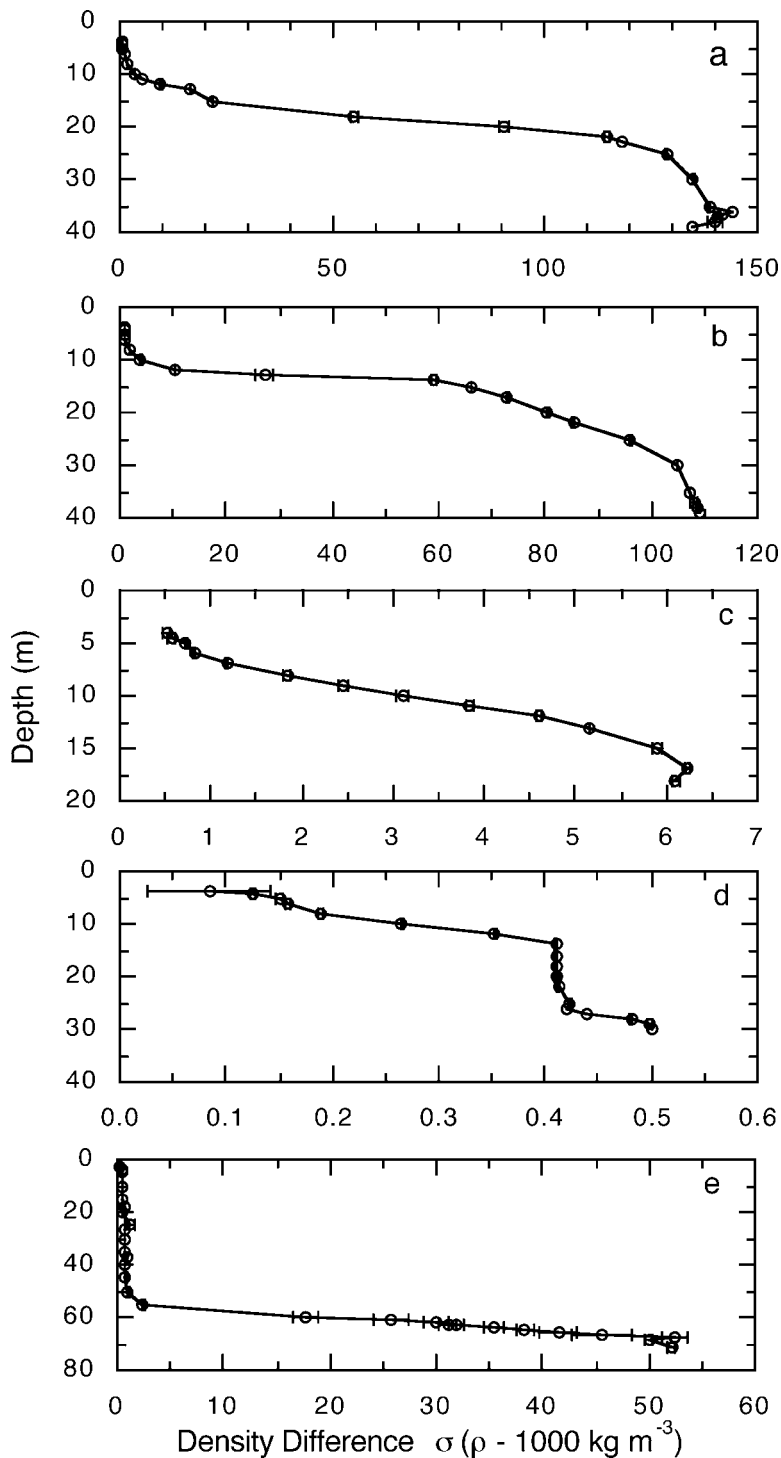


FIGURE 2. Depth profiles of water density (σ ; means \pm standard errors) in dry valley lakes: (a) east Lake Bonney, (b) west Lake Bonney, (c) Lake Fryxell, (d) Lake Hoare, and (e) Lake Vanda. Density calculated according to Gill (1982; $\sigma = \rho - 1000$, kg m^{-3}).

where I_0 is maximum PAR at the surface of the water beneath the permanent lake ice, k is the attenuation coefficient of the water column (0.05 m^{-1} ; Vincent, 1981; Howard-Williams et al., 1998), and d is depth in meters. In all cases, data identified as being unreliable or below detection limits were omitted from analyses.

STATISTICAL METHODS

Many of the data used in these analyses could not be transformed to meet the underlying assumption of normal distribution necessary for parametric tests. Therefore, nonparametric and distribution-free methods were used to evaluate relationships among variables. More-

over, observations were not balanced across time, lakes, and depths within lakes, suggesting a hierarchical approach to our investigation. Finally, two subsets of data were prepared for analyses: an unbound set that included data from all depths within each lake, and a bound set that was restricted to depths bracketing the DCM. The latter set was defined to reduce the influence of portions of the water column distant from the DCM, i.e., the high light and low nutrient environment in surface zones as well as dark, anoxic regions at greater depths. Bound data sets included depths approximately equidistant above and below the DCM, measured from the approximate location of the overlying minimum chlorophyll-*a* concentration. For example, the DCM for Lake Vanda occurs at 60 m with a minimum overlying chlorophyll-*a* concentration

at 55 m (Fig. 1). Therefore, the bound data set included data from 55 to 66 m. The DCM for West Bonney was estimated to be around 12 m, and the bound data spans 8 to 16 m. Fryxell's bound data lay between 5 and 12 m and Lake Hoare's bound data lay between 4 and 16 m. The DCM used for analyses of East Bonney is at 14 m, with bounds between 10 and 18 m. The second DCM in East Bonney at 30 m is biologically inactive and was examined separately (see below).

A suite of preliminary analyses was conducted to explore correlations between variables and patterns of variation in each variable over time, depth, and between lakes. First, all data were pooled and Spearman's rho was calculated for all pairs of variables: chlorophyll-*a* (CHL), DEN, DEL, DIN, PAR, DO, and SRP. Kruskal-Wallis one-way analysis for independent samples was used to test for significant differences in all parameter values between months and lakes. Data then were pooled by lake and Spearman's rho was used to assess correlations between variables within each lake. Kruskal-Wallis analysis was used to test for significant differences in all parameter values between months and between depths within each lake. Finally, data were pooled by month and Spearman's rho again was used to determine correlations between variables. Kruskal-Wallis analysis was used to test for significant differences in all parameter values between lakes by month. Lake Vanda was not included in the monthly analyses because data collected from this lake were not consistent across time with collections from the other lakes. Otherwise, these three sets of analyses were conducted for each of the bound and unbound sets of data previously described. Spearman rank correlations and Kruskal-Wallis tests were performed on raw (untransformed) data values with SPSS Version 9 (SPSS, Inc., 1998).

Multiple linear regression is commonly used to identify which combination of possible independent variables explains the greatest variation in a dependent variable. However, this method is based upon the assumption that data have normal distributions. An alternative approach has recently been developed, which can evaluate relationships among data that do not meet this assumption. Legendre et al. (1994) explained a partial Mantel method of performing multiple regression on distance matrices, with permutation testing of the regression parameters. Variables of the independent matrices remain fixed with respect to each other during permutation. We used the program, *Permute!* (Version 3.4), obtained from the Legendre laboratory via internet (Casgrain and Legendre, 2001) for our analyses. This program also will analyze vectors of data that have no inherent matrix structure, by permuting values of the dependent variable at random. Output includes estimated probability (*P*-values) of regression coefficients and associated R^2 values.

For our data, the dependent matrix consisted of simple Euclidian distances calculated between pairs of chlorophyll-*a* measures; independent matrices similarly consisted of distances between measures of DEN, DEL, DIN, PAR, and SRP (DO was considered to be more likely a result rather than a cause of chlorophyll concentrations and was not included in these analyses). We used the backward elimination procedure begun with entering all independent variables ($P = 0.10$ to remove) and compared the final model to one produced by the forward selection procedure ($P = 0.10$ to enter), because a stepwise method was not available. Analyses were performed on all data pooled from all lakes, for data pooled for each lake, and for data pooled by month. These analyses were repeated for bound and unbound data sets. Data from Lake Vanda were not included in the overall analysis of pooled data, because sampling regimes differed from other lakes, and too few bound data were available for specific examinations of Lake Vanda.

Results

Significant correlations existed between most water quality parameters: (1) when data from all lakes were pooled, (2) when data were analyzed by lake, and (3) when data were analyzed by month.

TABLE 1

Correlations between chlorophyll-*a* concentration (CHL) and other characteristics of the water column: dissolved oxygen (DO), density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP). Analyses performed for all depths (lower off-diagonal elements in table) and for depths bracketing deep chlorophyll maxima (upper off-diagonal elements).

	CHL	DO	DIN	DEN	DEL	PAR	SRP
CHL	1.000	0.049	-0.360	-0.434	-0.295	-0.382	-0.026
		0.323	0.001	0.001	0.001	0.001	0.594
		403	461	731	731	595	433
DO	0.494 ^a	1.000	-0.349	-0.229	0.003	0.140	-0.448
	0.001 ^b		0.001	0.001	0.959	0.005	0.001
	805 ^c		334	401	402	392	314
DIN	-0.543	-0.618	1.000	0.879	0.669	0.327	0.221
	0.001	0.001		0.001	0.001	0.001	0.001
	1016	706		482	483	424	399
DEN	-0.290	-0.504	0.846	1.000	0.789	0.445	0.285
	0.001	0.001	0.001		0.001	0.001	0.001
	1459	779	1064		752	593	454
DEL	0.031	-0.041	0.505	0.746	1.000	0.405	0.107
	0.257	0.264	0.001	0.001		0.001	0.021
	1368	753	991	1417		592	459
PAR	-0.358	0.200	0.062	-0.079	-0.072	1.000	-0.078
	0.001	0.001	0.075	0.008	0.016		0.123
	1123	690	816	1126	1101		398
SRP	-0.237	-0.486	0.423	0.359	0.077	-0.086	1.000
	0.001	0.001	0.001	0.001	0.024	0.021	
	887	621	872	931	868	716	

^a Spearman's rho.

^b *P*-value.

^c Number of observations.

This pattern was consistent for both data sets, including all depths (unbound set) and for depths bracketing the DCM (bound set). For example, only three pairs of parameters showed no significant correlation in the unbound set of data from all lakes combined: DEL and CHL, DEL and DO, and DIN and PAR (Table 1); only four pairs of parameters showed no significant correlation for the bound set of data: DO and CHL, DEL and DO, SRP and CHL, and SRP and PAR. These analyses also revealed that relationships between variables were sometimes inconsistent between bound and unbound data sets. For example, a significant, negative relationship existed between DO and CHL in the unbound set of data, but there was no relationship between these variables in the bound set (Table 1). Conversely, a significant, negative relationship existed between DEL and CHL in the bound set of data but not in the unbound set (Table 1). Thus relationships among some variables differed between the overall water column and in the vicinity of the DCM, as we suspected. Finally, some pairs of variables showed a very high strength of correlation. The strongest correlations were for DIN and DEN, with values of Spearman's rho exceeding 0.8 in both bound and unbound data sets (Table 1). Clearly, this level of correlation among variables complicates the interpretation of factors most likely to influence DCM formation.

When attention was focused on relationships between chlorophyll and the other water quality parameters, correlations with DIN were consistently among the strongest, with values of Spearman's rho ranging between -0.719 and 0.688, and averaging 0.662 (absolute values) for analyses of unbound data (Table 2). The relationships between chlorophyll and DEN were next in overall strength, ranging between -0.743 and 0.630, averaging 0.562 (based on absolute values). In both cases, correlations were negative for all analyses

TABLE 2

Correlations between chlorophyll-*a* concentration (CHL) and other characteristics of the water column: dissolved oxygen (DO), density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP). Analyses performed by lake (pooling months) on observations taken from the entire water column.

Parameter	All Lakes	E. Bonney	Fryxell	Hoare	Vanda	W. Bonney
DO	0.494 ^a	0.511	0.397	0.506	0.097	0.848
	0.001 ^b	0.001	0.001	0.001	0.361	0.001
	805 ^c	208	138	170	90	199
DIN	-0.543	-0.628	-0.715	-0.719	0.688	-0.679
	0.001	0.001	0.001	0.001	0.001	0.001
	1016	275	146	198	101	296
DEN	-0.290	-0.649	-0.461	-0.597	0.630	-0.743
	0.001	0.001	0.001	0.001	0.001	0.001
	1459	274	246	294	348	297
DEL	0.031	-0.330	0.323	0.405	0.411	0.359
	0.257	0.001	0.001	0.001	0.001	0.001
	1368	257	225	278	330	278
PAR	-0.358	0.535	0.362	0.696	-0.300	0.551
	0.001	0.001	0.001	0.001	0.001	0.001
	1123	218	145	181	353	226
SRP	-0.237	-0.368	-0.531	0.032	0.469	-0.371
	0.001	0.001	0.001	0.658	0.001	0.001
	887	214	180	196	66	231

^a Spearman's rho.

^b *P*-value.

^c Number of observations.

except Lake Vanda and for bound data from West Bonney. When analyses focused on the bound data set, correlations between chlorophyll and DIN remained among the strongest, with values of Spearman's rho ranging between -0.495 and 0.299, and averaging 0.367 (absolute values; Table 3). However, the relationship between chlorophyll and DEL was strongest, ranging between -0.463 and 0.640, averaging 0.337 (absolute values).

Although most variables showed significant correlation to chlorophyll in most analyses, important exceptions occurred. For example, SRP was correlated to chlorophyll in all lakes but Hoare from analyses of unbound data, but was significantly correlated to chlorophyll in only the bound data from Lake Fryxell. Similarly, SRP was correlated to chlorophyll in analyses of all months of unbound data, but was not correlated to chlorophyll in any months for bound data.

Kruskal-Wallis tests confirmed that significant differences existed between lakes in all water quality parameters, with the single exception of SRP for bound data in January ($P = 0.136$; results not shown). All water quality parameters also differed between depths within each lake for unbound data, and for nearly all water quality parameters in bound data. The major exception was that SRP showed significant differences with depth only in Lake Fryxell for analyses of bound data. Thus spatial differences (by depth) existed for almost all parameters in all lakes. Perhaps more interesting were results that showed few significant differences between months in values of DO, DIN, DEN, and DEL for any lake, from analyses of either bound or unbound data. In contrast, almost all lakes showed significant differences in chlorophyll, PAR, and SRP with month, in analyses of both bound and unbound data. Hence two groups of parameters seemed to exist, based on their variability over time, with this difference between groups being consistent among lakes.

The partial Mantel analysis of pooled data from all lakes entered DIN, DEL, and PAR into the regression model explaining chlorophyll

TABLE 3

Correlations between chlorophyll-*a* concentration (CHL) and other characteristics of the water column: dissolved oxygen (DO), density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP). Analyses performed by lake (pooling months) on observations taken from depths bracketing the location of the deep chlorophyll maximum in each lake.

Parameter	All Lakes	E. Bonney	Fryxell	Hoare	Vanda	W. Bonney
DO	0.049 ^a	0	0.221	0.097	0.189	0.271
	0.323 ^b	0	0.021	0.326	0.263	0.016
	403 ^c	75	109	104	37	78
DIN	-0.360	-0.439	-0.495	-0.441	0.299	0.165
	0.001	0.001	0.001	0.001	0.102	0.076
	461	95	103	115	31	117
DEN	-0.434	-0.379	-0.180	-0.159	0.310	0.191
	0.001	0.001	0.014	0.029	0.001	0.038
	731	95	187	190	141	118
DEL	-0.295	-0.463	0.199	0.233	-0.189	0.640
	0.001	0.001	0.006	0.001	0.027	0.001
	731	95	187	194	138	117
PAR	-0.382	0.195	0.311	0.550	0.451	-0.020
	0.001	0.061	0.001	0.001	0.001	0.841
	595	93	123	126	145	108
SRP	-0.026	-0.042	-0.251	0.134	-0.035	-0.023
	0.594	0.731	0.003	0.144	0.890	0.833
	433	70	136	120	18	89

^a Spearman's rho.

^b *P*-value. Same as in Tables 1 and 2.

^c Number of observations. Same as in Tables 1 and 2.

concentrations, based on unbound data (Table 4). The overall explanatory power of this model was low ($R^2 = 0.1356$) but highly significant ($P < 0.001$). Analysis of the bound data set also entered DIN and PAR, but added DEN and SRP. Again, the explanatory power of the model was highly significant but modest. Stronger relationships were identified for individual lakes (Table 5), suggesting that variations between lakes may have reduced the power of the model for pooled data from all lakes. For example, DEN, DEL, and PAR were entered into the model for East Bonney, based on unbound data, for an $R^2 = 0.4984$ ($P < 0.001$). However, little consistency was apparent in the strengths of the resulting models or the parameters selected, and physical variables (DEN and DEL) appeared as frequently as resource variables (DIN, SRP, and PAR), providing little resolution of our central hypothesis.

Partial Mantel analysis of data pooled by month provided more consistent results (Table 6). In almost all cases, DIN and PAR were entered as the only variables in regressions. The only other variable entered was DEN, in analyses of bound data for the months of November and December. Despite these consistent results, R^2 values were generally less than 0.3, although most relationships were highly significant ($P < 0.01$).

Discussion

Results of this study demonstrated that concentrations of chlorophyll-*a* were related to both resource availability (DIN, SRP, and PAR) and physical factors (DEN and DEL). Also, the relative importance of particular factors varied between analyses, suggesting that controls may differ between lakes and over time despite the permanent stratification of all dry valley lakes. When data were pooled (by lake and month), regressions included dissolved inorganic nitrogen (DIN) in both analyses of bound and unbound data (Table 4). When

TABLE 4

Results of partial Mantel analyses of data pooling lakes and months, for unbound and bound data sets. The independent variables were density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP).

Data	<i>N</i>	<i>R</i> ²	<i>P</i> -value ^a	Variable	<i>P</i> -value ^b
Unbound	583	0.1356	0.001	DIN	0.001
				DEL	0.005
				PAR	0.002
Bound	333	0.1096	0.001	DIN	0.001
				DEN	0.002
				PAR	0.004
				SRP	0.006

^a Overall model.

^b Individual parameter.

separate analyses were performed by lake, DIN was entered in six of nine analyses using backward elimination and four of nine analyses using forward selection procedures (Table 5). Thus inorganic nitrogen concentrations frequently explained a significant amount of variation in chlorophyll-*a* concentrations within lakes. These observations are consistent with earlier studies citing nutrient limitations on NPP as the probable cause of DCM location in dry valley lakes (Vincent and Vincent, 1982; Priscu et al., 1989; Priscu, 1995; Lizotte et al., 1996), as well as in other ecosystems (Marra et al., 1990; Revelante and Gilmartin, 1995; Wurtsbaugh et al., 2001; Camacho et al., 2003). Venrick et al. (1973) suggested that nutrient regime was the most important controlling factor when radiant energy is not limiting. However, these suggestions also imply a positive, causative relationship between DIN and chlorophyll concentration wherein relatively high concentrations of DIN at depths near the DCM drive primary production. In contrast, DIN was negatively correlated with chlorophyll-*a* concentrations in almost all of our analyses.

In most cases when a DCM is coincident with a nitracline, both nutrient and radiant energy regimes are important for the persistence of phytoplankton (Marra et al., 1990; Revelante and Gilmartin, 1995; Gecek and Legovic, 2001; Klausmeier and Litchman, 2001). In the dry valley lakes, PAR appeared in both analyses of pooled data (Table 4), in four of nine tests using backward elimination and five of nine analyses using forward selection procedures (Table 5). It was interesting that PAR was negatively correlated to chlorophyll-*a* concentration in overall analyses of data pooled by month and lake (Table 4), and when data were pooled by month (Table 6). However, correlations between these parameters usually were positive when data were pooled by lake. Thus relationships between PAR and chlorophyll that existed across months and depths within lakes were not consistent between lakes.

In addition to resource availability, water density (DEN) or change in density with depth (DEL) appeared in both analysis of bound and unbound data when all data were pooled (Table 4). When analyzed by lake, DEN or DEL appeared in three or four of the nine analyses, respectively (Table 5), so that at least one of the two parameters appeared in five of nine tests. These results support the notion that the DCM is related to density gradients within lakes (Steele and Yentsch, 1960; Steele, 1964; Pingree et al., 1975; Herbrand and Voituriez, 1979; Cullen, 1982). However, DEN and DIN were highly correlated (Table 1), so that much of the variation in chlorophyll-*a* concentration explained by one parameter could almost as readily be explained by the other variable. Indeed, DEN and DIN rarely co-occurred in regression models (Tables 4–6).

Different insights were provided by analyses performed on data pooled by month. Almost all regressions entered both DIN (10 of

TABLE 5

Results of partial Mantel analyses of data from each lake, using unbound and bound data sets. The independent variables were density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP).

Data	Lake	<i>N</i>	<i>R</i> ²	<i>P</i> -value ^a	Variable	<i>P</i> -value ^b
Unbound	East Bonney	164	0.4984	0.001	DEN	0.001
					DEL	0.005
					PAR	0.001
	West Bonney	185	0.5662	0.001	DIN	0.001
					DEL	0.001
					PAR	0.023
	Fryxell	109	0.1703	0.002	DIN	0.001
					PAR	0.001
	Hoare	121	0.2188	0.001	DIN	0.001
					PAR	0.013
	Vanda	48	0.8380	0.001	DEN	0.001
					SRP	0.001
Bound	East Bonney	68	0.1738	0.001	DEL	0.001 ^c
					West Bonney	89
	Fryxell	93	0.2101	0.001	DEN	0.001
					SRP	0.010 ^e
					DIN	0.001
	Hoare	83	0.0935	0.023	DIN	0.048
					PAR	0.039 ^f

^a Overall model.

^b Individual parameter.

^c Forward selection model included only DIN, *R*² = 0.1728, overall *P* = 0.001.

^d Forward selection model included only DEL, *R*² = 0.4312, overall *P* = 0.001.

^e Forward selection model also included PAR, *R*² = 0.2369, overall *P* = 0.002.

^f Forward selection model included only PAR, *R*² = 0.2603, overall *P* = 0.030.

10 analyses) and PAR (9 of 10 analyses). The only other variable ever entered was DEN, which occurred in analyses of bound data in both October and November (Table 6). Pooling by month emphasized the differences in parameter values between lakes, whereas pooling by lake emphasized differences between months. Kruskal-Wallis tests almost always revealed significant differences between lakes and months in both PAR and chlorophyll-*a* concentrations. In contrast, DIN, DEN, and DEL seldom differed between months although they almost always differed between lakes. The consistent inclusion of PAR and DIN in regressions explaining variation in chlorophyll within months (Table 6) and often in regressions explaining variations in chlorophyll within lakes (Table 5) suggested that this combination of resource variables explained both a component of variation in chlorophyll that varied over time (related to PAR), as well as a component that varied between lakes (related to DIN).

We expected PAR and nutrient concentration to influence DCM location in these lakes because: (1) several studies have shown that extreme shade-adaptation allows phytoplankton to survive at depths where PAR is very low (Lizotte and Priscu, 1992; Lizotte et al., 1996; Neale and Priscu, 1995); (2) Priscu (1995) already demonstrated nutrient limitations to phytoplankton productivity in these lakes and suggested this relationship as the primary control on DCM; and (3) Edwards and Priscu (1995) reported a positive relationship between DIN flux and net primary production of phytoplankton at the DCM in these lakes. However, we found that chlorophyll was usually negatively correlated to DIN and often negatively correlated to PAR. The explanation for this seeming anomaly is simple: chlorophyll-*a* concentrations are low at depths above the DCM where PAR is high and low at depths below the DCM where DIN is high. The resulting location of the DCM may be determined by a double-threshold

TABLE 6

Results of partial Mantel analyses of data from each month, using unbound and bound data sets. The independent variables were density (DEN), change in density/depth (DEL), dissolved inorganic nitrogen (DIN), photosynthetic active radiation intensity (PAR), and soluble reactive phosphorus (SRP).

Data	Month	N	R ²	P-value ^a	Variable	P-value ^b
Unbound	September	62	0.1901	0.006	DIN	0.002
					PAR	0.014
	October	94	0.1764	0.001	DIN	0.001
					PAR	0.009
	November	186	0.1679	0.001	DIN	0.001
					PAR	0.002
	December	166	0.1572	0.001	DIN	0.001
					PAR	0.001
	January	140	0.2480	0.001	DIN	0.001
					PAR	0.001
Bound	September	44	0.2600	0.012	DIN	0.024
					PAR	0.004
	October	48	0.1431	0.035	DIN	0.014 ^c
					DEN	0.046
					PAR	0.001
	November	106	0.2180	0.001	DIN	0.001
					DEN	0.020
					PAR	0.001
	December	97	0.0984	0.011	DIN	0.001
					PAR	0.012
January	38	0.3098	0.002	DIN	0.001	
				PAR	0.001	

^a Overall model.

^b Individual parameter.

^c Forward selection model included only DIN, $R^2 = 0.0805$, overall $P = 0.053$.

response of primary production to overlapping, minimum availabilities of PAR and DIN, which would appear as negative, individual relationships between chlorophyll and either resource. This is the general mechanism suggested to control the DCM in dry valley lakes (Edwards and Priscu, 1995).

THRESHOLD EFFECTS

In contrast to the mechanistic effects of PAR and nutrients on primary production, the passive concentration of particles along a density gradient is likely to be a threshold phenomenon that is independent of the number of particles that accumulate. If density were a controlling factor, then we argue that the location of the DCM should be consistent with respect to density, regardless of the concentration of chlorophyll that constitutes the DCM. In fact, the DCM in East Bonney, West Bonney, and Lake Vanda all occur at σ values ca. 20–29 kg m^{-3} , suggesting a consistent threshold response. However, the DCM in Lakes Fryxell and Hoare occur at ca. 2 and 0.3 kg m^{-3} , respectively. These observations are consistent with results of partial Mantel analyses performed by lake, in which DEN or DEL were included in regressions for East Bonney, West Bonney, and Lake Vanda, but not Fryxell or Hoare (Table 5), and suggest that the effect of water density on DCM depends on the absolute density gradient. The additional importance of resource availabilities within East Bonney, West Bonney, and Lake Vanda may reflect more continuous variations in concentrations of chlorophyll over depth than the actual location of the DCM. By the same logic, the importance of PAR and DIN in analyses of all lakes by month may reflect differences in resource availabilities between lakes.

An additional type of threshold response between chlorophyll-*a* and environmental parameters in these lakes is worth mentioning. A PAR intensity of 5–50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ was coincident with the

location of the DCM in these lakes. These intensities of radiant energy also correspond to values reported near DCM in other studies (Steele, 1964; Venrick et al., 1973; Moll et al., 1984; Larson et al., 1987; Revelante and Gilmartin, 1995). Typically, DCM are associated with radiant energy levels <1% ambient, and always below 5% ambient level (Fee, 1976; Moll and Stoermer, 1982; Larson, 2000; Perez et al., 2002). The calculated intensity of PAR at the DCM for Vanda (50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was <5% of incident levels, but much higher than in the other dry valley lakes (<5 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) because transmission through the permanent ice cover is much greater (5–20%). Although we previously discussed the positive influence that nutrients may have on DCM by stimulating primary production, negative impacts of very high concentrations of solutes below the DCM may inhibit biological activity. For example, Green et al. (1998) reported concentrations of metal ions beneath the DCM in Lake Vanda that may be toxic to many organisms. Thus, high concentrations of solutes in deeper waters of some dry valley lakes may impose a lower boundary on DCM through negative rather than positive impacts on primary production (but see below).

A DOUBLE DCM

The relationship between primary productivity and DCM was not the focus of this study, but the depth of maximum chlorophyll-*a* concentration frequently coincides with the location of highest primary production in a body of water (Cullen and Eppley, 1981). The DCM layer also may account for a major fraction of the phytoplankton standing crop (Jamart et al., 1977). In these dry valley lakes, Priscu (1995) found peaks in primary productivity coincident with DCM in Lake Fryxell, East Bonney, and at 14 m depth in West Bonney. A striking contrast to this pattern is the lack of detectable photosynthesis near a second, deeper DCM located at 30 m in East Bonney, repudiating the notion that biological activity is necessary to produce a DCM (Fig. 3). Our previous analyses did not include this deep DCM because we did not wish to prejudice results by including an example that lacked biological activity and thus was qualitatively distinct from the others. We now briefly compare the two DCM layers in East Bonney.

The DCM at 14 m in East Bonney corresponds with a peak in primary productivity and high respiration, whereas the peak at 30 m does not (Fig. 3). In fact, the peak at the 30 m corresponds with a layer of nearly anoxic water (ca. 0.2 $\mu\text{g O}_2 \text{L}^{-1}$), maximum density of the water column (ca. 135 kg m^{-3}), extremely low PAR (<1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), and high DIN (ca. 9–14 μM), suggesting physical rather than biotic control. Priscu (1995) noted that the organisms forming this peak are not photosynthetically viable, and therefore may be bacteria. A peak such as this in Antarctic lakes is not unique. Bell and Laybourn-Parry (1999) mentioned an apparent DCM in the anoxic monimolimnion in Ace Lake in the Vestfold Hills, and attributed its cause to photosynthetic bacteria. However, no photosynthetic activity has been detected (¹⁴C-uptake) near the deeper chlorophyll maximum in East Bonney, and respiration (measured as respiratory electron transport system activity in all aerobic organisms) associated with this layer is extremely low.

Partial Mantel analyses of bound data sets suggested that these two DCM were associated with different environmental controls, but results were equivocal. The backward elimination procedure included only DEL in the model explaining the DCM at 14 m ($R^2 = 0.1738$, $P = 0.001$), but the forward selection procedure entered only DIN (Table 5; $R^2 = 0.1728$, $P = 0.001$). In contrast, DEN was the only variable retained by backward elimination for the peak at 30 m, although the relationship was not significant ($R^2 = 0.3859$, $P = 0.124$) and forward selection added no variables to the model. The occurrence of two DCM in one body of water is rare. We are aware of only one other lake (Lake

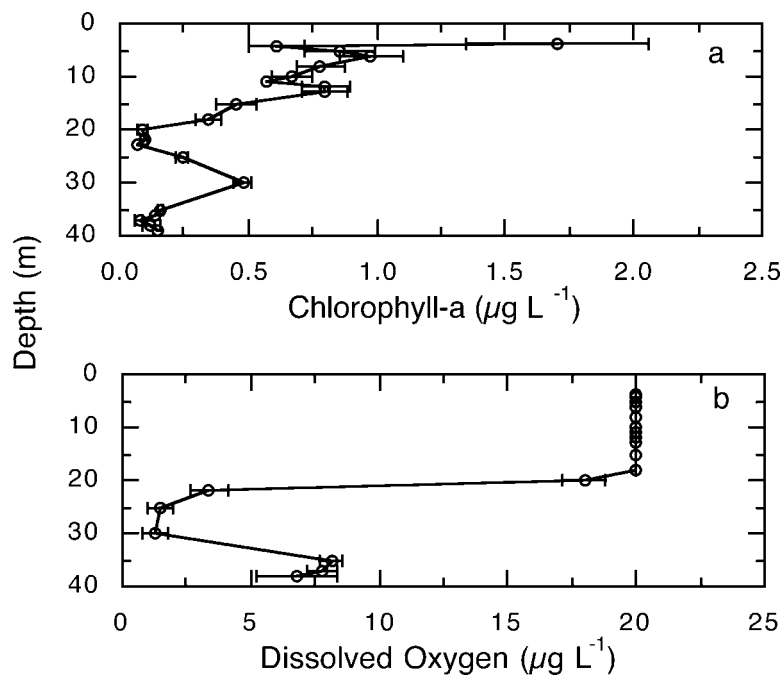


FIGURE 3. Depth profiles of chlorophyll-*a* ($\mu\text{g L}^{-1}$) and dissolved oxygen ($\mu\text{g O}_2 \text{L}^{-1}$) in east Lake Bonney (means \pm standard errors).

Tahoe, California, U.S.A.) that is reported to exhibit simultaneous, multiple DCM arising from different processes. There, a DCM at 100 m was attributed to a physiological response of the cells to higher nutrient concentrations, whereas a DCM at 320–350 m was credited to the passive sinking of phytoplankton (Kiefer et al., 1972). Unfortunately, results of our analyses for East Bonney are less certain.

Conclusions

Probably the most important result of this study was the implication that both density and resource availability control DCM in dry valley lakes. The frequency with which DIN and PAR appeared in regressions is consistent with the general hypothesis that resource availability strongly influences chlorophyll concentrations, as well as conclusions of earlier studies suggesting resource control of DCM in dry valley lakes (Vincent and Vincent, 1982; Priscu et al., 1989; Priscu, 1995; Edwards and Priscu, 1995; Lizotte et al., 1996). However, our analyses also found a consistent relationship between water density and DCM in the most oligotrophic of these lakes. Thus a distinction between chlorophyll concentration and DCM must be recognized because variations in chlorophyll concentrations within and between lakes may obscure relationships between DCM and environmental factors. Finally, cause-and-effect relationships between water chemistry and biological activity in these lakes may be more complicated than for many other systems, due to the long-term stability of the water column of dry valley lakes. Green et al. (1998) reported concentrations of metals beneath the DCM in Lake Vanda that may be toxic to biota, but conditions influencing solute chemistry (e.g., pH), in turn are affected by biological activities. Thus millennial-scale interactions between density gradient, resource availability, biological activity, and water chemistry may dynamically link these features of dry valley lakes and challenge the notion that any one explanation exists for DCM location.

In conclusion, Venrick et al. (1973) suggested that one clear explanation for the cause of a particular DCM should be found, implying that one could be found. However, we concur with Priscu and Neale (1995) that a number of interacting factors control DCM within the dry valley lakes. Other studies have reported that distributions of chlorophyll-*a* and primary production were regulated by the interaction of both density and nutrient concentration (Herbland and Voituriez,

1979), thus patterns within the dry valley lakes are not unique in this regard. Moreover, Jamart et al. (1977) concluded that the formation of a DCM requires a combination of many processes, including *in situ* production, with each process playing a rather specific role. It seems logical to assume that the relative importance of these processes may vary between systems as well as over time for a single system.

Acknowledgments

Financial support for this work was provided by grants from the U.S. National Science Foundation (OPP-0096250 and INT-9804949), and from the New Zealand Foundation for Research Science and Technology (CO1816).

References Cited

- Bell, E. M., and Laybourn-Parry, J., 1999: Annual plankton dynamics in an Antarctic saline lake. *Freshwater Biology*, 41: 507–519.
- Brooks, A. S., and Torke, B. G., 1977: Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. *Journal of the Fisheries Research Board of Canada*, 34: 2280–2287.
- Camacho, A., Wurtsbaugh, W. A., Miracle, M. R., Armengol, X., and Vicente, E., 2003: Nitrogen limitation of phytoplankton in a Spanish karst lake with a deep chlorophyll maximum: a nutrient enrichment bioassay approach. *Journal of Plankton Research*, 25: 397–404.
- Carlson, C. A., Phillips, F. M., Elmore, D., and Bentley, H. W., 1990: Chlorine-36 tracing of salinity sources in the dry valleys of Victoria Land, Antarctica. *Geochimica et Cosmochimica Acta*, 54: 311–318.
- Casgrain, P., and Legendre, P., 2001: The R package for multivariate and spatial analysis, version 4.0d6—user's manual. Département de sciences biologiques, Université de Montréal (<http://www.fas.umontreal.ca/BIOL/legendre/>).
- Coon, T. G., Lopez, M., Richerson, P. J., Powell, T. M., and Goldman, C. R., 1987: Summer dynamics of the deep chlorophyll maximum in Lake Tahoe. *Journal of Plankton Research*, 9: 327–344.
- Cullen, J. J., 1982: The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 803.
- Cullen, J. J., and Eppley, R.W., 1981: Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. *Oceanologica Acta*, 4: 23–32.

- Deksheniaks, M. M., Donaghay, P. L., Sullivan, J. M., Rines, J. E. B., Osborn, T. R., and Twardowski, M. S., 2001: Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. *Marine Ecology Progress Series*, 223: 61–71.
- Doran, P., Berger, G. W., Lyons, W. B., Wharton, R. A., Davisson, M. L., Southon, J., and Dobb, J. E., 1999: Dating Quaternary lacustrine sediments in the McMurdo Dry Valleys, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 147: 223–239.
- Dore, J. E., and Priscu, J. C., 2001: Phytoplankton phosphorus deficiency and alkaline phosphatase activity in the McMurdo Dry Valley lakes, Antarctica. *Limnology and Oceanography*, 46: 1333–1346.
- Edwards, R. L., and Priscu, J. C., 1995: McMurdo LTER: Relationships between vertical nutrient flux and phytoplankton biomass and productivity in lakes of the Taylor Valley, Antarctica. *Antarctic Journal of the United States*, 30: 294–295.
- Fee, E. J., 1976: The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. *Limnology and Oceanography*, 21: 767–782.
- Fountain, A. G., Lyons, W. B., Burkins, M. B., Dana, G. L., Doran, P. T., Lewis, K. J., McKnight, D. M., Moorhead, D. L., Parsons, A. N., Priscu, J. C., Wall, D. H., Wharton, R. A., and Virginia, R. A., 1999: Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience*, 49: 961–971.
- Gecek, S., and Legovic, T., 2001: Nutrients and grazing in modeling the deep chlorophyll maximum. *Ecological Modelling*, 138: 143–152.
- Gill, A. E., 1982: *Atmosphere-ocean dynamics*. New York: Academic Press.
- Green, W. J., Canfield, D. E., and Nixon, P., 1998: Cobalt cycling and fate in Lake Vanda. In Priscu, J. (ed.), *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica*. Washington, DC: American Geophysical Union, Antarctic Research Series, 72: 205–215.
- Herbland, A., and Voituriez, B., 1979: Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean. *Journal of Marine Research*, 37: 87–101.
- Howard-Williams, C., Schwarz, A., and Hawes, I., 1998: Optical properties of the McMurdo Dry Valley Lakes, Antarctica. In Priscu, J. (ed.), *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica*. Washington, DC: American Geophysical Union, Antarctic Research Series, 72: 189–203.
- Jamart, B. M., Winter, D. F., Banse, K., Anderson, G. C., and Lam, R. K., 1977: A theoretical study of phytoplankton growth and nutrient distribution in the Pacific Ocean off the northwestern U.S. coast. *Deep-Sea Research*, 24: 753–773.
- James, M. R., Hall, J., and Laybourn-Parry, J., 1998: Protozooplankton and microzooplankton ecology in lakes of the dry valleys, Southern Victoria Land. In Priscu, J. (ed.), *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica*. Washington, DC: American Geophysical Union, Antarctic Research Series, 72: 255–266.
- Jerlov, N. G., 1959: Maxima in the vertical distribution of particles in the sea. *Deep-Sea Research*, 5: 173–184.
- Jones-Lee, A., and Lee, G. F., 1993: The relationship between phosphorus load and eutrophication response in Lake Vanda. In Green, W. J., and Friedmann, E. I. (eds.), *Physical and biogeochemical processes in Antarctic Lakes*. Washington, DC: American Geophysical Union, Antarctic Research Series, 59: 197–214.
- Kiefer, D. A., and Kremer, J. N., 1981: Origins of vertical patterns of phytoplankton and nutrients in the temperate, open ocean: a stratigraphic hypothesis. *Deep-Sea Research*, 28A: 1087–1105.
- Kiefer, D. A., Holm-Hansen, O., Goldman, C. R., Richards, R., and Berman, T., 1972: Phytoplankton in Lake Tahoe: deep-living populations. *Limnology and Oceanography*, 17: 418–423.
- Klausmeier, C. A., and Litchman, E., 2001: Algal games: The vertical distribution of phytoplankton in poorly mixed water columns. *Limnology and Oceanography*, 46: 1998–2007.
- Larson, D. W., Dahm, C. N., and Geiger, N. S., 1987: Vertical partitioning of the phytoplankton assemblage in ultraoligotrophic Crater Lake, Oregon, U.S.A. *Freshwater Biology*, 18: 429–442.
- Larson, G. L., 2000: Chlorophyll maxima in mountain ponds and lakes, Mount Ranier National Park, Washington State, USA. *Lake Reservoir Management*, 16: 333–339.
- Legendre, P., Lapointe, F.-J., and Casgrain, P., 1994: Modeling brain evolution from behavior: a permutational regression approach. *Evolution*, 48: 1487–1499.
- Lizotte, M. P., and Priscu, J. C., 1992: Photosynthesis-irradiance relationships in phytoplankton from the physically stable water column of a perennially ice-covered lake. *Journal of Phycology*, 28: 179–185.
- Lizotte, M. P., Sharp, T. R., and Priscu, J. C., 1996: Phytoplankton dynamics in stratified water column of Lake Bonney, Antarctica. I. Biomass and productivity during the winter-spring transition. *Polar Biology*, 16: 155–162.
- Marra, J., Bidigare, R. R., and Dickey, T. D., 1990: Nutrients and mixing, chlorophyll and phytoplankton growth. *Deep-Sea Research*, 37: 127–143.
- Matsumoto, G. I., 1993: Geochemical features of the McMurdo Dry Valley Lakes, Antarctica. In Green, W. J., and Friedmann, E. I. (eds.), *Physical and biogeochemical processes in Antarctic Lakes*. Washington, DC: American Geophysical Union, Antarctic Research Series, 59: 95–118.
- Moll, R. A., and Stoermer, E. F., 1982: A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. *Archiv für Hydrobiologie*, 94: 425–440.
- Moll, R. A., Brahe, M. Z., and Peterson, T. P., 1984: Phytoplankton dynamics within the subsurface chlorophyll maximum of Lake Michigan. *Journal of Plankton Research*, 6: 751–766.
- Neale, P. J., and Priscu, J. C., 1995: The photosynthetic apparatus of phytoplankton from a perennially ice-covered Antarctic lake: Acclimation to an extreme shade environment. *Plant and Cell Physiology*, 36: 253–263.
- Neale, P. J., and Priscu, J. C., 1998: Fluorescence quenching in phytoplankton of the McMurdo Dry Valley lakes (Antarctica): implications for the structure and function of the photosynthetic apparatus. In Priscu, J. (ed.), *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica*. Washington, DC: American Geophysical Union, Antarctic Research Series, 72: 241–253.
- Parker, B. C., Simmons, G. M., Jr., Seaburg, K. G., Cathey, D. D., and Allnut, F. C. T., 1982: Comparative ecology of plankton communities in seven Antarctic oasis lakes. *Journal of Plankton Research*, 4: 271–285.
- Perez, G. L., Queimaliños, C. P., and Modenutti, B. E., 2002: Light climate and plankton in the deep chlorophyll maxima in North Patagonian Andean lakes. *Journal of Plankton Research*, 24: 591–599.
- Pingree, R. D., Pugh, P. R., Holligan, P. M., and Forster, G. R., 1975: Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature*, 258: 672–677.
- Priddle, J., Hawes, I., and Ellis-Evans, J. C., 1986: Antarctic aquatic ecosystems as habitats for phytoplankton. *Biological Reviews*, 61: 199–238.
- Priscu, J., 1995: Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology*, 34: 215–227.
- Priscu, J. C., and Neale, P. J., 1995: Phototactic response of phytoplankton forming discrete layers within the water column of Lake Bonney, Antarctica. *Antarctic Journal of the United States*, 30: 301–303.
- Priscu, J., Priscu, L. R., Vincent, W. F., and Howard-Williams, C., 1987: Photosynthate distribution by microplankton in permanently ice-covered Antarctic desert lakes. *Limnology and Oceanography*, 32: 260–270.
- Priscu, J., Vincent, W., and Howard-Williams, C., 1989: Inorganic nitrogen uptake and regeneration in perennially ice-covered Lakes Fryxell and Vanda, Antarctica. *Journal of Plankton Research*, 11: 335–351.
- Revelante, N., and Gilmartin, M., 1995: The relative increase of larger phytoplankton in a subsurface chlorophyll maximum of the northern Adriatic Sea. *Journal of Plankton Research*, 17: 1535–1562.

- Shortreed, K. S., and Stockner, J. G., 1990: Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 262–273.
- Spigel, R. H., and Prisco, J. C., 1998: Physical limnology of the McMurdo Dry Valleys Lakes. In Prisco, J. (ed.), *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica*. American Geophysical Union, Antarctic Research Series, 72: 153–187.
- SPSS Inc., 1998: Version 9.0. SPSS Inc., Chicago, IL, U.S.A.
- Steele, J. H., 1964: A study of production in the Gulf of Mexico. *Journal of Marine Research*, 22: 211–222.
- Steele, J. H., and Yentsch, C. S., 1960: The vertical distribution of chlorophyll. *Journal of the Marine Biological Association of the United Kingdom*, 39: 217–226.
- Torii, T., and Yamagata, N., 1981: Limnological studies of saline lakes in the dry valleys. In McGinnis, L. (ed.), *Dry valley drilling project*. American Geophysical Union, Antarctic Research Series, 33: 141–159.
- UNESCO, 1981: Tenth report of the joint panel on oceanographic tables and standards. UNESCO Technical Papers in Marine Science, no. 36. Paris: UNESCO.
- Venrick, E. L., McGowan, J.A., and Mantyla, A.W., 1973: Deep maxima of photosynthetic chlorophyll in the Pacific Ocean. *Fishery Bulletin*, 71: 41–52.
- Vincent, W. F., 1981: Production strategies in Antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. *Ecology* 62: 1215–1224.
- Vincent, W. F., and Vincent, C. L., 1982: Factors controlling phytoplankton production in Lake Vanda. *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 1602–1609.
- Wharton, R. A., Jr., Simmons, G. M., Jr., and McKay, C. P., 1989: Perennially ice-covered Lake Hoare, Antarctica: physical environment, biology, and sedimentation. *Hydrobiologia*, 172: 305–320.
- Wurtsbaugh, W. A., Gross, H. P., Budy, P., and Luecke, C., 2001: Effects of epilimnetic versus metalimnetic fertilization on the phytoplankton and periphyton of a mountain lake with a deep chlorophyll maxima. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2156–2166.

Revised ms submitted April 2005