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Phytoplankton nutrient deficiency in lakes of the McMurdo dry valleys, Antarctica

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SUMMARY

1. The influence of inorganic nitrogen and phosphorus enrichment on phytoplankton photosynthesis was investigated in Lakes Bonney (east and west lobes), Hoare, Fryxell and Vanda, which lie in the ablation valleys adjacent to McMurdo Sound, Antarctica. Bioassay experiments were conducted during the austral summer on phytoplankton populations just beneath the permanent ice cover in all lakes and on populations forming deep-chlorophyll maxima in the east and west lobes of Lake Bonney.

2. Phytoplankton photosynthesis in surface and mid-depth (13 m) samples from both lobes of Lake Bonney were stimulated significantly ($P < 0.01$) by phosphorus enrichment (2 µM) with further stimulation by simultaneous phosphorus plus NH_4^+ (20 µM) enrichment. Similar trends were observed in deeper waters (18 m) from the east lobe of Lake Bonney, although they were not statistically significant at $P < 0.05$. Photosynthesis in this lake was never enhanced by the addition of 20 µM NH_4^+ alone. Simultaneous addition of phosphorus plus nitrogen stimulated photosynthesis significantly ($P < 0.01$) in both Lake Hoare and Lake Fryxell. No nutrient response occurred in Lake Vanda, where activity in nutrient-enriched samples was below unamended controls; results from Lake Vanda are suspect owing to excessively long sample storage in the field resulting from logistic constraints.

3. Ambient dissolved inorganic nitrogen (DIN) ($NH_4^+ + NO_2^- + NO_3^-$) : soluble reactive phosphorus (SRP) ratios partially support results from bioassay experiments indicating strong phosphorus deficiency in Lake Bonney and nitrogen deficiency in Lakes Hoare and Fryxell. DIN : SRP ratios also imply phosphorus deficiency in Lake Vanda, although not as strong as in Lake Bonney. Particulate carbon (PC) : particulate nitrogen (PN) ratios all exceed published ratios for balanced phytoplankton growth, indicative of nitrogen deficiency.

4. Vertical nutrient profiles in concert with low advective flux, indicate that new (*sensu* Dugdale & Goering, 1967) phytoplankton production in these lakes is supported by upward diffusion of nutrients from deep nutrient pools. This contention was tested by computing upward DIN : SRP flux ratios across horizontal planes located immediately beneath each chlorophyll maximum and about 2 m beneath the ice (to examine flux to the phytoplankton immediately below the ice cover). These flux ratios further corroborated nutrient bioassay results and bulk DIN : SRP ratios indicating phosphorus deficiency in Lakes Bonney and Vanda and potential nitrogen deficiency in Lakes Hoare and Fryxell.

5. Neither biochemical reactions nor physical processes appear to be responsible for differences in nutrient deficiency among the study lakes. The differences may instead be related to conditions which existed before or during the evolution of the lakes.

Introduction

The study of phytoplankton nutrient deficiency has been a central theme of both limnology and oceanography for many years (e.g. Likens, 1972; Dodds, Johnson & Priscu, 1989; Elser & Hassett, 1994). Despite intensive research in this area, there remains debate on which nutrients limit the biological productivity of aquatic systems (Smith, 1984; Morel *et al.*, 1994). Several general concepts regarding nutrient deficiency have been put forward (Smith, 1984; Elser & Hassett, 1994). Smith contended that lakes are generally phosphorus deficient, whereas marine systems are nitrogen deficient. He based this differentiation on the balance between phosphorus input via advection and nitrogen gains and losses by N_2 fixation and denitrification, respectively. More recently, Elser & Hassett (1994), studying elemental ratios in various components of the food web, also concluded that phosphorus deficiency was more prevalent in lakes than in marine systems. The data bases used by both Smith and Elser focused on temperate systems; little attention was given to high-latitude aquatic systems. It is clear that high-latitude marine systems, given their relatively low phytoplankton biomass despite high nutrient concentrations, do not fit the paradigms proposed for temperate marine systems (e.g. Chisholm & Morel, 1991). High-latitude lakes, however, have not been included in general models regarding nutrient deficiency presumably because little data on this aspect of these systems exist.

Previous reports on nutrient deficiency in Antarctic lakes are based primarily on indirect evidence such as nitrogen to phosphorus ratios in the water column (Hoehn *et al.*, 1977), nutrient ratios in streams entering the lakes (Canfield & Green, 1985), photobiological responses of phytoplankton (Lizotte & Priscu, 1994; Neale & Priscu, 1995) and direct measurement of nitrogen uptake using 15-nitrogen labelled compounds (Priscu, Vincent & Howard-Williams, 1989; Priscu, 1989). The only detailed experimental bioassay work focused on coastal lakes and ponds on Ross Island (Vincent & Vincent, 1982a) and Lake Vanda (Vincent & Vincent, 1982b). With the recent inception of studies focusing on photosynthesis (Priscu *et al.*, 1990; Lizotte & Priscu, 1992a, 1994; Neale & Priscu, 1995) and nitrogen transformations (e.g. Priscu, Ward & Downes, 1993) in the permanently ice-covered lakes of the dry valley region of McMurdo Sound, knowledge of nutrient regulation of primary productivity in these systems is imperative. The paper reports results from experimental nutrient (nitrogen and phosphorus) bioassays conducted on Lakes Bonney (east and west lobes), Hoare, Fryxell and Vanda.

Materials and methods

Study sites

Studies were conducted in the east and west lobes of Lake Bonney, Lake Hoare, Lake Fryxell and Lake Vanda during November and December 1993. All of these lakes exist in ablation valleys of the Transantarctic Mountains adjacent to McMurdo Sound. The first three lakes reside in the Taylor Valley, whereas Lake Vanda lies in the Wright Valley (Chinn, 1993). All lakes are covered by 3–5 m of permanent ice and show varying degrees of chemical stratification with relatively nutrient-poor water overlying nutrient-rich deep water. Sodium chloride is the dominant salt in the deep waters of the Taylor Valley lakes, whereas $CaCl_2$ is the major salt in the deep waters of Lake Vanda. The trophogenic zone in these lakes usually extends from the bottom of the ice cover to the nutricline; between 1 and 5% of incident irradiance penetrates the ice covers (Priscu, 1991; Lizotte & Priscu, 1992b). Owing to low turbulence (Spigel, Sheppard & Priscu, 1990), phytoplankton form discrete layers with biomass maxima generally occurring just beneath the ice cover and immediately above the nutricline. Phytoplankton photosynthesis exists only for about 6 months per year when adequate light is present (Sharp, 1993; Lizotte, Sharp & Priscu, 1995). A major portion of the phytoplankton biomass in the study lakes is comprised flagellates (Vincent, 1981, 1982b; Sharp, 1993; Spaulding *et al.*, 1994) which appear to maintain their position in the water column partially through phototactic responses (J.C. Priscu, unpublished data). Detailed descriptions of these lake systems can be found in Green & Friedmann (1993).

Nutrient bioassays experiments

Nutrient bioassay experiments were conducted on phytoplankton populations from 5, 13 and 18 m, and 5 and 13 m in the east and west lobes of Lake Bonney, respectively, and at 5 m in Lakes Hoare, Fryxell and Vanda (all depths are from the piezometric water level in the sampling hole). The depths selected for Lake Bonney were immediately beneath the ice cover and from deep-water phytoplankton biomass and productivity maxima; those for the other lakes represent the phytoplankton assemblage immediately beneath the permanent ice covers. Logistics did not allow experiments to be conducted on deep phytoplankton maxima in lakes other than Bonney.

All bioassay experiments were conducted at Lake Bonney in a shore-side field camp during November and December 1993. A 20-l water sample was collected from each lake through a hole drilled in the ice cover. Samples collected from lakes other than Bonney were stored in the dark near 2 °C during transport by helicopter (within 30 min of collection) to the Lake Bonney laboratory where experiments were initiated immediately, except for the sample from Lake Vanda which, owing to helicopter logistics, was stored in the dark for about 10 h before the experiment could be set up. Once at the Lake Bonney laboratory, a 4-l subsample was enriched with ^{14}C-bicarbonate (0.1–0.8 μCi ml^{-1} final concentration) and 500 ml was decanted into each of eight acid-leached high-density polyethylene bottles. Nutrients were added to duplicate bottles to yield the following enrichments: 20 μM NH_4^+, 2 μM PO_4^{-3}, 20 μM NH_4^+ plus 2 μM PO_4^{-3}; two non-amended bottles served as controls. All samples were placed in an environmental chamber that simulated light and temperature from which the samples were collected. Subsamples (80 ml) were removed from each bottle at 24 h intervals over a 144-h period and filtered through Whatman GF/F filters. The filters were acidified with 0.5 ml 3 N HCl and dried at 50 °C to remove unincorporated isotope. Radioactivity on the filters (which is referred to hereafter as photosynthetic activity) was determined by standard liquid scintillation spectrometry at McMurdo Station.

Chemistry and particulate matter

Ammonium, NO_2^-, NO_3^- and soluble reactive phosphorus (SRP) were measured on filtered (Whatman GF/F) samples according to Parsons *et al.* (1984), modified to accommodate a 10-ml sample. Samples exceeding sea water salinity were diluted with deionized water to yield final salinities below that of sea water. Recovery of internal nutrient standards varied between 90 and 110%. Phaeophytin-corrected chlorophyll *a* was quantified by comparing fluorescence (Turner Designs AU10 fluorometer) of samples filtered on to Whatman GF/F filters and extracted overnight in 90% acetone with pure chlorophyll *a* standards (Holm-Hansen *et al.*, 1965). Tests on Lake Bonney samples showed that this extraction protocol was as efficient as samples that had been homogenized with a glass-Teflon tissue homogenizer before extraction (Lizotte & Priscu, 1992b). Particulate carbon (PC) and particulate nitrogen (PN) were measured on samples filtered on to precombusted (450 °C for > 4 h) Whatman GF/F filters with a Carlo Erba model 1500 elemental analyser standardized with acetanilide. Temperature and conductivity profiles were measured with a Seabird SBE 25 CTD system fitted with both fine structure and microstructure sensors.

Primary productivity

Vertical profiles of primary productivity were made by measuring ^{14}C-bicarbonate incorporation into particulate matter over a 24-h *in-situ* incubation. Separate experiments in the east lobe of Lake Bonney showed that rates from a single 24 h incubation were not statistically different from the sum of 4–6 h incubations (Sharp, 1993). Samples were filtered on to Whatman GF/F filters, acidified with 0.5 ml 3 N HCl, air dried at 50 °C and counted using standard scintillation spectrometry. Dissolved inorganic carbon, required for productivity rate calculations, was determined by passing the gas from acid-sparged samples through a calibrated infra-red gas analyser.

Diffusion model

Upward diffusion of inorganic nitrogen and phosphorus across specified horizontal planes was computed according to the following equation:

$$\frac{dC}{dt} = \frac{\delta}{\delta z}\left(K_z \frac{\delta C}{\delta z}\right)$$

where: dC/dt = upward flux of nutrient (μmol m^{-2} day^{-1}), K_z = vertical diffusion coefficient (10^{-9} m^2 s^{-1}), z = depth (m).

The planes of calculation for the equation were at 6 m for the flux to the phytoplankton community immediately beneath the ice cover (i.e. above 6 m) and 1 m below the depths were deep chlorophyll maxima occurred. Depth (z) was defined as positive downwards so that negative fluxes indicate negative nutrient gradients (i.e. concentration decreased with depth over the plane of calculation). The vertical diffusion coefficient (which for the Antarctic lakes under consideration is essentially at the molecular level) was based on examination of micro-structure (3-mm resolution) profiles of temperature and conductivity obtained with the Seabird SBE 25 CTD system described earlier. These data indicate that turbulence in the main body of these lakes is virtually non-existent (Spigel *et al.*, 1990; R.H. Spigel & J.C. Priscu, unpublished data). Because turbulent mixing does not occur in the main body of these lakes (at least when advective stream flow is absent; which was the case during our study and is so most of the time), we used the value of 10^{-9} m^2 s^{-1}, which is representative of molecular diffusion coefficients for dilute solutions in water (Cussler, 1984). This diffusion coefficient is also applicable for lakes with thermohaline convection cells because vertical transfer will still be controlled by molecular diffusion across the relatively thin 'sheets' that separate the much thicker convecting layers.

Statistical analysis

Estimates of relative growth rates of phytoplankton during the bioassay experiments were obtained by taking slopes of regressions of the natural log of average d.p.m. for each treatment against time. Slopes of nutrient-amended samples were then compared with the control using a t-test (Steele & Torrie, 1960). Although ^{14}C-bicarbonate fixation may not always be coupled to growth, previous experiments in Lakes Fryxell and Vanda (Priscu *et al.*, 1987, 1988) have shown that a major portion of the ^{14}C fixed is partitioned into protein. Hence, the isotopic activity reported here should be directly proportional to growth, particularly given the long incubation time (144 h) of the bioassay experiments which would allow for equilibrium labelling among all macromolecular pools.

Results

Hydrographic parameters

The maximum temperature in all lakes occurred well below the ice–water interface (Fig. 1). This feature is particularly evident in the east lobe of Lake Bonney, Lake Fryxell and Lake Vanda where maximum temperatures occurred at 14, 9 and 68 m, respectively. The lowest temperature (–4.5 °C) was measured near the bottom at 37 m in the west lobe of Lake Bonney. Conductivities below the chemocline reached maximum levels in the east and west lobes of Lake Bonney and in Lake Vanda where they greatly exceeded sea water. Conductivities in the upper water columns of all lakes are indicative of relatively fresh water. The unusual temperature profiles result from solar heating coupled to extreme hydraulic stability associated with strong chemical gradients, low advective stream inflow and no wind-forced mixing. Radiant energy and salt levels are appropriate for the establishment of thermohaline convection cells below 13 m in Lake Hoare and between 5 and 20 m and 27–42 m in Lake Vanda (denoted by the lack of gradients in temperature and conductivity in these layers). Apparently, low irradiance, coupled with strong salt gradients, preclude such circulation in the other lakes.

Nitrogen and phosphorus levels generally increased sharply in the chemocline (or thermocline of Lake Hoare) of all lakes (Fig. 2). Exceptions are for NO_3^- in the west lobe of Lake Bonney, Lake Fryxell and Lake Vanda where anoxic conditions support denitrification (Vincent, Downes & Vincent, 1981; J.C. Priscu, unpublished data). Nitrate reached almost 200 μM below 20 m in the east lobe of Lake Bonney in apparently anoxic conditions (O_2 data not shown); there is no simple explanation for the presence of NO_3^- in the region of this lake which should support denitrification. The highest nitrogen and phosphorus levels occurred in the deep waters of Lakes Vanda and Fryxell where NH_4^+ and SRP reached 1515 and 9 μM, and 360 and 38 μM, respectively.

Phytoplankton vertical distribution in the study lakes was characterized by conspicuous deep-chlorophyll maxima (DCM) and often a less prominent peak immediately beneath the ice cover (Fig. 3). The DCM at 30 m in the east lobe of Lake Bonney is well below the euphotic zone in anoxic water; displacement experiments have shown that organisms forming this maximum are not photosynthetically viable (Sharp, 1993). The maxima at 12 m in Lake Fryxell also occurs in anoxic water and is associated with a population of purple sulphur bacteria shown to exist in this area (Priscu *et al.*, 1987). The photosynthetically viable DCM in all of the lakes appears just above the nutricline.

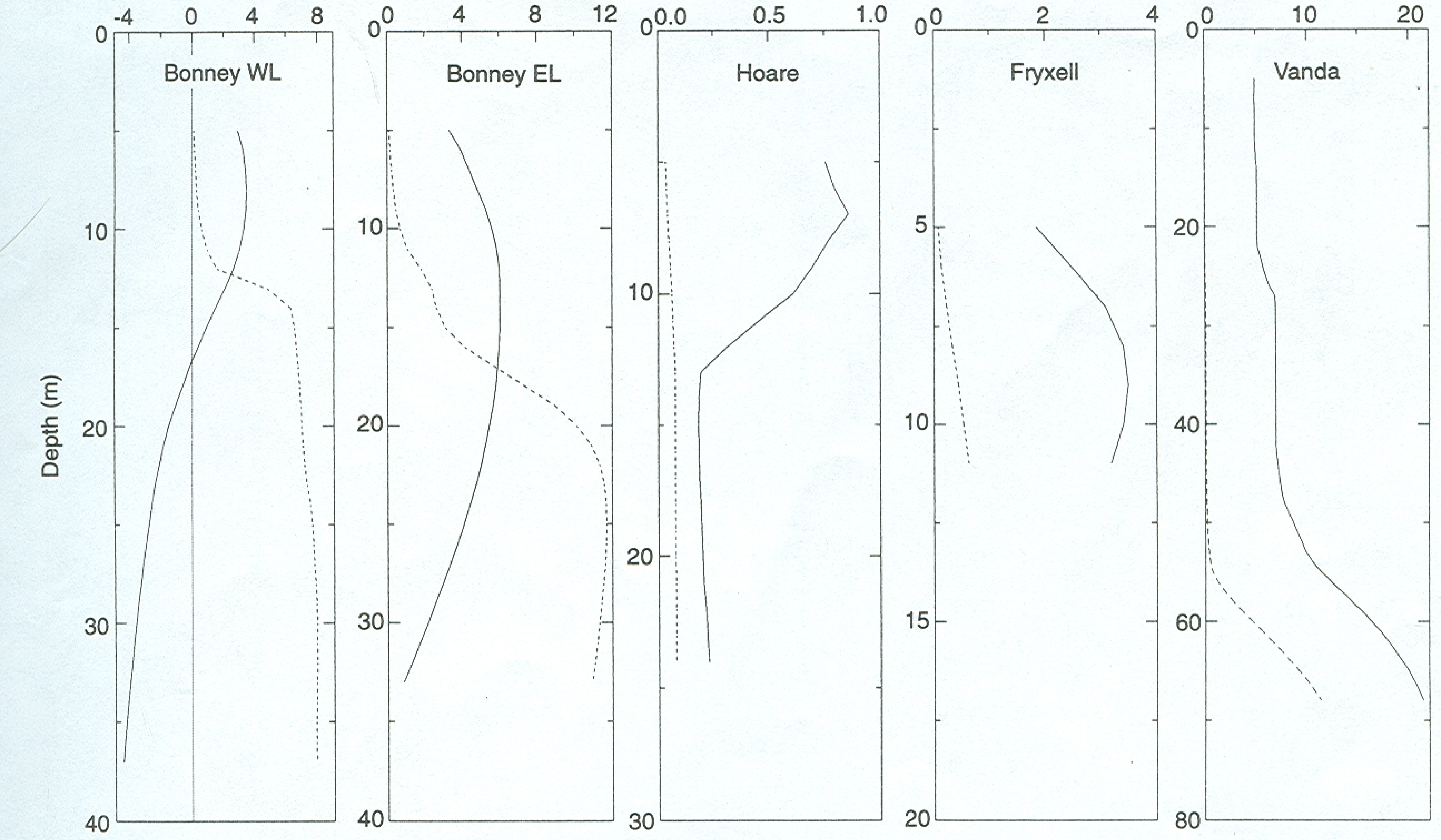

Fig. 1 Temperature (—,°C) and conductivity (···, S m^{-1}) fine-scale profiles in the study lakes. Readings begin near the bottom of the ice cover in each lake. Measurements in Lake Fryxell were terminated at 11 m to avoid sulphide precipitation on the conductivity sensor. The vertical dotted line in the panel for the east lobe of Lake Bonney denotes 0 °C.

Logistics precluded measurement of *in situ* primary productivity in Lake Vanda although previous work (Vincent & Vincent, 1982b; Priscu *et al.*, 1987) showed a clear productivity maximum associated with the DCM. Irradiance throughout the water column of the lakes is generally insufficient to saturate photosynthesis (Lizotte & Priscu, 1992a) and is usually near 0.1% of incident at the depth of the DCM (Lizotte & Priscu, 1992b, 1994). The DCM are thought to exist in part because the quantum yield of photosynthesis is enhanced by the deep nutrient pools (Lizotte & Priscu, 1992a). In general, photosynthetically viable phytoplankton exist throughout the water column above the nutricline but form maxima just above the nutricline.

Particulate carbon (PC) and particulate nitrogen (PN) concentrations in the trophogenic zones of the lakes were significantly ($P < 0.01$) correlated to chlorophyll (chl) (PC, $r = 0.70$, d.f. = 32; PN, $r = 0.63$, d.f. = 32) and yielded ratios (g : g) similar to that of viable phytoplankton (PC : CHL = 66.9; PN : CHL = 6.6, Lorenzen, 1968) indicating that much of the particulate organic matter in the trophogenic zone is comprised of phytoplankton (Fig. 4). The PC and PN maxima near the bottom in the east lobe of Lake Bonney and Lake Vanda are presumably associated with detrital material. The PC : PN ratios in all lakes exceed the Redfield ratio (6.6 by atoms; Redfield, 1958) which is an index of chemical composition of phytoplankton during balanced growth.

Nutrient bioassay experiments

Photosynthesis in most phytoplankton populations sampled from Lake Bonney was stimulated significantly ($P < 0.01$), relative to the non-amended controls, by phosphorus enrichment alone (Fig. 5). Simultaneous enrichment with phosphorus plus nitrogen further enhanced photosynthesis over that of phosphorus alone in the 5 and 13 m samples from both lobes. No significant ($P < 0.05$) nutrient stimulation occurred in the 18 m sample from the east lobe of this lake, although photosynthesis in the phosphorus alone and nitrogen plus phosphorus treatments were greater than the control. Samples from Lake Bonney were never stimulated by the addition of nitrogen alone at the $P < 0.05$ level.

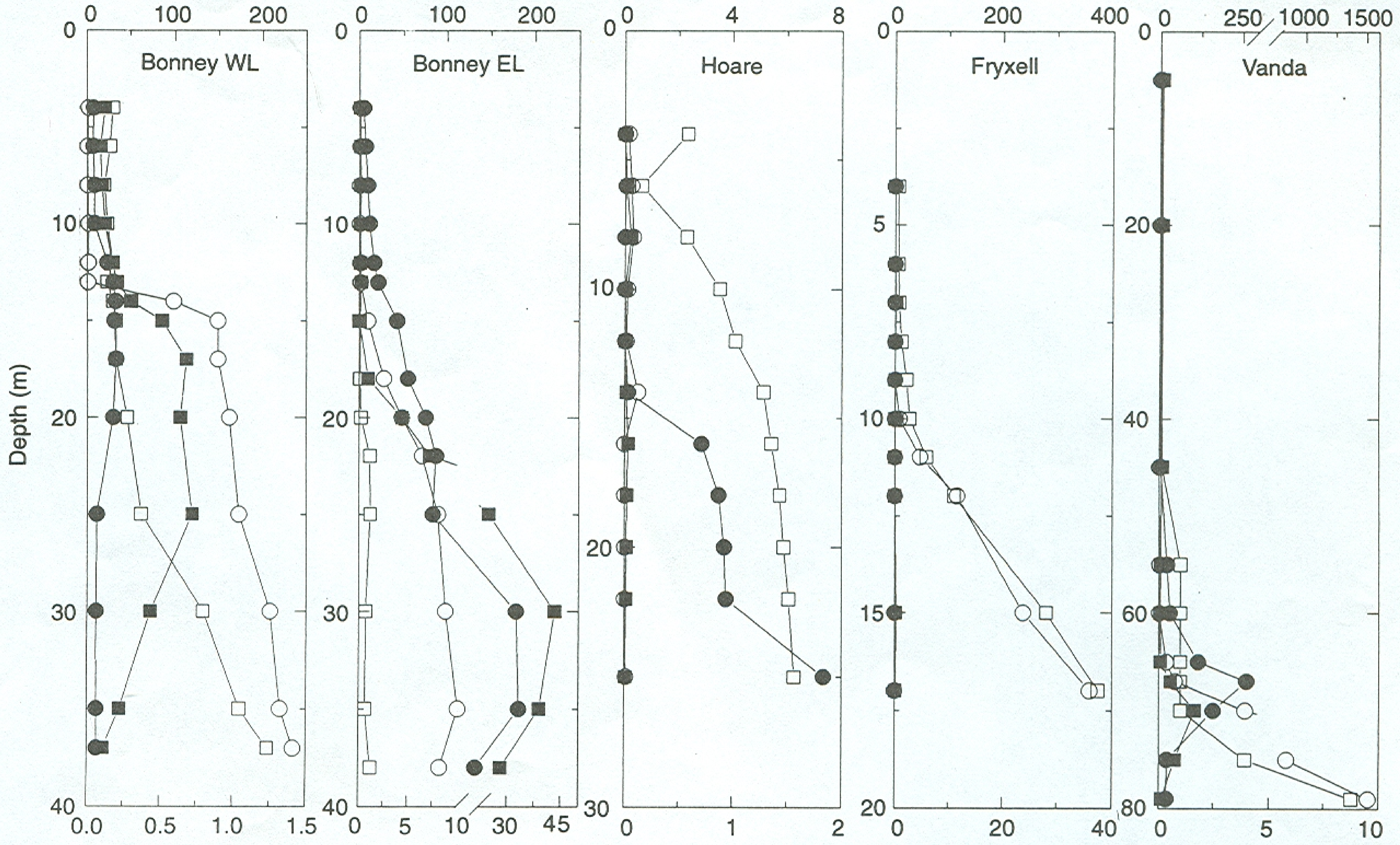

Fig. 2 Profiles of inorganic nitrogen (µM) and phosphorus (µM) in the study lakes. The shallowest sample was collected near the bottom of the ice cover. Note the axes breaks for NO_2^- and NH_4^+ in the east lobe of Lake Bonney and in Lake Vanda, respectively. Upper axis: ○, NH_4^+; ●, NO_3^-. Lower axis: □, SRP; ■, NO_2^-.

Simultaneous addition of phosphorus and nitrogen also resulted in a significant ($P < 0.01$) increase in photosynthesis in Lakes Hoare and Fryxell. Single additions of phosphorus and nitrogen elevated photosynthetic rates over the control in both of these lakes, although not significantly ($P < 0.05$) so.

Bioassay results from Lake Vanda showed that nutrient additions actually lowered photosynthetic activity relative to the control. The time-course profile indicated that there was no net photosynthetic activity in the sample from the time of the first measurement (24 h) to 120 h and that activity in the control exceeded that in nutrient-amended samples. It should be noted that, owing to helicopter logistics, the sample collected at Lake Vanda remained in the dark for more than 10 h in the collection carboy before processing. Together, these facts imply that the phytoplankton suffered physiological damage during sample storage. Consequently, bioassay results from Lake Vanda should be treated as suspect.

Dissolved inorganic nitrogen (DIN = $NH_4^+ + NO_2^- + NO_3^-$) : SRP ratios in Lake Bonney greatly exceeded the Redfield ratio for balanced growth (16 : 1 by atoms) ranging from 52.5 at 5 m in the west lobe to 856.2 at 18 m in the east lobe (Table 1). These high DIN : SRP ratios support results from the bioassay experiments showing phosphorus deficiency. DIN : SRP ratios for phytoplankton maxima in Lakes Hoare and Fryxell ranged from 0.2–1.2, well below the Redfield ratio. The ratios in Lakes Hoare and Fryxell partially support bioassay results for these lakes which show no significant ($P < 0.05$) stimulation by the addition of P alone. Although not statistically significant at $P < 0.05$, photosynthetic activity at the last time-point in the N-treatment of the Lake Fryxell experiment was 72% greater than the control whereas that of the P-enriched sample was only 18% greater than the control. DIN : SRP ratios imply nitrogen deficiency in the DCM in Lakes Hoare and Fryxell. Although the bioassay results for Lake Vanda are inconclusive, DIN : SRP ratios provide evidence for moderate phosphorus deficiency at 5 m and strong phosphorus deficiency for the populations forming the DCM. Particulate carbon : PN ratios for all lakes exceeded the Redfield proportions for these compounds (Table 1). The lowest ratio (10.5) was measured at 5 m in Lake Fryxell,

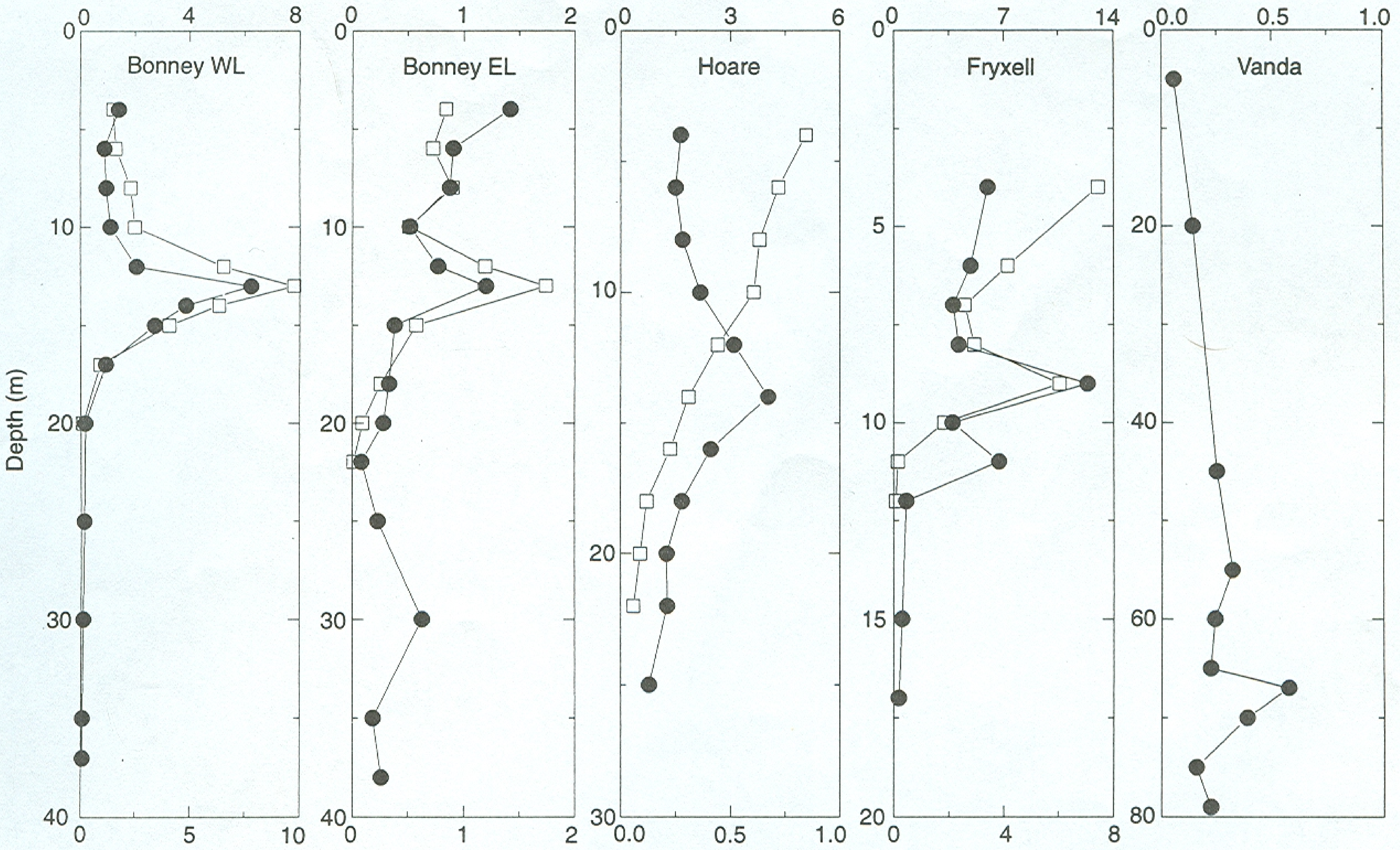

Fig. 3 Profiles of chlorophyll *a* (●, μg l^{-1}; upper axis) and primary productivity (□, μgC l^{-1} day^{-1}; lower axis). The shallowest sample was collected immediately beneath the ice cover. The deepest sample for primary productivity in each lake was made at the approximate depth where light bottle activity was not different from dark bottle activity (i.e. the bottom of the trophogenic zone). Primary productivity measurements were not made in Lake Vanda for this study.

supporting the relative lack of phosphorus deficiency in this lake shown by the bioassay experiments. Overall the PC : PN ratios show no clear pattern of nutrient deficiency.

Discussion

Few studies have addressed experimentally nutrient deficiencies in lakes of the McMurdo dry valleys, or for that matter, Antarctic lakes in general. Experimental data that have been published are often contradictory. For example, early studies in Lake Vanda (Goldman, 1964) showed that nitrogen enrichment almost doubled the photosynthetic rate in littoral water, whereas recent experimental work by others has produced different conclusions. The low half-saturation coefficients for NH_4^+ uptake and tight coupling between NH_4^+ uptake and regeneration at 5 m in Lake Vanda also implies a nitrogen-deficient system (Priscu *et al.*, 1989). Conversely, experiments on sestonic changes in N : P ratios and the degree of enhancement of dark inorganic carbon uptake upon NH_4^+ addition has shown water from different depths in this lake to be primarily phosphorus deficient (Vincent & Vincent, 1982). Although the nutrient bioassay experiments were inconclusive in Lake Vanda, the DIN : SRP ratios measured in this lake support phosphorus deficiency as do those of Canfield & Greene (1985). The discrepancy between Goldman's observation and those from more recent studies could result from that fact that littoral water has completely different nutrient dynamics than water from the central portion of the lake or that phytoplankton nutrient requirements have changed over the ≈ 20-yr period between experiments. Earlier work on Lake Fryxell, based on experimental manipulation and direct measurement of nitrogen uptake using the stable isotope ^{15}N, indicated potential nitrogen deficiency (Vincent, 1981; Vincent & Vincent, 1982; Priscu *et al.*, 1989) a result supported by the current bioassay experiments.

Past studies on the east lobe of Lake Bonney, based on ambient nitrogen and phosphorus concentrations, concluded that phytoplankton growth was not nitrogen deficient, and may be phosphorus deficient during

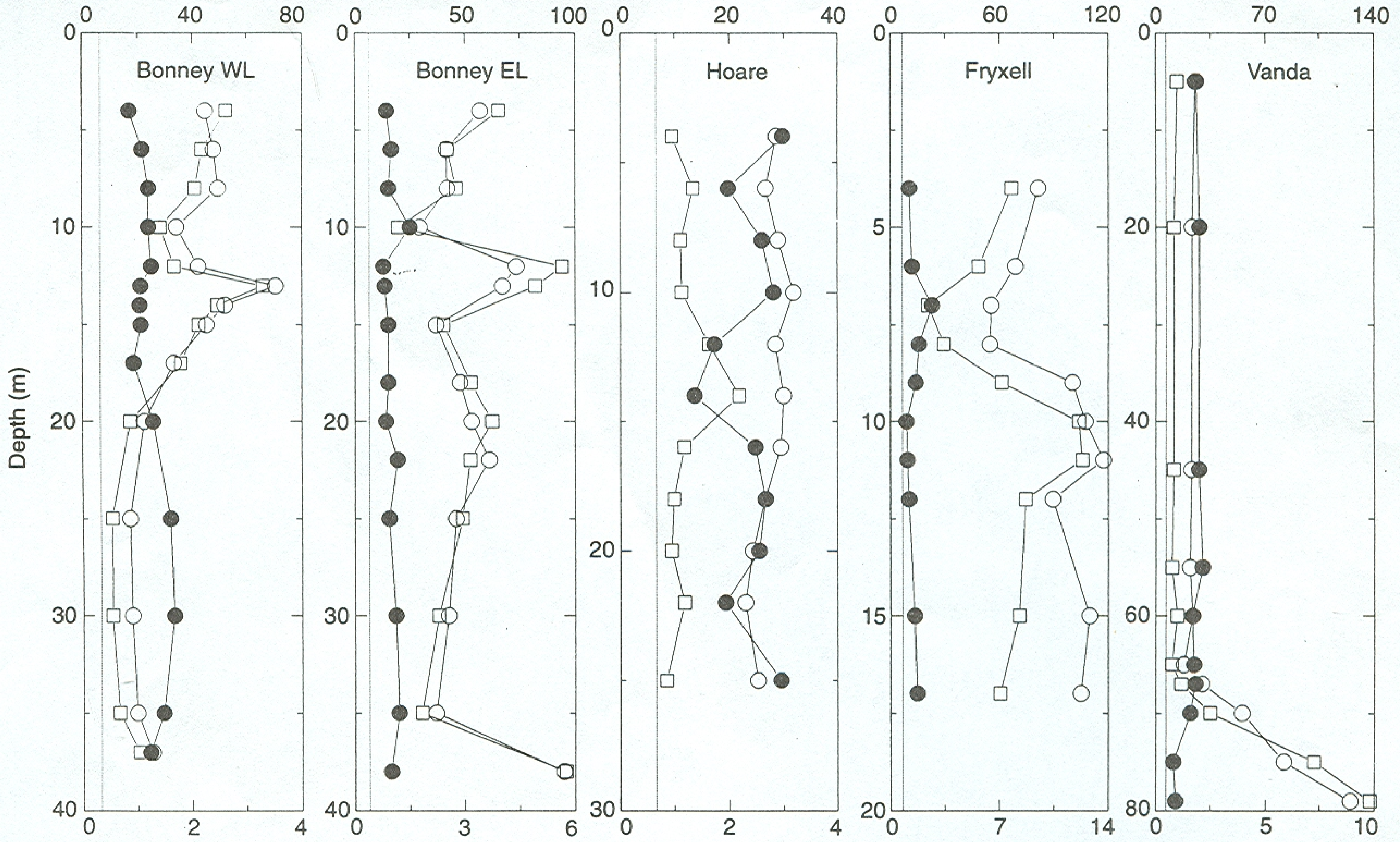

Fig. 4 Profiles of particulate carbon (○, PC, μM; upper axis), particulate nitrogen (□, PN, μM; lower axis) and the ratios of PC : PN (●, by atoms; upper axis). The dotted vertical line denotes the Redfield PC : PN ratio (6.6).

a portion of the year (Hoehn *et al.*, 1977). My experimental results corroborate these conclusions and, based on consistently high DIN : SRP ratios in this lake over the phytoplankton growth period (Sharp, 1993), phosphorus deficiency would predominate throughout the year. Nutrient deficiency, at least for the shallower depths in the east lobe of Lake Bonney, have been suggested by Lizotte & Priscu (1992a, 1994) who observed elevated photosynthetic efficiency in the deeper, more nutrient rich waters. No published reports currently exist on the nutrient status of Lake Hoare or the west lobe of Lake Bonney.

It should be noted that conclusions based on ambient nutrient ratios can be misleading without information on the turnover rates of the individual nutrient pools. Sestonic PC : PN ratios can also yield an unreliable index of phytoplankton nutrient status to the extent that detrital and bacterial PC and PN contribute to the ratio. In general, conclusions regarding nutrient limitation based on any single type of nutrient deficiency index can be misleading (Dodds & Priscu, 1990). However, comparative tests of a suite of different types of bioassay experiments and static physiological parameters (Dodds & Priscu, 1990) have shown that long-term, growth based nutrient bioassay experiments such as those employed in the current study provide the most reliable information on the nutrient status of phytoplankton populations.

The Antarctic lakes included in this study are all terminal lakes; they lack surface outflow and presumably have little or no groundwater outflow (Chinn, 1993). The primary source of new nutrients to the trophogenic zones of these lakes is from intermittent stream flow, which occurs only when temperatures approach or exceed 0 °C (about 6 weeks yr^{-1}). Stream flow had not started during the period when the current bioassay experiments were conducted (early November until mid-December) making the lakes essentially closed systems during this period, a conclusion made previously based on NH_4^+ dynamics (Priscu *et al.*, 1989). Assuming that no new nutrients entered the lake during the experimental period, the only sources of nutrients for phytoplankton growth would be internal recycling, possible release from the permanent ice cover and upward diffusion from the deep-water nutrient pool, the latter of which is a conspicuous feature in each of the lakes (Fig. 2).

Because internal cycling cannot support indefinitely

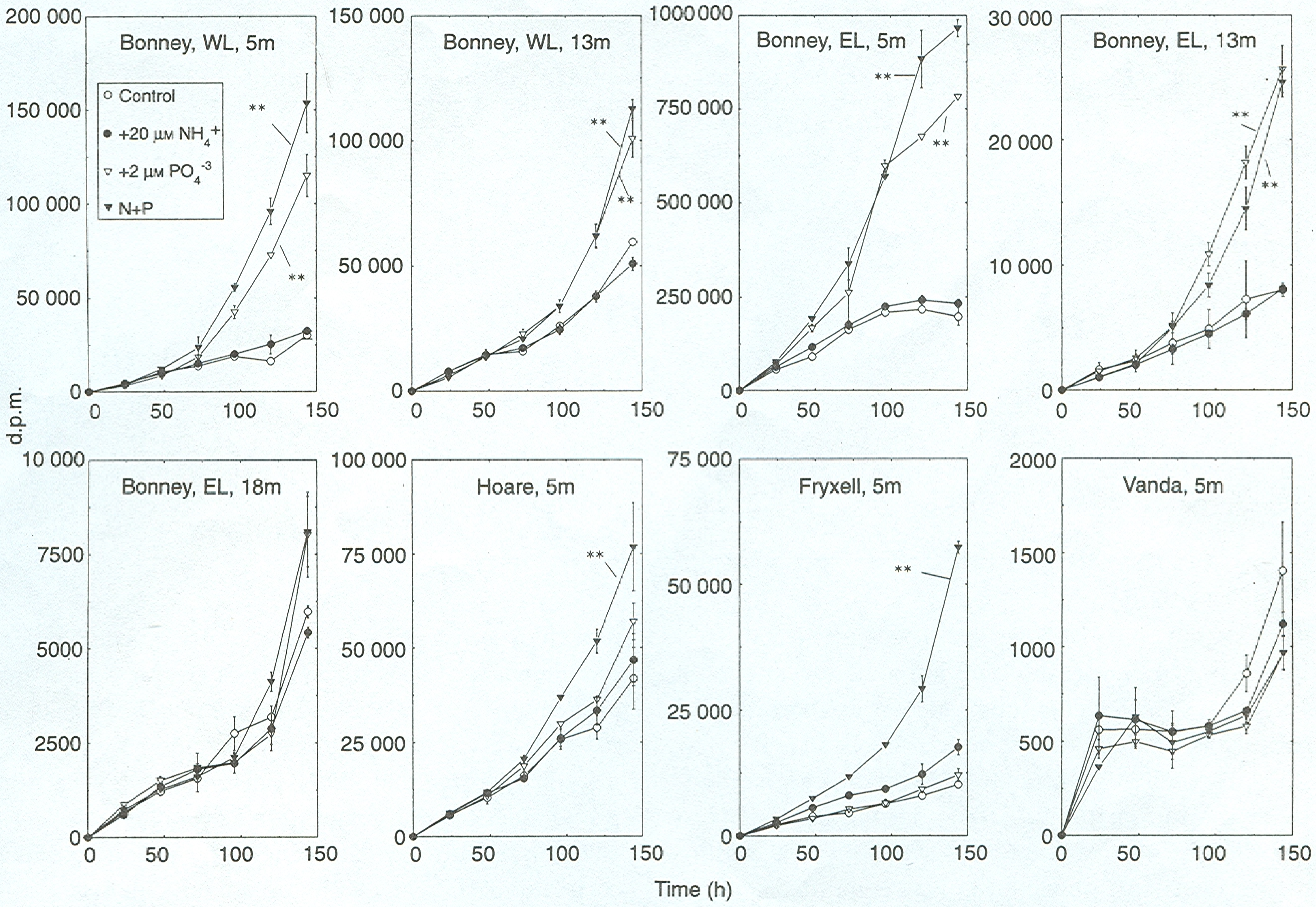

Fig. 5 Relationships between photosynthesis (disintegrations per minute of ^{14}C incorporation, d.p.m.) and time under different nutrient amendments. WL and EL represent the west and east lobes of Lake Bonney, respectively. Error bars represent the range of two replicate samples. * and ** denote significant differences from the control at $P < 0.05$ and $P < 0.01$, respectively.

Table 1 Ambient concentration (µM) of various forms of nitrogen and phosphorus, DIN ($NH_4^+ + NO_2^- + NO_3^-$) : SRP ratios (by atoms) and particulate carbon : particulate nitrogen ratios (PC : PN, by atoms) from the study lakes. Data are presented for depths were nutrient bioassay experiments were conducted and for depths where phytoplankton maxima occurred but logistics precluded experimental manipulation. Bonney WL, west lobe; Bonney EL, east lobe. Redfield ratios (by atoms) for N : P and C : N are 16 : 1 and 6.6 : 1, respectively

Lake	Depth(m)	NH_4^+	NO_2^-	NO_3^-	DIN	SRP	DIN : SRP	PC : PN
Bonney WL	5	1.63	0.13	7.69	9.45	0.18	52.5	17.1
	13	1.43	0.21	30.13	31.77	0.14	226.9	21.3
Bonney EL	5	1.30	0.06	4.74	6.10	0.10	61.0	14.5
	13	1.72	0.19	21.54	23.45	0.19	123.4	13.6
	18	28.74	0.94	55.94	85.62	0.10	856.2	15.1
Hoare	5	0.14	0.00	0.01	0.15	0.59	0.3	29.8
	14	0.49	0.02	0.12	0.63	1.29	0.5	13.7
Fryxell	5	0.76	0.02	0.00	0.78	0.64	1.2	10.5
	9	0.41	0.02	0.00	0.43	2.12	0.2	14.0
Vanda	5	0.16	0.12	3.24	3.52	0.08	44.0	25.7
	67	49.62	0.54	268.09	318.25	0.99	321.5	25.3

steady-state phytoplankton biomass with respect to time (i.e. cycling is not 100% efficient), upward diffusion of nutrients must play a major role in supporting phytoplankton growth in the DCM in each of the lakes; potential nutrient release from the ice (if any) is apparently lower or in balance with phytoplankton

Table 2 Vertical nutrient fluxes (µmol m^{-2} day^{-1}) across horizontal planes (m) located immediately below phytoplankton biomass maxima. DIN (NH_4^+ + NO_2^- + NO_3^-) : SRP flux ratios are also presented when they represent upward flux across the specified plane. Negative flux values denote downward flux, indicative of decreasing nutrient concentration with depth.

	Flux (µmol m^{-2} day^{-1})						
Lake	Plane	NH_4^+	NO_2^-	NO_3^-	DIN	SRP	DIN : SRP
Bonney WL	6	–0.0184	–0.0001	0.0169	–0.0022	–0.0013	NA
	14	6.3707	0.0130	0.0635	6.4472	1.0026	2487.3
Bonney EL	6	–0.0158	0.0009	0.1074	0.0925	0.0009	107.0
	14	0.3676	–0.0082	0.9405	1.2999	–0.0030	NA
	19	0.8912	0.1482	0.8834	1.9228	0.0043	445.1
Hoare	6	0.0037	0.0013	0.0002	0.0052	–0.0002	NA
	15	–0.0212	0.0009	0.0320	0.0117	0.0030	3.9
Fryxell	6	–0.0061	–0.0002	0.0000	–0.0063	0.0104	NA
	10	2.0062	0.0007	0.0004	2.0073	0.1616	12.4
Vanda	6	0.0004	–0.00006	0.0006	0.0009	–0.0001	NA
	68	6.1546	0.0320	–2.9264	3.2602	0.00003	108 673

uptake (which is also low, Fig. 3) because no consistent gradients in nutrients occur immediately under the ice cover (Fig. 2). The importance of upward nutrient diffusion is qualitatively supported by the fact that the predominant chlorophyll maxima are associated with the top of the nutricline, despite relatively low irradiance. To corroborate this claim, the upward flux of nitrogen and phosphorus was computed and the corresponding DIN : SRP flux ratios at horizontal planes located 1 m below the phytoplankton maxima in each lake. If these fluxes do indeed drive new production (*sensu* Dugdale & Goering, 1967) in the lakes, the flux ratios should determine which nutrients are regulating phytoplankton productivity (assuming the turnover rates of the pools are similar). In general the DIN : SRP flux rates support the bioassay data showing a high degree of phosphorus deficiency in Lakes Bonney (east and west lobes) and Vanda; upward DIN : SRP flux ratios to the DCM in Lakes Hoare and Fryxell imply nitrogen deficiency (Table 2). The negative flux values denote that nutrient flux was downward (i.e. nutrient concentration decreased with depth), and occur mainly just beneath the ice (i.e. the 6-m plane). These negative values are usually much lower than upward fluxes and may result from exsolution (i.e. freeze-out) of salts during freezing of the ice cover. It would appear that the surface phytoplankton maxima receive some new nutrients from the ice covers, whereas the deeper-water maxima obtain all of their new nutrients from upward diffusion from the deep nutrient pools.

Correlations of chlorophyll and phosphorus flux, and chlorophyll and DIN flux (omitting negative flux data) revealed a significant positive association for phosphorus ($r = 0.84$, $P < 0.05$) but not DIN ($r = 0.33$, $P > 0.05$). That the positive association is stronger for phosphorus than DIN presumably reflects the predominance and magnitude of phosphorus deficiency over nitrogen deficiency. The overall positive correlations between phytoplankton biomass (i.e. chlorophyll *a*) and upward nutrient flux supports the contention that new phytoplankton production, particularly in the DCM, is supported to a large extent by upward diffusing nutrients in these Antarctic lakes. The phytoplankton forming the DCM would then act as a 'biofilter' reducing and modifying the diffusive nutrient supply to surface populations.

It is interesting to speculate as to why phytoplankton in lakes within the same general proximity show such different responses to nitrogen and phosphorus enrichment. Smith (1984), attempting to reconcile differences between marine and freshwater systems, argued that it is the balance between the physical processes of advection and eddy diffusion, and the biochemical processes governing the sources and sinks of nitrogen that determine if phytoplankton will be deficient in nitrogen or phosphorus. Because advection and diffusion are similar in all of the study lakes (except for apparent thermohaline convection cells below 13 m in Lake Hoare and between 5 and 20 m and 27–42 m in Lake Vanda denoted by the lack of gradients in temperature and conductivity in these regions, Fig. 1), physical processes do not appear to be responsible for differences in nutrient deficiency among lakes. Based on my nutrient flux analysis, which shows that nitrogen and phosphorus diffusion rates are positively related to phytoplankton biomass and that upward DIN : SRP diffusion ratios contribute to phosphorus or nitrogen deficiency, biochemical processes influencing the nitrogen and phosphorus concentration below the nutricline would control nutrient availability to phytoplankton in the trophogenic zone. Because of the different oxygen (and presumably redox) states below the nutriclines, an obvious biogeochemical process to consider would be denitrification. Nitrate profiles in the deep waters of the west lobe of Lake Bonney, Lake Fryxell and Lake Vanda all suggest that denitrification is occurring in this region of the lakes. Direct measurements of denitrification have indeed shown that denitrification is responsible for the lack of NO_3^- in the anoxic regions of the west lobe of Lake Bonney and Lake Vanda (Vincent *et al.*, 1981; J.C. Priscu unpublished data). If denitrification does lower the upward flux of DIN, indications of nitrogen deficiency should be seen in the west lobe of Lake Bonney, Lake Fryxell and Lake Vanda. However, bioassay results and DIN : SRP flux ratios indicate potential nitrogen deficiency in Lake Fryxell and Lake Hoare only, the latter of which shows no sign of denitrification. Hence, it is difficult to attribute differences in nutrient deficiency among the lakes to nitrogen losses via biochemical processes. The only biochemical source of new nitrogen to the lakes would be through microbial N_2 fixation, an O_2 and DIN sensitive process, via the enzyme nitrogenase. However, the high DIN concentrations below the nutricline should suppress nitrogenase activity in this zone, and the low abundance or complete lack of known N_2-fixing phytoplankton species, in concert with extreme O_2 supersaturation, would eliminate N_2 fixation as a major source of new DIN to the trophogenic zone of these lakes.

The absolute size of the DIN and SRP pools in the deep waters of the lakes overrides the impact of contemporaneous biochemical transformations. For example, even though NO_3^- has been denitrified below the chemoclines of the west lobe of Lake Bonney, Lake Fryxell and Lake Vanda, extremely large pools of NH_4^+ exist (exceeding 1.5 mM in Lake Vanda). The origin of deep-water nutrients in most temperate lakes results from decomposition of autotrophically produced organic matter that has settled out of the trophogenic zone (e.g. Priscu *et al.*, 1986). This paradigm does not apply to the Antarctic lakes where Lake Vanda, which has the lowest primary productivity of any of the lakes (Fig. 3, see also Vincent & Vincent, 1982b; Priscu *et al.*, 1987) has one of the highest deep-water DIN and SRP concentrations.

Perhaps the most likely source of variation in deep water nutrients in these lakes relates to the origin and evolution of the lakes (see Chinn, 1993). It is thought that the lakes originated from brine pools which accumulated salts over many years via evaporation and sublimation of glacial meltwater (Chinn, 1993). Freshwater then overflowed the brine pools resulting in the present physical and chemical structure of the lakes. Given this scenario, lakes originating from large or highly concentrated brine pools would show the highest degree of chemical stratification (assuming similar mixing process among lakes). Lakes fitting into this category would be Bonney, Vanda and Fryxell. Conversely, Lake Hoare does not exhibit strong chemical stratification, nor does it have nitrogen levels reaching that in the other lakes. Consequently, the nutrient concentrations and ratios currently observed in these lakes probably reflect conditions during the period of salt concentration and during the physical evolution of the lakes. It should be noted that, owing to the overall dominance of molecular diffusion in all of the lakes, a lake 40 m deep (such as Bonney) would have a mixing time of more than 50 000 years. In other words, the nutrient gradients shown in Fig. 2 may have formed when the lakes originated (≈ 10 000 years ago; Chinn, 1993) and have been modified little by biogeochemical or mixing processes (except perhaps in Lake Hoare where thermohaline convection extends to the bottom). Hence, it is no simple task to determine factors producing the present day deep-water nutrient conditions and associated nutrient deficiencies in phytoplankton. Moreover, because little is known about temporal dynamics (i.e. turnover times) of phosphorus and nitrogen pools in these lakes (although preliminary rate measurements indicate that nitrogen turnover is low relative to temperate systems, e.g. Woolston, 1994), implications regarding nutrient deficiencies based on pool sizes can be misleading and remain equivocal.

These nutrient bioassay experiments and flux determinations are the first to address collectively nutrient deficiency in lakes of the McMurdo dry valleys. To obtain a more thorough view of nutrient deficiency in these lakes, experiments should be conducted over the phytoplankton growing season and should include samples from the phytoplankton maxima within each lake. In addition, information on nitrogen and phosphorus pool dynamics must be known and compared with diffusive fluxes. Although Antarctic lakes appear to present 'simple' systems (i.e. diffusion dominated, little advective input, no crustaceous zooplankton, no fish), they have other complexities that must be considered.

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