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Nutrients and Their Effects on Phytoplankton Populations in Lakes on Signy Island, Antarctica

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Summary. Seasonal changes in nutrient concentrations, phytoplankton biomass and nutritional state were followed in two contrasting Antarctic lakes. Oligotrophic Sombre Lake receives little phosphate from its catchment and this limits the standing crop of phytoplankton which can develop in spring and summer. This situation appears to be typical of unenriched Maritime Antarctic lakes. Large numbers of seals and seabirds in the catchment of nearby Heywood Lake increase its phosphate loading and allow a much denser growth of phytoplankton. The N:P ratio is low and nitrogen rather than phosphate is the most limiting nutrient. Despite limitation of standing crop, photosynthetic rates in both lakes are relatively high and recycling of nutrients within the lake may be rapid.

Introduction

The 17 freshwater lakes on Signy Island (60°43′S, 45°38′), South Orkney Islands are thought to provide examples of most lake types known to occur in the Maritime Antarctic (Heywood 1978). Continuous monitoring of a number of physicochemical parameters in these lakes has revealed considerable differences in nutrient concentrations and phytoplankton abundance. These differences appear to be related in part to the extent of natural enrichment of their catchment areas by summer bird and seal populations (Priddle and Heywood 1980).

The interdependence of nutrient loading, nutrient concentration and standing crop is a consistent feature of phytoplankton ecology and has been widely documented in temperate lakes (Schindler et al. 1978; Dillon and Rigler 1974). Rigler (1978) concluded that similar relationship held in high Arctic lakes, despite the restrictions on production imposed by the extreme environmental conditions. Information on nutrient/phytoplankton interactions in Antarctic freshwater lakes is scarce, though Samsel and Parker (1972) found that nutrient enrichment increased phytoplankton densities in lakes on Anvers Island. The present study describes the dynamics of nutrients and their effects on phytoplankton in lakes on Signy Island. It forms part of a continuing study of the limnology of the area by the British Antarctic Survey.

Materials and Methods

Study Area

Characteristics of the lakes of Signy Island are given in Heywood (1967, 1968) and Heywood et al. 1980. The two lakes chosen for detailed study lie close together in a single geological formation (Fig. 1) but

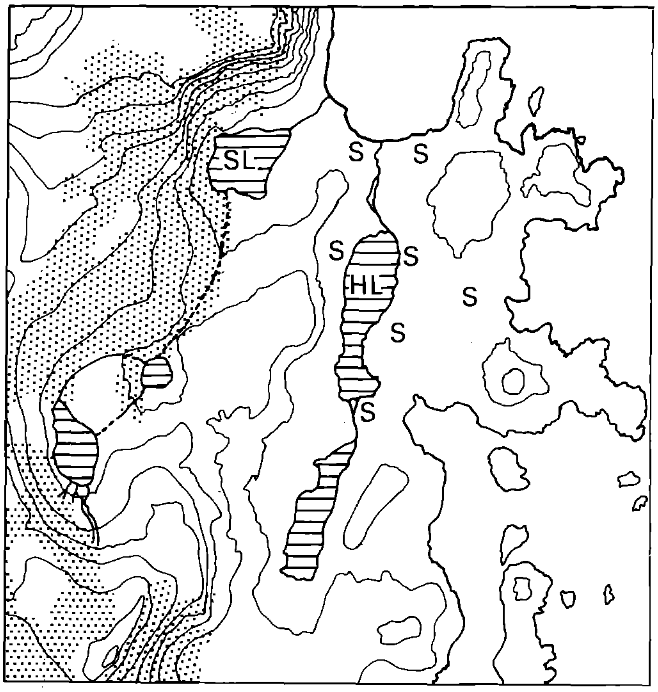

Fig. 1. The location of Heywood Lake *(HL)* and Sombre Lake *(SL)* in the north-east corner of Signy Island (60°43′S, 45°38′W). Permanent ice cover is shown stippled and *S* represents areas of moss carpet frequented by elephant seals. Contour interval 20 m

Table 1. Limnological characteristics of Sombre and Heywood Lakes

	Sombre Lake	Heywood Lake
Area (ha)	2.43	4.17
Mean depth (m)	5.0	2.0
Max depth (m)	11.4	6.2
Volume (m^3)	132600	96200
Duration of ice cover (months)	10	9
Max temperature (°C)	4.5	5.3
Stratification	None	None
Catchment area (ha)	48	41
% permanent ice cover in catchment	73	0

are of contrasting character. Heywood Lake lies in a lowland catchment with extensive moss carpet cover and is subject to enrichment from the large bird and seal population present during the summer months. Nutrient concentration are high and an extensive phytoplankton develops. Sombre Lake, in contrast, lies at the end of a chain of three lakes in a barren valley where rock, scree and permanent ice fields predominate. There are few animals associated with this catchment and enrichment is minimal. The lake is nutrient poor and develops only a sparse phytoplankton during the summer. Some important characteristics of the two lakes are summarized in Table 1.

Water Sampling and Analysis

Water samples were pumped from the required depth into light-proof polythene bottles using a hand operated 'Whale Gusher' diaphragm pump. With care, this system proved operational at air temperatures down to $-28\,°C$. Samples were either handled immediately in a small, lakeside hut or transported to the laboratory at the research station within 1.5 h. On extremely cold days, vaccum flasks were used to prevent samples freezing.

Total inorganic carbon was measured using the Gran titration technique described by Talling (1973). The remainder of the sample was filtered (Whatman GF/C), the filter being used for determination of chlorophyll-*a* and phaeopigment concentrations and the filtrate for chemical analyses.

Chlorophyll-*a* concentration was determined spectrophotometrically at 665 mn after extraction into cold 95% acetone for 24 h. Following acidification to 0.003 N with hydrochloric acid, phaeopigments were determined by comparison of the absorbance at 665 mn with that of the unacidified extract. The equations of Vollenweider (1969) were used throughout, the absorption coefficient of chlorophyll being taken as 84 g cm^{-1}.

Nitrate and nitrite concentrations were determined by the method described by Wood et al. (1967), ammonia according to Chaney and Marbach (1962); chloride, Goltermann (1969) and soluble reactive phosphate according to the method of Strickland and Parsons (1972). In addition, sestonic material was collected on acid washed GF/C filters, frozen at $-40\,°C$ and transported to the UK for analysis of particulate carbon, nitrogen and phosphorous, using methods described in Allen et al (1974).

Photosynthesis

In situ estimates of rates of photosynthesis were obtained using the ^{14}C method of Vollenweider (1969). Duplicate 125 ml bottles were incubated at each of the seven depths sampled for 4 – 6 h with approximately 5 μCi of activity. Under ice, the samples were suspended from a 2 m aluminium arm to protect them from abnormal light conditions close to the sampling hole. Bottle contents were filtered immediately after recovery (0.45 μm membrane filters) under gentle suction (less than 100 mg Hg). Filters were then fumed over concentrated hydrochloric acid to remove any remaining inorganic ^{14}C and stored at $-40\,°C$. Radioactivity was determined by liquid scintillation counting up to 20 months later. Dark uptake controls were run on top and bottom samples only and ^{14}C incorporation in these was subtracted from that of the light bottles.

A similar technique was used for laboratory estimates of photosynthesis, with light provided by Grolux fluorescent tubes. Acrylic plastic incubation chambers were employed throughout, as these have been shown to have superior light transmission properties to most forms of glass (Ilmavirta 1977). At all times the phytoplankton were protected from high light intensities to prevent damage to the photosynthetic apparatus (Goldman 1963).

Inflows and Outflows

All flow rate determinations were made using standard dilution gauging techniques. Either lithium chloride or sodium chloride was used as the tracer and concentrations determined by flame photometry and conductivity respectively. Conductivity measurements were made in situ using a Yellow Springs Instruments Model 33 conductivity meter. Lake outflow rates were determined weekly. At monthly intervals, nutrient analyses were carried out on all inflow and outflow streams. During January and February 1981, the flow rates of these inflows were also determined and used to quantify earlier visual estimates. Subtraction of surface inflow from outflow rates provided estimates of groundwater seepage (assuming evaporation and precipitation to be negligible). First order estimates of inorganic nutrient loadings could then be calculated. Groundwater was extracted for analysis by sampling water entering pits dug at intervals around the lakes or by forcing water out of moss carpet samples in a 500 ml syringe. For estimates of nutrient loadings a constant seepage rate was assumed for the whole shoreline.

Bioassays

Two bioassay techniques were used to investigate nutrient limitation. One employed a unialgal culture of a *Chlorella* sp. isolated from Sombre Lake whilst the other used natural phytoplankton assemblages.

Bioassays using the natural population involved enrichment of 450 ml aliquots of fresh lake water, from which the large zooplankton had been removed using a 200 μm filter, with a nutrient or combination of nutrients as follows:

1. Unenriched control
2. 30 $\mu g\ l^{-1}$ Phosphate-phosphorous als Na_2HPO_4
3. 300 $\mu g\ l^{-1}$ Ammonia-nitrogen as NH_4Cl
4. 3 $mg\ l^{-1}$ Bicarbonate-carbon as $NaHCO_3$
5. 30 $\mu g\ l^{-1}$ Phosphate-phosphorous and 300 $\mu g\ l^{-1}$ Ammonia-nitrogen
6. As 5 with trace elements also added.

The trace element solution contained Fe, Zn, Cu, B, Mg, Mn and Mo to give a final concentration one tenth that of the culture medium described by Lund et al. (1975).

Samples were incubated at saturating light levels of 130 $\mu E\ m^{-2}s^{-1}$ with daily manual agitation. After 72 h, ^{14}C uptake rates of duplicate subsamples from each were determined at the same light intensity. A third subsample was analysed for total inorganic carbon, by Gran titration (Talling 1973) to enable the photosynthetic rate to be calculated.

The second type of bioassay was a standard algal growth potential (AGP) test. Triplicate 15 ml samples of filtered lake water (Whatman GF/C) in 20 ml culture tubes were enriched with the following combinations of nutrients:

1. No enrichment	2. NH_4 only	3. NO_3 only
4. PO_4 only	5. Trace elements	6. NH_4 and PO_4
7. NO_3 and PO_4	8. NH_4, PO_4 and trace elements.	

Tubes were innoculated to give an initial cell concentration of approximately $10^4\ ml^{-1}$, and incubated on a shaker tray at 8 – 12 °C and 110 μEm^{-2} for 10 days. This light intensity was sufficient to light saturate growth. Cell concentrations were then determined using a haemocytometer. The effectiveness of each treatment in promoting growth was assessed on a scale of 0 – 6.

To examine the general applicability of data from Heywood and Sombre Lake a further series of AGP tests were undertaken to determine growth potential and major limiting nutrients in summer samples taken from seven other lakes on Signy Island. Each of these lakes has been sampled for major nutrient and chlorophyll-*a* three times annually since 1974 (Heywood et al. 1980).

Results

Standing Crop and Productivity

In Heywood Lake, an under-ice chlorophyll maximum developed on commencement of detectable photosynthesis in spring (Fig. 2a). This declined rapidly before production of a second, smaller peak during summer. Small chrysophytes and chlorophytes (notably an *Ankistrodesmus* sp.) were dominant during spring while cryptophytes were most abundant in summer. Chlorophyll-*a* levels increased more slowly in Sombre Lake and there was no pronounced spring maximum (Fig. 2b). Depth/time distributions of chlorophyll-*a* (Fig. 3a, b) reveal further differences between the two lakes. Although during winter chlorophyll-*a* was confined to the surface of both, the spring increase in Heywood Lake was distributed evenly down the water column, while in Sombre Lake, the maximum chlorophyll concentration accumulated towards the bottom (5 – 11 m). *Ankistrodesmus falcatus* was particularly abundant in this deep maximum while cryptophytes occurred in midwater and surface samples. In summer these gave way to a collection of small chlorophytes. In both, vertical homogeneity was maintained throughout the summer by wind-induced turbulence.

Production rates (Fig. 2a, b) showed similar patterns in the two lakes, commencing in September/October and remaining at constant low levels until ice cover was lost. Rates then increased to summer maxima before decreasing rapidly with the onset of winter conditions. Heywood Lake consistently showed a higher rate of production than Sombre Lake, particularly during the open period.

Nutrients

Winter. Nutrients concentrations increased after ice formation, reaching a peak in late winter (Figs. 4 and 5). As inflows and outflows were frozen during this period, the increases were derived solely from autochthonous sources. Of these, mineralisation and sediment release were probably most important. The concentrating effect

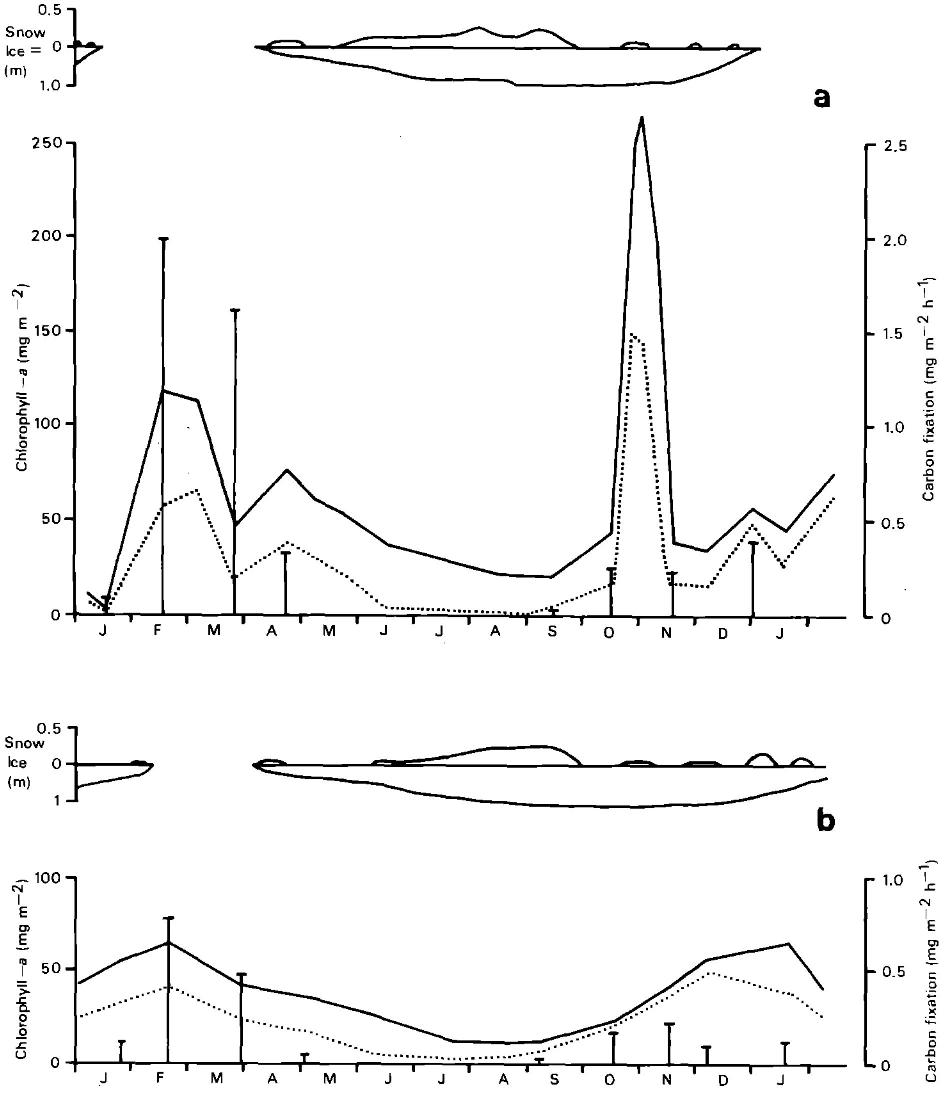

Fig. 2. Changes in concentration of total chlorophyll-*a* *(solid line)* and chlorophyll-*a* corrected for phaeopigments *(dotted line)* and phytoplankton photosynthesis *(vertical bars)* during 1980 in **a** Heywood Lake and **b** Sombre Lake. Areal values are given for the deep-spot sampling site (6 m and 11 m, respectively). Photosynthesis was measured over a 4 – 6 h period at mid-day

of solute exclusion during ice formation can be eliminated by calculation of nutrient: chloride ratios, chloride acting as a conservative ion. These ratios (Table 2) show differences in both the extent and location of nutrient regeneration in the two lakes.

In Heywood Lake, N regeneration was initially more rapid than P and the N: P ratio rose (Table 3), though by August comparable proportional increases had occurred. Considerably less accumulation was observed in midwater and surface samples taken from Sombre Lake, N barely doubling and P increasing only threefold. N: P ratios reached a minimum in late winter, but remained an order of magnitude higher than those of Heywood Lake (Table 3). From July onwards, large amounts of both phosphate and ammonia were released to the bottom water, comparable to the phosphate maximum recorded at 6 m in Heywood Lake during September. N: P ratios at depth were depressed by the high phosphate concentrations. Although oxygen concentrations were not recorded during the study period unpublished data from previous yerars show this release to be associated with the development of anoxia in the water overlying the sediment. Accumulation of ammonia reflects the anaerobic sediment metabolism which Ellis-Evans (1982) found after ice formation in Signy Island lakes.

Spring and Summer. The two events characterizing the beginning of spring were the opening of inflows and outflows and the commencement of algal growth. These combined to bring about a rapid reduction in nutrient concentrations (Figs. 4 and 5) which then remained low throughout the summer. Phosphate and ammonia dropped to near undetectable levels in Sombre Lake though concentrations at the base of the water column remained high until ice cover was lost. Both midwater and bottom N: P ratios rose as phosphate declined and high values

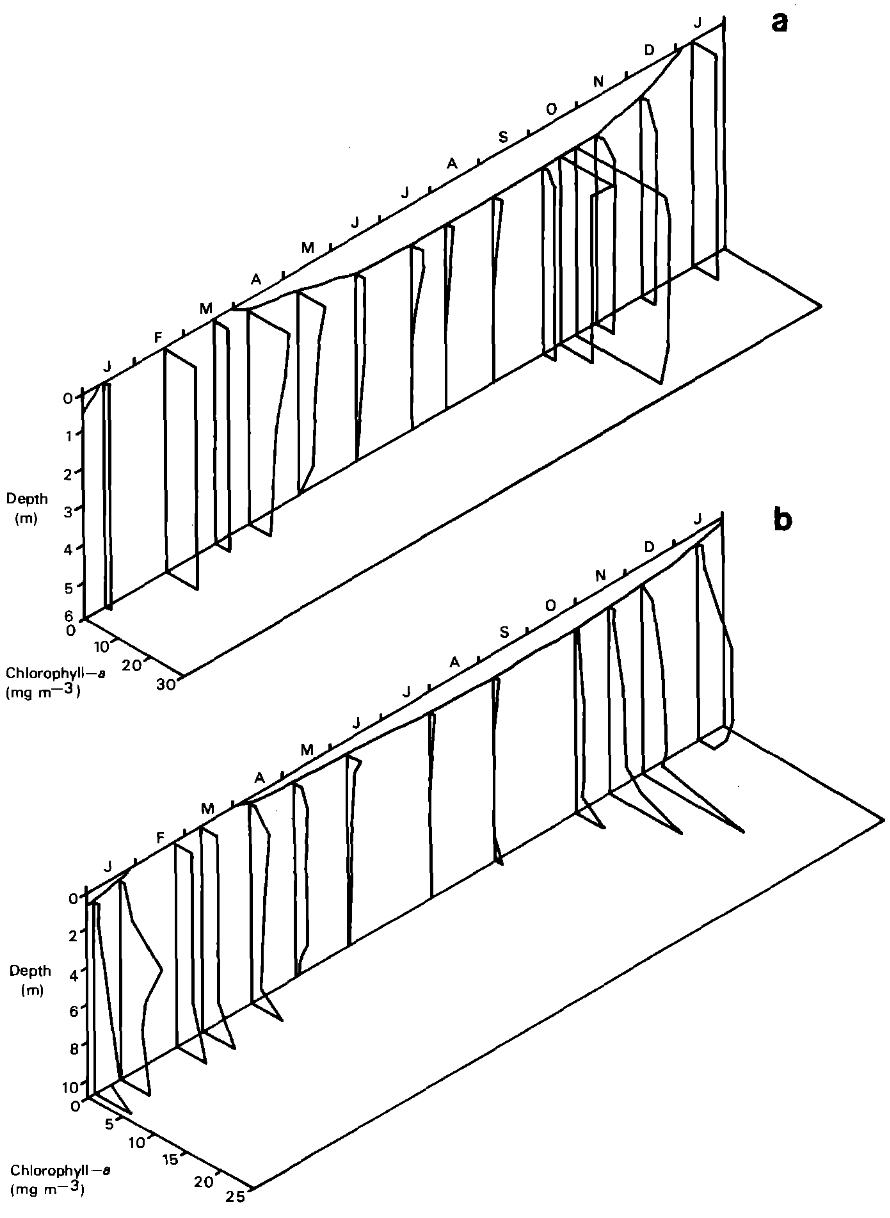

Fig. 3. Depth-time distribution of chlorphyll-*a* (corrected for phaeopigments) in **a** Heywood Lake and **b** Sombre Lake during 1980

were prevalent throughout in summer. In Heywood Lake, nitrate concentrations also fell to low levels while after the spring decrease, summer phosphate concentrations were relatively high and the N:P ratio was low (Table 3).

Increases in biomass bound much of the inorganic nutrients available at the end of winter in particulate form. Analysis of this particulate matter suggests that up to 50 μg/l P and 180 μg/l N was consumed in the production of the Heywood Lake spring bloom and 7 μg/l P and 30 μg/l N was absorbed from the water column of Sombre Lake up to the loss of ice cover. This consumption represents 72% of the P and 22% of the N available at the end of winter in Heywood Lake and 40% of P and 12% of N in Sombre Lake. A considerable amount of this material was flushed out of the lakes, particularly Heywood Lake, where peak outflow rates coincided with the biomass maximum.

Estimates of inorganic nutrient input to and outflow from the lakes during this period show a further net loss

Table 2. Concentration of some inorganic nutrients as ratios to chloride (by wt) during the winter of 1980, prior to the opening of inflows. All values have been multiplied by 10^3

A *Sombre Lake*

	Phosphate			Nitrogen		
Date	Surface	Mid-depth	Bottom	Surface	Mid-depth	Bottom
12 Mar	0.02	0.02	0.02	6.0	6.0	6.0
10 Apr	0.02	0.02	0.05	9.8	8.2	15.7
7 May	0.05	0.04	0.19	13.1	11.4	20.0
9 Jun	0.03	0.05	0.15	10.0	10.4	18.5
31 Jul	0.06	0.05	8.18	10.9	10.7	35.2
9 Sep	0.06	0.06	10.55	11.2	11.1	25.0

B *Heywood Lake*

	Phosphate			Nitrogen		
Date	Surface	Mid-depth	Bottom	Surface	Mid-depth	Bottom
18 Mar	0.21	0.23	0.25	2.5	2.3	2.3
14 Apr	0.13	0.43	0.59	8.6	10.6	14.1
9 May	0.56	0.68	1.15	11.8	13.0	17.4
14 Jun	0.79	1.09	1.38	13.9	16.5	19.1
26 Jul	1.08	1.31	1.56	16.7	18.5	17.0
18 Aug	1.12	1.22	1.88	15.6	18.1	17.2
11 Sep	1.10	1.27	7.04	18.0	17.9	15.3

Table 3. Ratios by wt of inorganic N: inorganic P during 1980

A *Sombre Lake*

Date	Surface	Mid-depth	Bottom
3 Jan	124	675	2720
12 Mar	215	286	531
10 Apr	470	472	367
7 May	265	316	108
9 Jun	322	219	121
31 Jul	150	198	8.28
14 Aug	198	231	4.32
9 Sep	203	171	2.40
28 Oct	163	1570	3.24
19 Nov	108	1580	13.4
11 Dec	151	907	229

B *Heywood Lake*

Date	Surface	Mid-depth	Bottom
18 Jan	3.13	3.18	3.16
18 Mar	11.8	10.2	9.42
14 Apr	6.57	24.4	23.3
9 May	21.2	19.1	15.3
14 Jun	17.8	15.1	13.9
26 Jul	15.4	14.1	10.9
18 Aug	13.9	14.1	5.52
11 Sep	16.4	14.1	2.18
26 Oct	18.6	18.8	18.6
17 Nov	5.25	5.24	5.25
5 Dec	5.27	4.30	4.48

Table 4. Concentrations of some plant nutrients in some representative streams entering Heywood and Sombre Lakes, 1980–1981. All values in mg N or P m^{-3}. Stream types are *i* Direct snow melt; *ii* Snowmelt passing over rocks, moss and scree; *iii* Flowing through areas occupied by nesting sea birds; *iv* Flowing through areas occupied by seals; *v* Inflows from other lakes; *vi* Outflows

	Stream type	Oct			Nov			Dec			Jan			Feb			Mar		
		NO_3	NH_4	PO_4	NO_3	NH_4	PO_4	NO_3	NH_4	PO_4	NO_3	NH_4	PO_4	NO_3	NH_4	PO_4	NO_3	NH_4	PO_4
Heywood Lake	i	None occurring																	
	ii	–	–	–	–	–	–	200	35	28	243	9	6	483	7	4	80	20	6
	iii	–	–	–	–	–	–	315	44	18	340	14	35	224	11	12	865	8	6
	iv	–	–	–	–	–	–	100	46	60	224	48	70	146	25	40	482	23	21
	v	44	12	4	20	12	9	50	24	25	92	8	7	98	25	9	90	14	7
	vi	199	0	18	118	54	21	95	40	13	46	0	31	40	2	7	60	0	8
Sombre Lake	i	–	–	–	–	–	–	90	12	4	283	26	1	250	20	3	1048	19	12
	ii	–	–	–	–	–	–	125	55	5	243	9	6	250	13	6	80	20	6
	iii	–	–	–	–	–	–	270	6	25	1155	16	25	950	16	25	2000	6	25
	iv	None occurring																	
	v	–	–	–	*	*	*	80	11	4	291	21	0	150	10	3	544	15	8
	vi	*	*	*	173	19	2	125	5	3	200	4	3	120	2	3	110	0	0

– No significant flow
* Flowing but not sampled

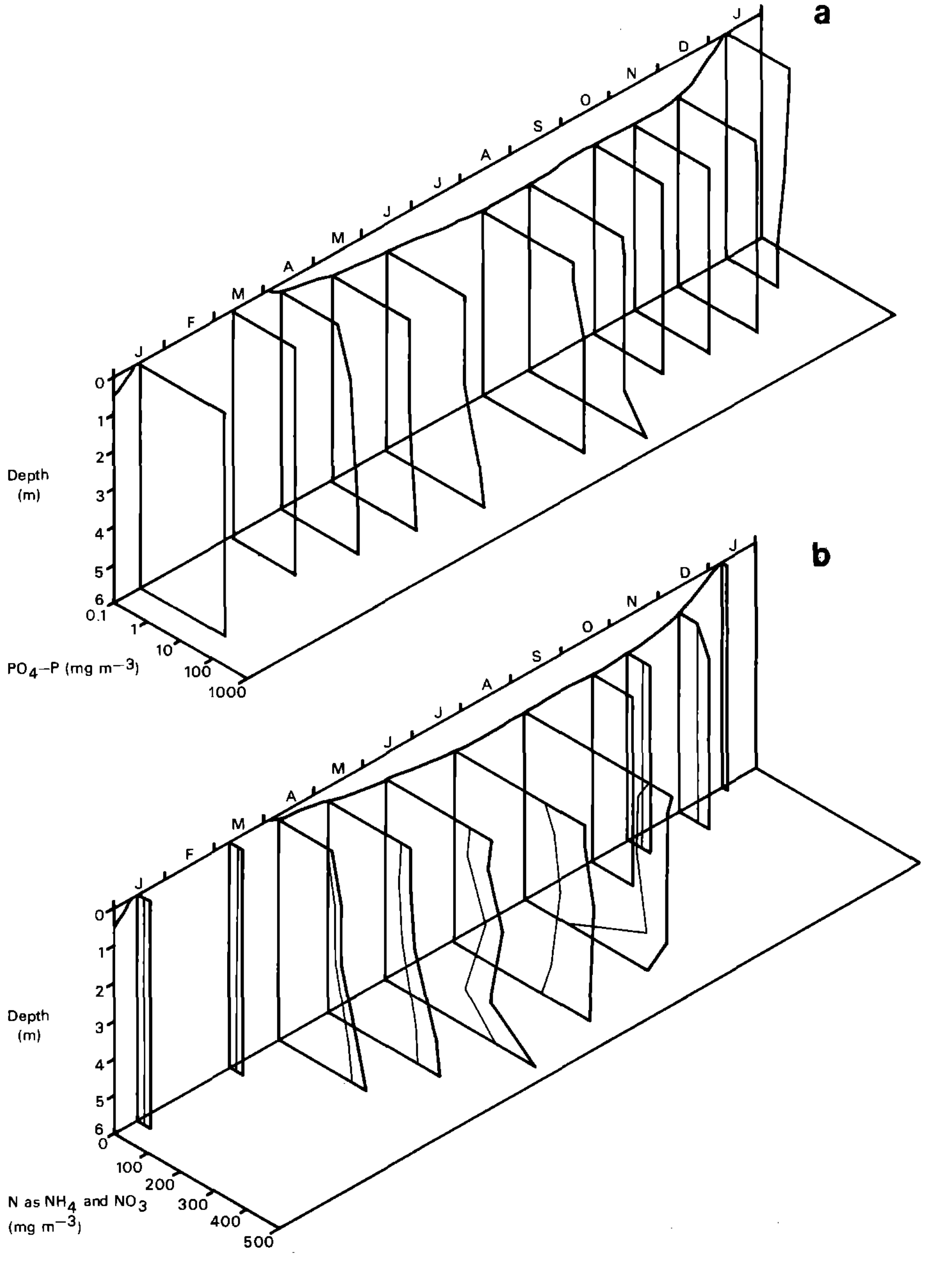

Fig. 4. Depth-time distribution of **a** Soluble reactive phosphate and **b** Inorganic nitrogen in Heywood Lake during 1980. In **b** the *thin line* represents (NO_3 + NO_2) – N concentration and the *thick line* (NO_3 + NO_2 + NH_4) – N concentration. All concentrations mg m^{-3}

of both N and P from Heywood Lake and a small loss of N from Sombre Lake. There was however a slight gain of P in the latter, due to the extremely low P content of the resident surface water. During the early stages of flow, the inflowing water consisted primarily of freshly melted snow. It had a dilute composition and was often colder than the lake water. At times, this resulted in the inflow forming a discrete low density layer immediately under the ice (as reported for an arctic lake by Rigler 1978) and is apparent from the chemical differences between surface and subsurface water (Figs. 4 and 5). Differences in the composition of inflow and outflow waters does however indicate that some interchange was occurring with resident lake water.

As the winter snow accumulation receded and the surface layers of the moss carpet melted, the importance of small run-off streams entering around the lake margins in supplying nutrients increased. Though flow rates were low, these streams could accumulate high nutrient concentrations where they passed over moss or scree enriched by animals (Table 4). The amount of phosphate reaching Heywood Lake in particular increased considerably. Because of the geological similarity of the two lake catchments, leaching rates of nutrients are likely to be similar and animals represent the major importers of nutrients to Heywood Lake. The concentration of nitrate in inflows was relatively high even where no enrichment occured and the N loadings of the two lakes were broadly similar. Estimates of groundwater seepage showed that during the summer months Heywood Lake received up to 54% of its water via this route, whereas Sombre Lake received only 2–3%. Ground-

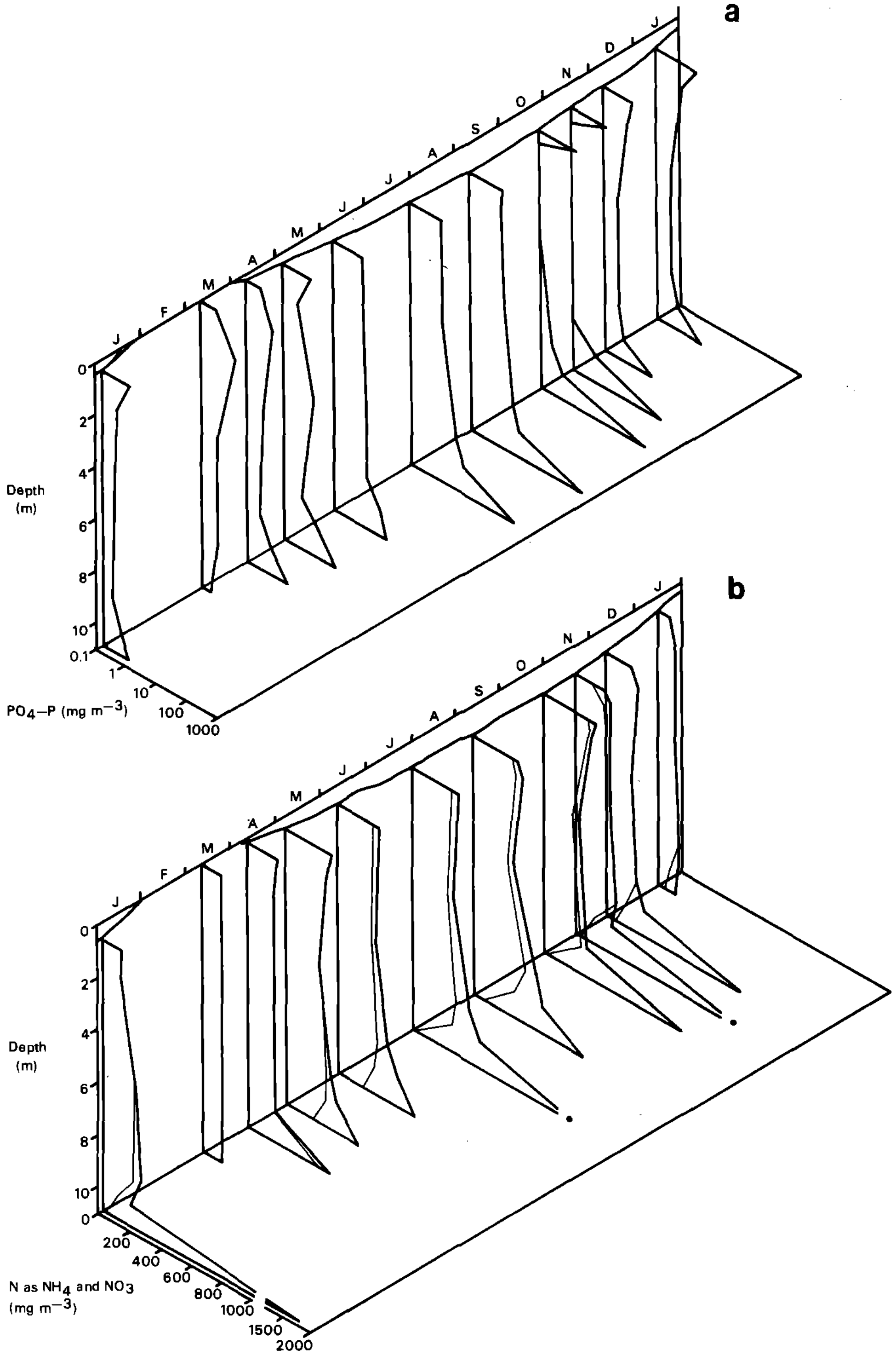

Fig. 5. Depth-time distribution of **a** Soluble reactive phosphate and **b** Inorganic nitrogen in Sombre Lake during 1980. In **b** the *thin line* represents (NO_3 + NO_2) – N concentration and the *thick line* (NO_3 + NO_2 + NH_4) – N concentration. All concentrations mg m^{-3}

water extracted from moss banks fringing Heywood Lake again contained exceptionally high amounts of phosphate, up to 360 $\mu g\ l^{-1}$. Values for N and P loading (Table 5) to the lakes were derived from these data but are rough estimates. Only inorganic forms were analysed, samples were taken infrequently, no direct input from seals swimming in the lakes was included and visual estimates of flow rates were sometimes used. Despite this, these values indicate that, as a result of catchment enrichment, Heywood Lake receives considerably greater amounts of phosphate than Sombre Lake, particularly during the summer period, but a similar amount of inorganic nitrogen. However, most of the N and P input to Sombre Lake was towards the end of the growing season while in Heywood Lake it coincided with peak activity in January/February.

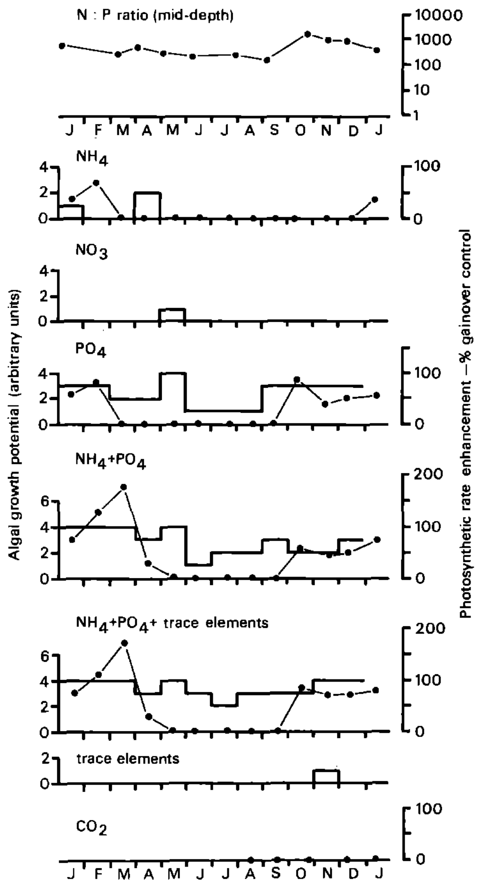

Fig. 6. Results of bioassays on Sombre Lake. Histograms represent increase in algal growth potential for each nutrient enrichment over the control on scale of 0–6 *(left-hand scale)*. Lines show % enhancement of photosynthetic rate over 72 h by nutrient enrichment *(right-hand scale)*. Lake mid-depth N : P ratios are also shown

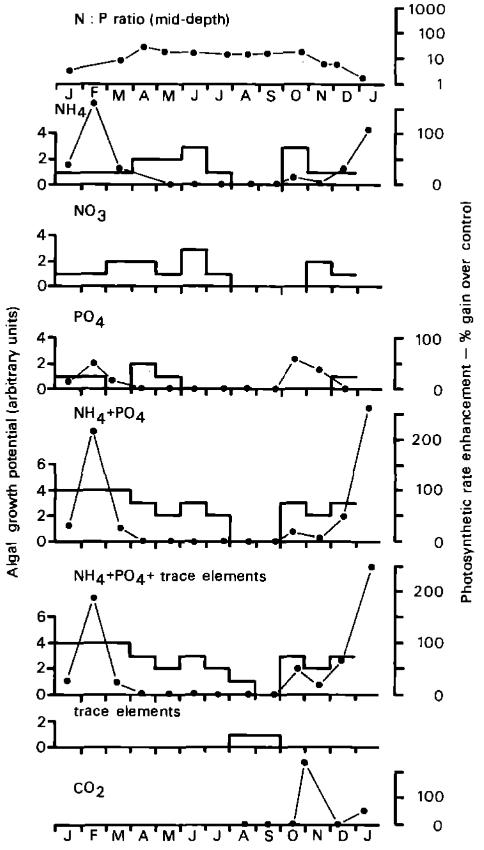

Fig. 7. Results of bioassays on Heywood Lake. Histograms represent increase in algal growth potential for each nutrient enrichment over the control on scale of 0–6 *(left-hand scale)*. Lines show % enhancement of photosynthetic rate over 72 h by nutrient enrichment *(right-hand scale)*. Lake mid-depth N : P ratios are also shown

Table 5. Estimated fluxes of inorganic nitrogen and phosphorus into and out of Heywood and Sombre Lakes. Values given in $\mu g\ m^{-2}\ d^{-1}$

A *Heywood Lake*	P in	P out	N in	N out
November	0.08	0.25	0.08	2.06
December	1.50	0.719	1.69	3.52
January	4.94	2.25	10.04	5.84
February	5.68	1.73	10.40	5.72
March	0.37	0.11	1.64	1.12
B *Sombre Lake*	P in	P out	N in	N out
November	0.02	0.01	1.65	1.56
December	0.06	0.02	1.98	2.23
January	0.02	0.09	4.77	13.95
February	0.19	0.07	8.68	12.63
March	0.57	0.00	39.75	6.91
C *Annual totals*	$mg\ m^{-2}\ yr^{-1}$ P in	P out	N in	N out
Heywood Lake	350	140	660	530
Sombre Lake	23	5	1580	1017

Nutrient Limitation

Sombre Lake. Algal growth potential (AGP) tests showed N to have little importance compared to P in limiting the potential crop in Sombre Lake (Fig. 6). This is consistent with the high N : P ratio of both the lake and its inflows. Only during summer did N have any effect on AGP and then only when P was also provided. ^{14}C assays suggested, however, that despite continual limitation of growth potential, the lake population was not nutrient limited between April and October when photosynthesis was undetectable due to low light levels under ice cover. Only with the onset of spring growth did P limitation become effective. By November, as ambient concentrations declined, addition of ammonia also stimulated photosynthesis and a dual enrichment gave maximum enhancement until April when the lake returned to its winter state.

Heywood Lake. Results of the AGP tests for Heywood Lake contrast with those for Sombre Lake. During late winter, nutrients were sufficiently abundant to render the technique incapable of identifying any of those tested as being potentially limiting (Fig. 7). During the summer, nitrate and ammonia were the nutrients most limiting growth potential. Phosphate, which remained in relatively high concentrations, rarely had any effect.

As in Sombre Lake, ^{14}C bioassays showed no evidence of nutrient limitation during winter. P was more important than N during spring growth, but as algal population size and N : P ratio declined, ammonia limitation became prevalent. A dual enrichment of phosphate and ammonia gain produced maximum enhancement.

At the height of the spring bloom evidence was obtained suggesting that carbon dioxide availability limited photosynthetic rate. Samples incubated with ^{14}C immediately after collection showed a substantially greater rate of photosynthesis after enrichment with CO_2 bubbled water (Fig. 8). An investigation of diurnal fluctuations of dissolved inorganic carbon (DIC) showed that free CO_2 concentration was reduced by half over the course of the day to 50 $\mu m\ l^{-1}$. The change in total DIC was largely accounted for by the change in free CO_2, and it would appear that bicarbonate is not an important source of carbon. A considerable depletion of DIC had occurred during the spring from maximum winter levels of 420 M (total) and 165 μM (free CO_2). During summer, higher values were again found at 121 μM free CO_2 and 281 μM total DIC (samples taken at 1000 h).

Other Lakes. Primary limiting nutrients identified for other Signy Island lakes are indicated in Fig. 9. Also included are average winter inorganic-N : $PO_4 - P$ and SiO_4; Si : $PO_4 - p$ ratios (both on a weight basis) and average summer chlorophyll-*a* concentrations for the period 1974 – 80. N : P ratios above 20 – 30 were associated with phosphate limitation and low summer chlorophyll concentrations. Decreasing N : P ratio was accompanied by an increse in chlorophyll development and a change from P to N limitation. The Si : P ratio has been used as an indicator of the degree of P enrichment of natural river waters. Golterman (1975) took a value of 110 to represent unenriched water and considered lower ratios to be indicative of catchment enrichment. Ratios in oligotrophic Signy Island lakes which receive minimal biotic enrichment, were considerably in excess of this

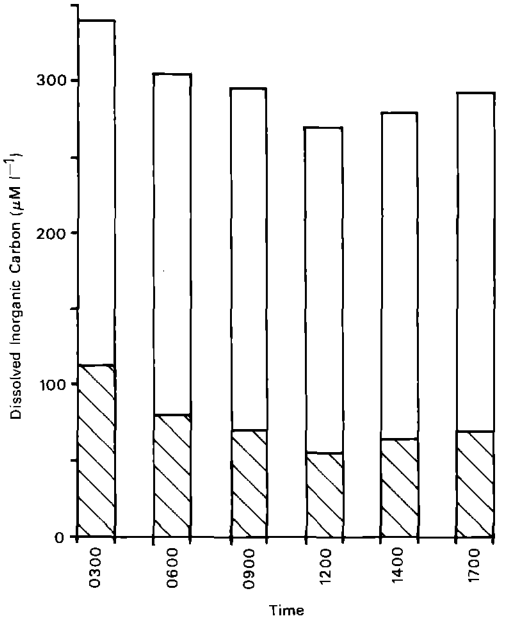

Fig. 8. Concentration of dissolved inorganic carbon in Heywood Lake at 1.5 m on 13th November 1980. Histogram represents total inorganic carbon, shaded area free carbon dioxide

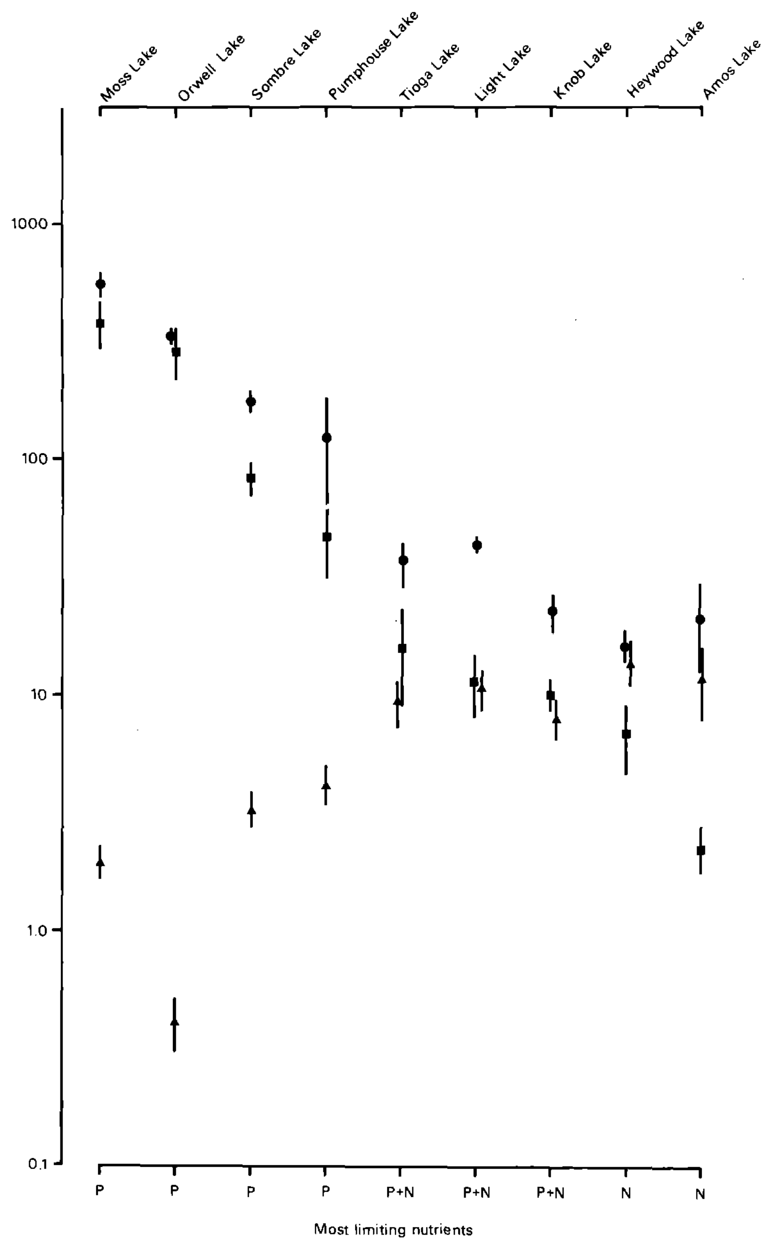

Fig. 9. Mean summer chlorophyll-*a* concentration *(triangles* mg m^{-3}), mean winter $SiO_4 -$ Si : $PO_4 -$ P ratios *(squares)* and mean winter (NO_3 + NH_4) – N : PO_4 – P ratios *(circles)* for a number of Signy Island lakes. Data for 1974 – 80 was used to calculate means. Bars represent SE. Most limiting nutrients *(N* or *P)* during summer 1980, as identified by growth potential bioassay are also indicated

value and may reflect the large volumes of water which enter directly as snowmelt with little or no contact with rock. The tendency for N : P and Si : P ratios to decline in parallel, coupled with the high N concentrations observed in oligotrophic lakes (300 $\mu g\ l^{-1}$ in Moss Lake during winter) confirm the findings from Heywood and Sombre Lake that catchment enrichment primarily results in increased P rather than N loading.

Discussion

The identification of nutrient limitation in this study depended on the two bioassay techniques. Of these, the batch culture assay is generally accepted as providing reasonably accurate information on which nutrients most limit potential biomass production (O'Brien and Denoyelles 1976). It does not reveal actual limitation in the natural population, as shown by the P limitation indicated in Sombre Lake at midwinter when photoautotrophic growth was impossible. The bioassay using the natural population is of more potential relevance, but has been criticised recently by Healey (1979) who found short term photosynthetic response to nutrient additions too unpredictable to confidently identify limitation. However, where 72 h incubations are employed, more satisfactory results are normally obtained (Lean and Pick 1981). The possibility of cell number increases during this incubation period means that an increase in ^{14}C uptake could represent either an increase in biomass or activity per cell.

Nutrient limitation can affect both final cell yield and/or growth rates (O'Brien 1972). Apparent limitation of growth rate has been demonstrated on several occasions in laboratory cultures (Senft 1978; Laws and Bannister 1980), though recent work has shown that many phytoplankton species can maintain high growth rates down to effectively undetectable nutrient concentrations (Goldman and McCarthy 1978; Smith and Kalff 1981). Although low rates of photosynthesis in situ have been ascribed to nutrient limitation (Pechlaner 1971) others have found that rapid recycling of nutrients within the trophogenic zone can permit high photosynthetic rates to be maintained despite limitation of standing crop (Morris et al. 1971). Rates of photosynthesis in both Heywood and Sombre Lakes were high during summer despite the evidence for nutrient limitation. Light et al. (1981) reported assimilation numbers in Heywood Lake to be among the highest on record. Fluctuations of both biomass and nutrient concentrations during summer were relatively small despite this extensive photosynthesis and it is likely that rapid recycling and the net nutrient input were permitting the maintenance of such high growth rates, while the available pool of nutrients imposed a restriction on the standing crop. Kalff and Welch (1974) found that nutrient concentrations limited biomass rather than production per unit biomass in two High Arctic lakes with comparable temperature regimes to those described here.

A special case for direct nutrient limitation of photosynthetic rate can be argued for inorganic carbon (Talling 1976). When the rate of CO_2 uptake exceeds the rate of supply limitation may occur, though lasting effects on standing crop are unusual due to gas exchange with the atmosphere (Schindler and Fee 1973). Under the conditions prevailing in Heywood Lake at the height of the spring bloom where a dense phytoplankton population was isolated from the atmosphere by thick ice cover, the rate of supply was insufficient to satisfy the demands of photosynthesis. Limitation of photosynthesis resulted which, together with the onset of N and P limitation and heavy algal losses to outflows, appears to have been responsible for the termination of the bloom. Concentrations of CO_2 were greater than those found limiting by Talling (1976) and Schindler and Fee (1973). Standing crops in Sombre Lake never reached sufficient density for inorganic carbon to become limiting because of the effect of low P availability.

Where summer phytoplankton development is determined by nutrient availability, regeneration of inorganic forms during winter may be of particular significance (Burns and Ross 1972). Such regeneration was a feature of both Heywood and Sombre Lakes. In the latter, it provided over twice as much phosphate and in the former 1.8 times as much nitrogen as was received annually from the catchment. This contrasts with the situation in Char and Meretta Lakes in the Canadian High Arctic which, though receiving similar nutrient loadings and undergoing similar periods of ice cover, do not regenerate significant quantities of either nutrient. Consequently considerably sparser, nutrient-limited phytoplankton populations develop during the summer (Kalff and Welch 1974). The underice bloom in Heywood lake is dependent on the regenerated nutrients and continues until the supply is nearly exhausted. Much of the winter regeneration in Signy Island lakes is likely to result from the continuing microbial activity reported by Ellis-Evans (1981a, b, 1982). Microbial populations both mineralize organic material and create the anoxic conditions essential for chemical release of sediment-bound phosphate. Accumulation of high concentrations of inorganic nutrients over winter in Heywood Lake, compared to the amount received annually from its catchment, suggests that both autochthonous and allochthonous organic material is available for decomposition. Such ready availability of substrates explains the much greater activity seen here than in Sombre Lake where the unenriched catchment is likely to have provided considerably fewer organics.

The localisation of P and N increases in Sombre Lake to the 9 – 11 m strata, while accumulation occurred at all depths in Heywood Lake reflects the location of microbial activity. Ellis-Evans (1981a, b) found an active heterotrophic population throughout the water column of Heywood Lake, while in Moss Lake (comparable in trophic state to Sombre Lake) it was largely confined to the bottom waters and sediments. As a result the growth potential of most of Sombre Lake remained low and maximum chlorophyll concentrations were recorded close to the nutrient rich sediment-water interface, despite lower radiation levels at this depth. Comparable deepwater maxima, in response to nutrient availability, have been reported by Pechlanter (1971) and Vincent (1981). The abundance of non-motile chlorophytes at this maximum suggests growth at this depth rather than vertical migration of flagellates. This phenomenon was never seen in this study though common in other ice covered lakes (Tilzer 1973). The less dense population of chrysophytes in midwater may however have been capable of limited migration to utilize phosphate available at depth. In contrast to Sombre Lake, high nutrient concentrations throughout Heywood Lake at the beginning of spring growth permitted the rapid development of an extremely dense phytoplankton population at all depths. Hawes (1983) describes how under-ice mixing processes in Heywood Lake increase the availability of nutrients and light to the developing phytoplankton. This mixing is responsible for the vertical homogeneity of the lake during spring growth and is facilitated by the weak density gradient prevailing at the end of winter. In Sombre Lake, the density gradient was found to be much stronger and mixing was negligible. This density gradient in Sombre Lake restricted upward movement of both chlorophyll and phosphate.

By increasing the amount of P entering lakes without a corresponding N increase, catchment enrichment results in a decrease in the N:P ratio of resident lake water. This ratio is often important in determining which nutrient is most limiting to phytoplankton (Forsberg et al. 1978; Yull Rhee 1978) and data presented in Fig. 8 suggests that this holds true for Signy Island lakes. In Heywood Lake, the N:P ratio before the spring-bloom was considerably higher than in summer when the P-rich inflows were running. Consequently P limitation was observed before N limitation. Only when the N:P ratio fell, largely because of net loss of N to the outflow (Table 3) and algal activity, did N limitation become prevalent. Both nitrate and ammonia were depleted during summer while phosphate concentrations remained high and it was therefore the rate of autochthonous supply and internal cycling of N that controlled phytoplankton growth.

N:P ratios remained very high in Sombre Lake throughout the summer, P availability limited phytoplankton and consequently nitrate levels were not depleted. However, a requirement for ammonia was indicated by the ^{14}C bioassays, though of secondary importance. This ammonia requirement suggests that despite the low observed concentrations, the phytoplankton was predominantly utilizing this N form throughout the summer rather than the more abundant nitrate. The implication is that autochthonous and allochthonous supply was sufficient to satisfy demand. Ilmavirta (1982) reached a similar conclusion for a range of brown-water Finnish lakes, where high rates of photosynthesis were maintained by internal cycling.

It is concluded from this study that nutrient limitation of algal standing crops is widespread in a variety of Maritime Antarctic lakes. In unenriched catchments, phosphate is the single most limiting nutrient and phytoplankton is sparse, though photosynthetic rates can remain relatively high. Where seals and birds encroach into the lake catchment and terrestrial vegetation is more extensive, phosphate inputs are increased, permitting an extensive phytoplankton to develop, which may become nitrate limited. Despite low temperatures, internal recycling appears to be a significant process and the long, dark winter period, when photosynthesis was not detected, allows accumulation of nutrients before spring growth commences.

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