

PHYTOPLANKTON PRODUCTION AND WINTER MIXING: CONTRASTING EFFECTS IN TWO OLIGOTROPHIC LAKES

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SUMMARY

(1) Two deep oligotrophic lakes in the centre of North Island, New Zealand, shared several limnological features but differed in their seasonal patterns of algal production.

(2) Lake Waikaremoana followed, in its thermal stratification, the classic pattern for temperate warm-monomictic lakes. During winter circulation, light availability to the phytoplankton was reduced by a factor of at least 13 relative to that in spring and summer, and there was no increased supply of phosphorus, which later controlled the amount of growth of its phytoplankton. Concentrations of algal biomass and algal production rates were predictably low, but rose rapidly with increased irradiance in spring.

(3) Lake Taupo experienced similar thermal stratification and mixing, but concentrations of algal biomass and algal photosynthetic production rose to maxima for the year during winter isothermy when temperatures were at their annual minimum and when mixing extended to the bottom of the lake. Winter circulation brought an increased supply of phosphorus and, more importantly, nitrogen which later controlled the amount of algal growth in the euphotic zone. This increased availability of potentially limiting nutrients offset the effects of low light availability and low temperature.

(4) Lake Taupo, and other nearby lakes which behave similarly, form intermediates between temperate lakes with typical winter minima of algal production and many tropical lakes which experience maximum phytoplankton production during storminduced mixing.

INTRODUCTION

Winter isothermy in warm-monomictic lakes has been described traditionally as a time of low concentrations of algal biomass and minimum productivity. In English Lake District lakes, phytoplankton population density declines during late autumn mixing and remains low until the spring diatom increase (e.g. meso-eutrophic Windermere (Lund 1950; Talling 1971), oligotrophic Wastwater (Vincent 1981 a)). This pattern appears also to be typical of monomictic lakes in eastern Europe (e.g. Lake Ohrid, Yugoslavia (Oceviski & Allen 1977); Lake Mikolajskie, Poland (Szczepanski 1966)), the Laurentian Great Lakes, U.S.A. and Canada (Dobson, Gilbertson & Sly 1974) and Lake Washington, U.S.A. (Edmondson 1969). This has led Round (1971) to identify mid-winter as a 'cardinal point' in the algal growth cycle, a time of year when unfavourable environmental conditions restrict population development to an annual minimum.

Early investigations suggested that several of the lakes on North Island, New Zealand, do not follow this pattern. McColl (1972) reported that phytoplankton chlorophyll concentration, in three productive lakes of the region, apparently was higher in winter than at other times of the year, and concluded that algal growth in these lakes was not seriously limited by minimum winter temperatures. Winter chlorophyll concentration maxima have

subsequently been observed in a range of nearby lakes of differing fertilities (Fish 1975; W. F. Vincent, unpublished). A pronounced peak of *Melosira* and the yearly maximum in chlorophyll *a* concentration in the largest waterbody of this region, Lake Taupo (White *et al.* 1980) occur in winter.

The present study has investigated factors controlling these winter maxima in algal biomass. Two nearby lakes of similar fertility, but apparently dissimilar production cycles, were selected for study of seasonal patterns of productivity, chlorophyll *a* concentration and planktonic nutrient demands.

THE STUDY SITES

Lakes Taupo (38°45'S, 175°50'E) and Waikaremoana (38°45'S, 177°05'E) are warm-monomictic waters on the central volcanic plateau of North Island, New Zealand. They have similar mean depths, hydraulic residence times and minimum water temperatures during winter isothermy (Table 1) but differ in water clarity and geochemistry and other characteristics of their catchments.

Lake Taupo is New Zealand's largest lake. It lies in the middle of a volcanic plateau and is surrounded by a varied catchment that includes pasture, native forest, scrub, alpine tussock vegetation and two small towns. The inflows to the lake are high in phosphorus concentration relative to that of nitrogen. White & Downes (1977) report an overall N : P ratio in the inputs of 5-7: 1 (weight/weight) which results from the unusual geochemistry of pumice and ignimbrite substrata of the area (M. H. Timperley, unpublished).

Lake Waikaremoana is a smaller, but deeper lake, completely surrounded by dense forest (podocarp/southern beech) on the edge of a plateau where volcanic influence is much reduced. Low phosphorus concentration and high ratios of inorganic N : P in the inflows (many greater than 20:1 by weight) reflect its geochemically distinct catchment of sedimentary rock.

TABLE 1. General characteristics of Lakes Taupo and Waikaremoana, New Zealand

	L. Taupo	L. Waikaremoana
Altitude (m)	357	585
Area (km ²)	612	51
Catchment area (km ²)	2849	371
Maximum depth (m)	163	248
Average depth (m)	97	93
Residence time (year)	12	8
Secchi disc depth (range in m)	14-21	7-15
Minimum winter temperature (°C)	10.5	9.0
Maximum windfetch (km)	39	11
Shoreline length (km)	153	93
Shoreline length/lake area (km km ⁻²)	0.25	1.81

METHODS

Samples were collected with an opaque Van Dorn water sampler from the middle of each lake at depths of 5 to 25 m in a series of visits spanning the range of a calendar year. For productivity estimates, sub-samples were dispensed into duplicate 125-ml transparent and opaque bottles, injected with ¹⁴C-bicarbonate (final activity of 0.04 #Ci ml⁻¹) and incubated *in situ* for 4 h from 10.00 to 14.00 h local time (Goldman 1963). At the end of

the incubation the plankton was filtered through 0.22 μm pore size Millipore membrane filters which were then air-dried. The activity of these cells was determined by liquid scintillation spectrometry. Dissolved inorganic carbon concentration was measured by infrared gas analysis after acidification.

Plankton for chlorophyll *a* analysis was filtered through a 4.25 cm diameter Whatman GF/C glass-fibre filter which was then homogenized in 90% v/v acetone with a Teflon tissue grinder. The extract was cleared by centrifugation and the chlorophyll *a* concentration assayed by fluorometry before and after acidification (Strickland & Parsons 1968). Coefficients of variation for these estimates were typically less than $\pm 15\%$.

Water samples for chemical analysis were filtered through acid-washed GF/C filters within 4 h of collection, frozen and then stored. All analyses were performed on a Technicon AutoAnalyzer II. Nitrate was reduced to nitrite by hydrazine and then analysed by the method of Downes (1978a); ammonium was analysed by the method of Crooke & Simpson (1971), and soluble reactive phosphorus (SRP) by a modified molybdenum-blue method (Downes 1978b). Detection limits with these analytical procedures were 0.4 mg SRP m^{-3} , 0.4 mg $\text{NO}_3^- \text{N}$ m^{-3} and 0.5 mg $\text{NH}_4\text{-N}$ m^{-3} (Downes 1978a, b). In this paper 'dissolved inorganic nitrogen' (iN) refers to $\text{NO}_3^- \text{N}$ plus $\text{NH}_4\text{-N}$, and all N to P quotients are expressed on a weight/weight basis.

Four bioassays for nitrogen and phosphorus demand were carried out on each lake. First, $^{32}\text{P}\text{-PO}_4$ was injected into samples of lakewater and its loss from solution recorded after 1, 2, 4, 8, 16, 30, 60 and 120 min. Results were expressed as the time required for complete removal (turnover time). Secondly, samples were incubated with $^{14}\text{C}\text{-HCO}_3^-$ in the dark without ammonium ions added and with ammonium-N to give a final concentration of 100 mg m^{-3} . The percentage change in dark fixation of carbon over 4 h was measured. Thirdly, lakewater samples were incubated with ammonium ions ($\text{NH}_4^- \text{N}$ 100 mg m^{-3}) plus phosphate ($\text{PO}_4\text{-P}$ 10 mg m^{-3}) for 2 hours. The nitrogen and phosphorus content of the filtered seston was measured before and after enrichment. Specific accumulation rates for nitrogen (in days^{-1}) were calculated by the formula:

$$V'_N = 12 \ln [(\text{seston N after 2 h}) / (\text{seston N initially})]$$

The factor 12 converts uptake rates from h^{-1} to d^{-1} . Seston concentrations of N were measured per unit volume of water. Phosphorus accumulation rates were treated similarly. V'_N and V'_P provide theoretical measures of maximum potential growth rate in terms of N or P (but not total biomass). The methodology, and theoretical background to this, as well as to the other assays are given in Vincent (1981b, c).

Concentration of alkaline phosphatase in the cells was also measured as a further guide to phosphorus deficiency. Maximum potential rates of enzyme activity were determined by fluorometry using high concentrations of the artificial substrate O-methylfluorescein phosphate (O-MFP) (Healey & Hendzel 1979). Samples of lakewater (4 ml) were incubated with 0.5 ml of MFP (final concentration 10 μM) in fluorometer cuvettes held in a water bath at 35 $^\circ\text{C}$. The increase in fluorescence within the cuvettes was measured over 1 h with a Turner 111 fluorometer fitted with a Corning 47B filter over the excitation beam and a 2A-12 filter on the emission side. The assay was calibrated against known concentrations of the enzymatic reaction product, O-methylfluorescein. Alkaline phosphatase activities (O-methylfluorescein produced, nmol per h) were expressed per unit mass of adenosine triphosphate (ATP) which was determined with a JRB ATP photometer (JRB Associates, California) on Tris buffer extracts (extraction and measurement according to Holm-Hansen & Booth 1966).

In vivo fluorescence of chlorophyll *a* was measured before (F_a) and after (F_b) the addition of 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) injected to give a final concentration of 10^{-5} M. These values were used to calculate the index 'cellular fluorescence capacity' (CFC) defined as $(F_b - F_a)/F_b$. This quotient (the CFC index) ranges, on a theoretical scale, from 0 to 1.0 and indexes the photosynthetic capacity per unit chlorophyll of phytoplankton populations (Vincent 1980). Algal cells capable of photosynthesis have CFC indices much greater than zero; this index was therefore used as a biological tracer to determine the extent of mixing below the euphotic zone.

Penetration of photosynthetically active radiation (PAR) was measured with a Lambda quantum irradiance probe. Temperature was recorded with a submersible Yellow Springs Instrument Co. thermistor probe down to 70 m or, at greater depths, with a mercury thermometer placed in the Van Dorn sampler and read immediately on recovery of the sample.

Daily surface radiation (I_o) was measured with a Kipp recording radiometer over the waveband 300-2500 nm. Incident PAR (400-700 nm) just beneath the water surface (I_t) was approximated as $0.46I_o$ (Talling 1957).

Absorbance scans of lakewater were obtained with a Cary 219 spectrophotometer after correction for differences between the 10-cm pathlength cuvettes.

RESULTS

Mixing cycles

A range of biological, chemical and physical properties was used to follow the stratification and mixing characteristics of each lake. Two particularly useful and complementary tracers of vertical circulation were DCMU-induced fluorescence (CFC) and nitrate concentrations. An increase in fluorescence after addition of DCMU (CFC values greater than zero) is characteristic of algal cells that have recently been active in the euphotic zone; it is therefore a tracer of water mixed down into aphotic strata from above. In lakes with aerobic hypolimnia, such as Taupo and Waikaremoana, nitrate is released by nitrifying bacteria in the surface sediments (Vincent & Downes 1981). During stratification this ion therefore accumulates in the bottom waters of the lake, and during winter circulation, is a tracer of deep hypolimnetic water moving upwards.

In January (mid-summer) 1979 Lake Taupo was well stratified with a deep mixed layer and thick metalimnion (Fig. 1). The temperature gradient at the thermocline fell slightly in March (maximum $0.6\text{ }^{\circ}\text{C m}^{-1}$ in January, $0.4\text{ }^{\circ}\text{C m}^{-1}$ in March) and the detectable nitrate concentration at 60 m suggested that turbulent mixing through the upper hypolimnion had begun by March. By late autumn (May), the mixed zone had extended to 40 m and on 21 June the uppermost 60 m were almost isothermal. Changes in the CFC index with depth on this date, however, demonstrated that partial circulation had extended only to 80 m depth. No DCMU-induced fluorescence was detected below this depth, although chlorophyll *a* was distributed to 150 m depth (Fig. 2). By 13 August the top 60 m of the lake were isothermal at Lake Taupo's winter minimum temperature (about $10.5\text{ }^{\circ}\text{C}$). Changes in the CFC index with depth suggested complete mixing to 110 m, but partial mixing to the bottom since measurable, but reduced, CFC values were recorded in the bottom-most region, 110-150 m (Fig. 2). Minimum temperatures were maintained in the surface waters at least until 27 September, but by this date mixing had apparently slowed down so that turbulence was no longer adequate to maintain the winter algal populations in suspension. Chlorophyll *a* concentration increased with increasing depth to

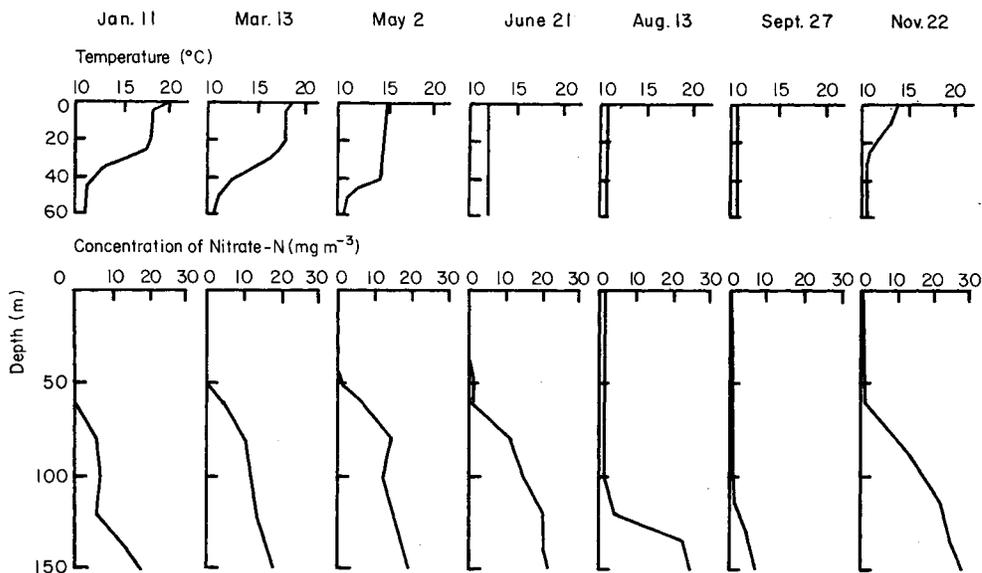


FIG. 1. Depth profiles of temperature to 60 m depth and concentration of nitrate-nitrogen, to 150 m depth in Lake Taupo, New Zealand.

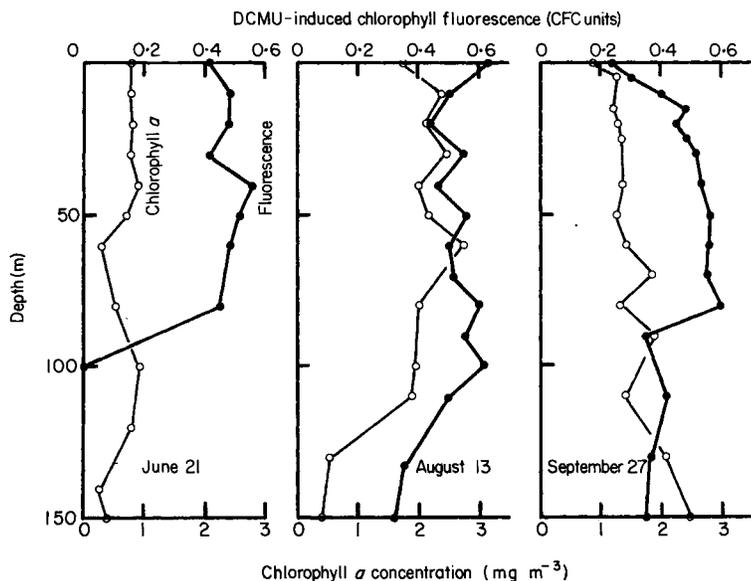


FIG. 2. Changes with depth of: (●), DCMU-induced chlorophyll fluorescence; and (○), chlorophyll a concentrations in Lake Taupo, New Zealand between mid- and late winter.

the bottom of the lake (0.9 mg m^{-3} at 0 m, 2.5 mg m^{-3} at 150 m). The CFC indices (y) were logarithmically related to increasing depth, (z) to 80 m ($y = 0.08 \ln z + 0.24$; $r^2 = 0.93$; $n = 10$) suggesting a population of dense cells with high CFC indices sedimenting from the surface (Vincent 1981 a). The CFC indices markedly declined below

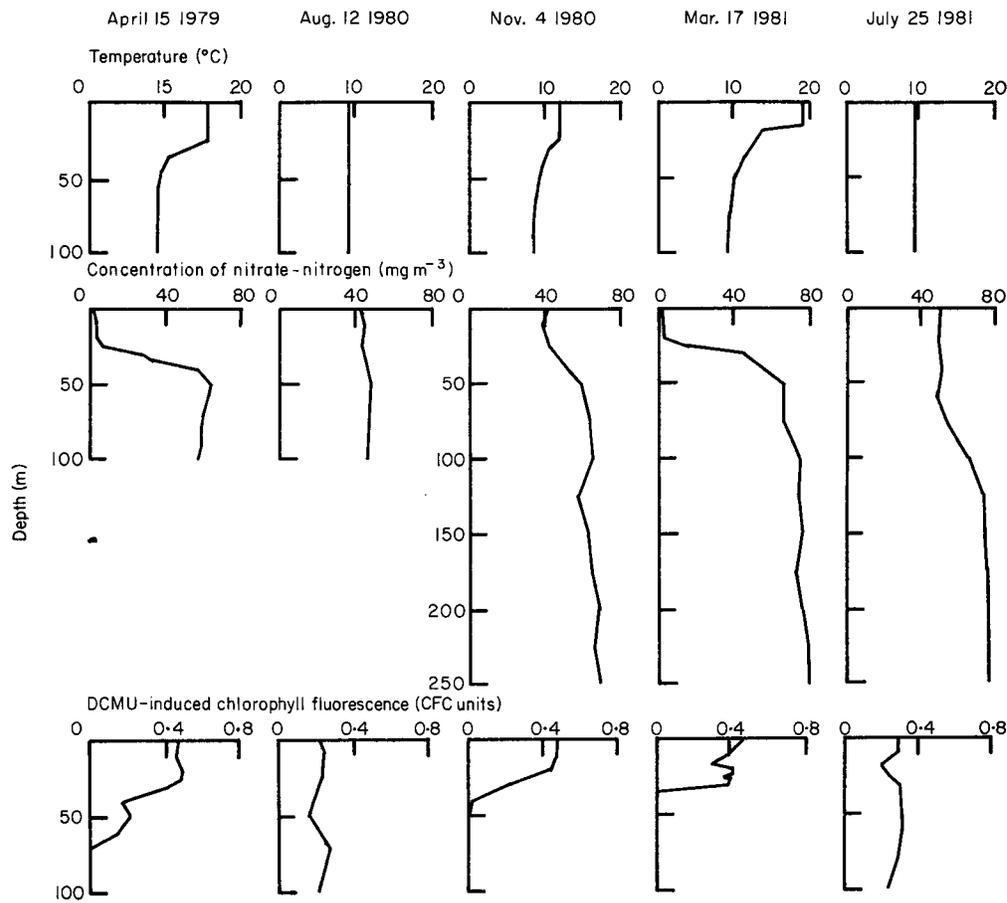


FIG. 3. Changes with depth throughout 1979 in Lake Waikaremoana, New Zealand of temperature, nitrate-nitrogen concentration and DCMU-induced chlorophyll fluorescence.

80 m suggesting that the algal cells in the deep layers had left the euphotic zone a long time previously. By November, thermal stratification was well established with a very large increase in concentration of nitrate in the hypolimnion that possibly began as early as September (Fig. 1).

Sampling of Lake Waikaremoana on 15 April 1979 showed CFC values greater than zero below the euphotic zone (estimated compensation depth 20 m, see below) which suggested that downward extension of the mixed zone had begun (Fig. 3). On 12 August the lake was isothermal at the minimum winter temperature (about 9.0 °C) from the surface to 100 m. Homogeneous nitrate concentration and values of CFC on this date demonstrated that the water mass was almost fully circulating. On three subsequent dates, sampling was extended to 250 m. In spring 1980 (4 November) stratification had begun; the euphotic zone had CFC values of 0.4 or greater and slightly reduced nitrate concentrations relative to those at aphotic depths. In late summer-early autumn (17 March) the distinction between euphotic and aphotic strata was more pronounced-CFC values were zero below 30 m and NO_3^- -N concentrations rapidly rose with depth below 20 m. On 25 July 1981 the lake was almost isothermal and CFC values were approximately

the same at all depths to 100 m (\bar{x} CFC \pm 2 S.E. = 0.264 + 0.025). Inspection of the profiles of nitrate concentration, however, showed that circulation was incomplete between 80 and 100 m, and little mixing had taken place at greater depths. Below 100 m there was no detectable chlorophyll *a* and hence no measurable CFC index.

Lakes Taupo and Waikaremoana therefore shared very similar stratification and mixing cycles. In both lakes the mixed layer began to deepen during late summer-early autumn (March), but complete overturn was not accomplished until late winter (August) each year. Turbulent mixing appears to slow down in early spring (September) and by late spring (November) stratification was well established in both water bodies.

Phytoplankton community composition

The two lakes contained very different algal floras. Lake Taupo's winter (June-August) community was dominated each year by a large-celled (about 2800 μm^3) *Melosira* which Florin (1970) considers morphologically similar to *M. baikalensis* (K. Meyer) Wislouch. Other important constituents of the phytoplankton at this time were *Asterionella formosa* Hass., *Cyclotella meneghiniana* Kutz., *C. stelligera* (Cleve & Grun.) Van Heurck, *Fragilaria crotonensis* Kitt., and *Synedra ulna* (Nitzsch.) Ehr. In summer (December-February), small-celled coccoid and ovoid chlorococcaleans, and flagellates such as *Chroomonas* sp. and *Dinobryon divergens* Imhof. were proportionately more important contributors to total algal biomass. During late summer diatoms, particularly *Asterionella formosa*, accumulated in the metalimnion (25-40 m).

In Lake Waikaremoana, the sparse winter community was dominated by *Chroomonas minuta* (Skuja) Bourrelly and *Cyclotella stelligera*. Both species were more abundant from spring to autumn, but during these seasons the dominant was *Sphaerocystis Schroeteri* Chod. which achieved maximum population density in the metalimnion. Also common then were *Chlamydomonas* sp., *Cryptomonas erosa* Ehr., *Peridinium* sp. and *Staurastrum floriformum* West & West.

Further descriptions of the phytoplankton in Lakes Taupo and Waikaremoana include White *et al.* (1980) and Cassie (1978), respectively.

Photosynthesis and chlorophyll concentration

The seasonal patterns of algal biomass concentration and production differed greatly between the two lakes. In Lake Waikaremoana chlorophyll *a* concentration and ^{14}C uptake rates were low during winter, but rose rapidly during spring (Fig. 4, Table 2). Maximum productivity and biomass were recorded in the late summer sampling (March 1981). There was then a pronounced metalimnetic chlorophyll maximum (Fig. 5), and photosynthesis by algae in deep water was probably responsible for the pronounced bulge in the profile of carbon uptake with depth, at 20 m (Fig. 4). This metalimnetic maximum was marked by high CFC values and high photosynthetic rates per unit chlorophyll and unit irradiance (Fig. 5). In July 1981 mixing was incomplete (see above), but both algal concentration and productivity were greatly reduced relative to those in late summer (Table 2). Much lower chlorophyll *a* concentration and photosynthetic rates were recorded during late winter of the previous year (August 1980).

Maximum photosynthetic carbon uptake rates (A_{max}) in the water column were always attained in Lake Waikaremoana at or near 5 m depth (Fig. 4), although in winter, productivities close to A_{max} were recorded down to 10 m (August 1980) or 7.5 m (July 1981).

A_{max} values (as carbon fixed) were highest in spring and late summer (both c. 3 $\text{mg m}^{-3} \text{h}^{-1}$), and minimum A_{max} was measured in late winter 1980 (0.5 $\text{mg m}^{-3} \text{h}^{-1}$).

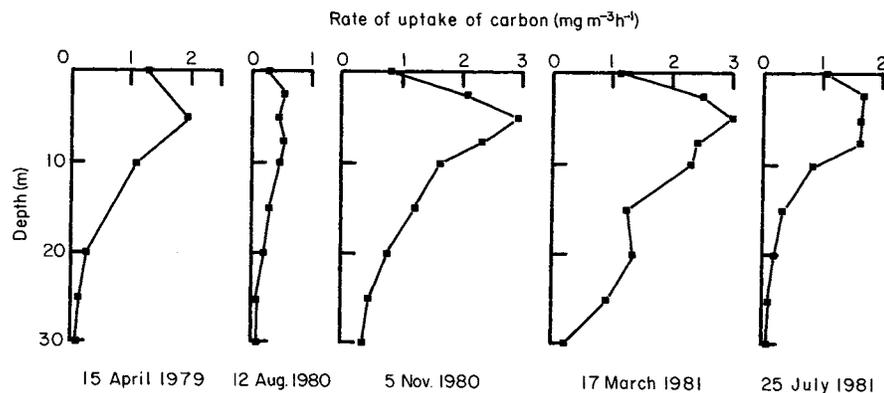


FIG. 4. Rates of photosynthetic carbon uptake with depth at different seasons in Lake Waikaremoana, New Zealand. Each point represents the difference between the mean values of uptake in duplicate clear and opaque bottles incubated *in situ* for 4 h.

TABLE 2. Integral rates of photosynthetic carbon uptake (ΣP , $\text{mg m}^{-2} \text{h}^{-1}$) in the euphotic zone (0–30 m) and chlorophyll *a* densities (ΣB , mg m^{-2}) in the euphotic zone and in the 0–90 m layer in Lake Waikaremoana, New Zealand, in 1979–81. The units of the quotient $\Sigma P/\Sigma B$ are carbon taken up per unit chlorophyll *a* and unit time ($\text{mg mg}^{-1} \text{h}^{-1}$).

Season	Date	ΣP	0–30 m ΣB	$\Sigma P/\Sigma B$	0–90 m ΣB
Autumn	15 Apr 1979	24.1	24.7	0.98	32.4
Winter	12 Aug 1980	9.9	15.8	0.63	44.6
Spring	5 Nov 1980	38.3	30.6	1.25	59.2
Summer	17 Mar 1981	47.9	44.1	1.09	59.1
Winter	25 Jul 1981	17.9	17.5	1.02	34.0

In contrast, carbon uptake rates and chlorophyll *a* concentration in summer in Lake Taupo were minimal for the year (Fig. 6, Table 3). As the epilimnion gradually was deepened, from February to March, carbon uptake and biomass concentration increased, rising to the annual maxima in August. With the onset of stratification there was a rapid decline in both chlorophyll concentration and photosynthetic rates and this decline continued into summer.

Carbon uptake rates per unit biomass also differed between the two lakes in both size and seasonality. The quotient of integrated rates of photosynthetic carbon uptake and densities of chlorophyll *a* in the euphotic zone ($\Sigma P/\Sigma B$) was maximal in Lake Taupo during summer and decreased through autumn and winter. Minimum $\Sigma P/\Sigma B$ was recorded in early spring during the rapid decline of the winter phytoplankton population. In Lake Waikaremoana this quotient was less variable, but a minimum was recorded during late winter isothermy (August) and a maximum in spring (November). This maximum was less than one-third of Lake Taupo's January peak (Tables 2, 3).

The A_{max} in Lake Taupo was generally attained at 10 m depth, except during the clear-water period (see below) in spring and summer when it dropped to 20 m or below. In midsummer (January) photosynthetic rates (as carbon) close to the annual minimum A_{max}

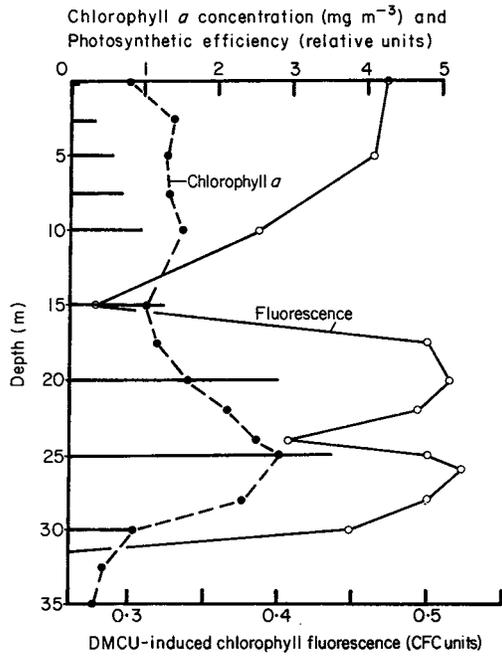


FIG. 5. Changes with depth of: (●), chlorophyll *a* concentration; (○), DCMU-induced chlorophyll fluorescence; and (bars), photosynthetic efficiency (carbon uptake per unit chlorophyll *a*, unit time and unit irradiance) in Lake Waikaremoana, New Zealand on 17 March 1981.

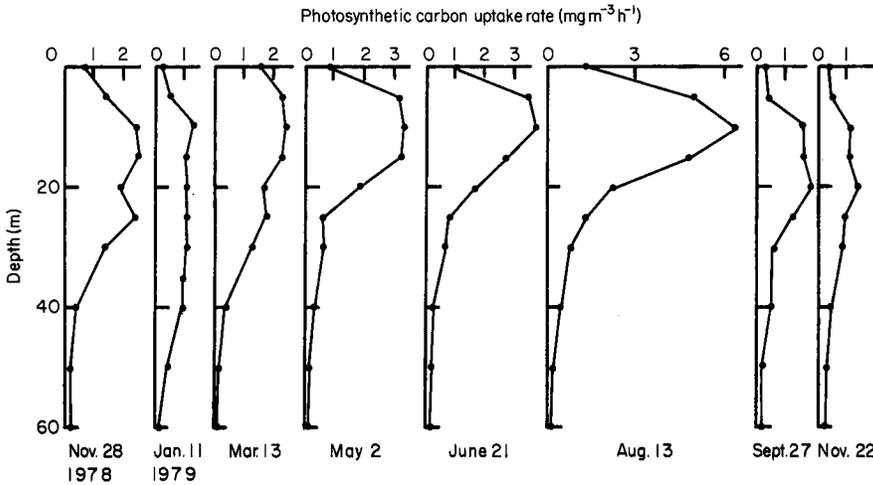


FIG. 6. Rates of photosynthetic carbon uptake with depths at different seasons in Lake Taupo, New Zealand. Each point represents the difference between the mean values of uptake in duplicate clear and opaque bottles incubated *in situ* for 4 h.

($1.26 \text{ mg m}^{-3} \text{ h}^{-1}$) were, achieved down to 40 m. Maximum A_{max} for the year was in late winter (August) ($6.26 \text{ mg m}^{-3} \text{ h}^{-1}$), and was over ten times greater than A_{max} in Lake Waikaremoana at the same time of year.

TABLE 3. Integral rates of photosynthetic carbon uptake (ΣP , $\text{mg m}^{-2} \text{h}^{-1}$) in the euphotic zone (0-50 m), and chlorophyll *a* densities (ΣB , mg m^{-2}) in the euphotic zone and in the 0-100 m layer in Lake Taupo, New Zealand, in 1978-79. The units of the quotient $\Sigma P/\Sigma B$ are carbon taken up per unit chlorophyll *a* and unit time ($\text{mg mg}^{-1} \text{h}^{-1}$).

Season	Date	ΣP	0-50 m		0-100 m	
			ΣB	$\Sigma P/\Sigma B$	ΣB	$\Sigma P/\Sigma B$
Spring	28 Nov 1978	69.5	29.6	2.35	57.1	
Summer	11 Jan 1979	45.4	12.0	3.78	26.6	
	13 Mar 1979	68.4	26.5	2.58	31.7	
Autumn	2 May 1979	69.0	44.2	1.56	50.0	
Winter	21 June 1979	76.3	39.9	1.91	67.9	
	13 Aug 1979	113	115	0.99	233	
Spring	27 Sep 1979	40.8	75.2	0.54	154	
	22 Nov 1979	39.6	27.1	1.46	64.6	

Photosynthesis and irradiance

Figure 7 compares the relationship between specific photosynthetic rate and relative irradiance for Lakes Taupo and Waikaremoana on selected dates during stratification and mixing. Samples of phytoplankton for these curves were taken from throughout the euphotic zone and incubated at their depth of origin. During late winter isothermy in both lakes, maximum photosynthesis per unit chlorophyll (P_{max}) was greatly reduced relative to that in summer (about a threefold reduction in both lakes) and surface phytoplankton was photoinhibited to a greater extent than in summer (Taupo: rate at surface was 26% of P_{max} in winter cf. 86% in summer; Waikaremoana: 51% P_{max} in winter cf. 72% in summer).

In both lakes the winter plankton was probably physiologically adjusted to a lower light regime. However, I_k values, which indicate the irradiance at which the onset of light

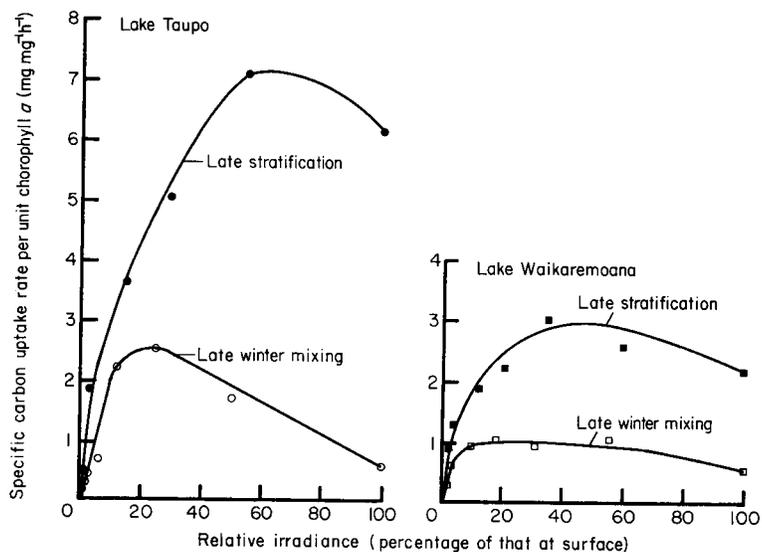


FIG. 7. Relationships between specific photosynthetic rate as carbon taken up per unit chlorophyll *a* and per unit time and relative irradiance (as percentage of surface irradiance) in two New Zealand lakes. Circular symbols, Lake Taupo: (●), 13 March 1979 (late stratification); (○), 13 August 1979 (late winter mixing). Square symbols, Lake Waikaremoana: (■), 17 March 1981 (late stratification); (□), 10 August 1980 (late winter mixing).

saturation of photosynthesis occurs (intercept between the initial slope of the photosynthetic rate/light curve and P_{max} , Talling 1957) did not vary markedly between the two seasons (about 10-12% of surface irradiance in Lake Taupo and 5-8% in Lake Waikaremoana). In both lakes this was because of relatively steep initial photosynthesis/light gradients in summer, suggesting that their metalimnetic algal populations were metabolically adjusted to low irradiance. As noted above, the deeper euphotic zones of both lakes during late stratification contain a floristically, as well as physiologically, distinct algal assemblage.

Although the relative relationship between photosynthetic rate and irradiance in each lake varied similarly from summer to winter, in absolute terms the lakes differed markedly (Fig. 7). Winter P_{max} in Lake Taupo was almost as high as the summer P_{max} in Lake Waikaremoana. During summer, Lake Taupo was more than twice as productive per unit chlorophyll as Lake Waikaremoana. The onset of light saturation was at a lower irradiance in Waikaremoana, although this may simply have been a consequence of the much reduced P_{max} .

Availability of light

In both lakes the availability of light for algal photosynthesis was greatly reduced in winter. Average daily surface irradiance in central North Island of New Zealand drops from about $2340 \text{ J cm}^{-2} \text{ day}^{-1}$ in mid-December to $702 \text{ J cm}^{-2} \text{ day}^{-1}$ in June. In both lakes, the underwater irradiances experienced by the plankton were further reduced by decreased water transparency in winter. In Lake Taupo the white light extinction coefficient (k) increased from an early summer minimum of 0.07 in units m^{-1} to winter values in the range 0.13-0.15 in units m^{-1} . This seasonal variation in k was not correlated

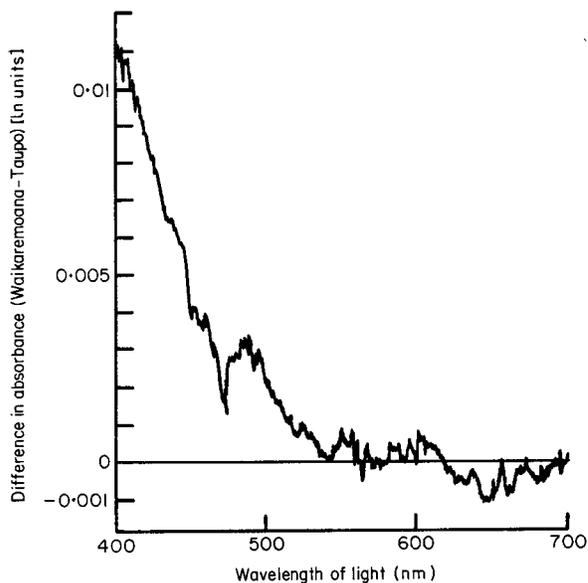


FIG. 8. Relationship between the differences in absorbance (10-cm pathlength) and wavelength of light along the spectrum from 400 nm to 700 nm, between water collected in November 1980 from Lakes Taupo and Waikaremoana, New Zealand.

TABLE 4. Availability of light for algal growth in Lakes Taupo and Waikaremoana, New Zealand, in winter (July and August) and spring (November) 1979.

	Winter	Spring
Radiation		
I_0 ($\text{J cm}^{-2} \text{d}^{-1}$)	591	1698
I'_0 ($\text{J cm}^{-2} \text{d}^{-1}$)	267	765
Lake Taupo		
k (m^{-1})	0.14	0.07
z_d (m)	97	65
I_{av} ($\text{J cm}^{-2} \text{d}^{-1}$)	19.6	168
I_{min} ($\text{J cm}^{-2} \text{d}^{-1}$)	3.9	—
D_c (m)	147	—
Lake Waikaremoana		
k (m^{-1})	0.23	0.16
z_d (m)	93	29
I_{av} ($\text{J cm}^{-2} \text{d}^{-1}$)	12.6	168
I_{min} ($\text{J cm}^{-2} \text{d}^{-1}$)	4.8	—
D_c (m)	90	—

I_0 : average daily surface irradiance in central North Island (1979 data for months specified).

I'_0 : average daily PAR immediately beneath the water surface.

k : measured extinction coefficient for PAR.

z_d : average depth at which photosynthetically active algae can be present—estimated as the 1% of surface light level in spring and the average depth of mixing in winter.

I_{av} : average PAR experienced by the phytoplankton from the surface to z_d .

I_{min} : average irradiance experienced by phytoplankton circulated to the deepest part of each lake (middle of Waitahanui Basin, L. Taupo, or Panekiri Basin, L. Waikaremoana).

D_c : Sverdrup's critical depth, calculated as $I'_0/(k \cdot I_k \cdot 24)$ where I'_0 and k are as above, 24 converts I'_0 to an average PAR input per hour, and I_k is the compensation irradiance estimated as $0.54 \text{ J cm}^{-2} \text{ h}^{-1}$ (Sverdrup 1953).

—: not applicable.

with changes in surface chlorophyll a concentrations ($r^2 = 0.06$), although the plankton increase in winter may have contributed towards decreased transparency.

The inflows to Lake Waikaremoana are heavily stained with humic substances and absorbance of light by this lakewater is predictably relatively high at the blue end of the spectrum compared with that of either distilled or Lake Taupo water (Fig. 8). The consequently high (relative to that of Lake Taupo) k value for PAR increases further in winter (from 0.16 m^{-1} in spring to 0.23 m^{-1}) probably as a result of increased runoff of humic-rich river waters into the lake. At this time of year the extinction coefficient for blue light increases to a much greater extent than those for green and red, which is consistent with increased input humic materials from runoff during winter rainstorms.

These low light conditions are aggravated in both lakes by winter mixing which circulates phytoplankton cells to depths well below the euphotic zone. Table 4 summarizes the combined effects of all three factors (clarity, mixing, and surface irradiance) which control the underwater light climate in each lake. For these calculations winter mixing is assumed to be complete, at which time the average depth of circulation (z_d) approximates the average depth of the lake. Average irradiance was estimated as the total PAR, from the

surface to the average greatest depth at which metabolically active algae occurred (z_d during late-winter mixing) expressed per unit depth:

$$\begin{aligned} I_{av} &= \frac{1}{z_d} \int_{z=0}^{z=z_d} I dz \\ &= \frac{1}{z_d} \int_0^{z_d} I'_0 e^{-kz} dz \end{aligned}$$

The solution of this integral is:

$$I_{av} = \frac{I'_0}{z_d} \left[\frac{1}{-k} e^{-kz} \right]_{z=0}^{z=z_d}$$

This solution is evaluated as:

$$I_{av} = \frac{I'_0}{-z_d k} [e^{-kz} - 1]$$

which for all but shallow ponds of high transparency approximates to $I'_0/(z_d k)$. Average daily surface irradiance decreased by a factor of about three between spring and winter, but for phytoplankton mixed through the lake, average irradiance fell to 11.8% (Taupo) or 7.6% (Waikaremoana) of the spring I_{av} value (Table 4). Maximum light limitation is experienced by algal cells circulated to the greatest depths in each lake. The minimum average irradiance for these cells is only 7.5% (Taupo) and 2.9% (Waikaremoana) of the spring value (Table 4).

Light availability is therefore greatly depressed in both lakes during winter, but much more so in Lake Waikaremoana. A comparison of critical depths (D_c the depth at which respiration in the overlying water column equals gross photosynthesis in that column) also suggests that light availability may be a greater problem for Waikaremoana plankton, since D_c was less than z_d (Table 4). In Panekiri Basin, the main region of open water in Lake Waikaremoana, the average depth is 129 m which greatly exceeds the calculated D_c value; light limitation may therefore be particularly severe in this portion of the lake during the final weeks of winter circulation.

Nutrient concentration

Throughout stratification both nitrate and SRP were released from the sediments of Lake Taupo and accumulated in the deep hypolimnion (Table 5, Fig. 1). These nutrients were mixed into the euphotic zone by autumn and winter mixing (March-September) and during this time the concentration of dissolved inorganic nitrogen (iN) and phosphorus (SRP) in the surface waters of the lake rose from almost undetectable in late summer ($<0.5 \text{ mg m}^{-3}$) to a maxima (4-6 mg m^{-3} , 1-2 mg m^{-3} , respectively) in August.

The quotient of iN to SRP in Lake Taupo remained low throughout the year (Table 6), particularly in the euphotic zone. Lowest quotients (< 1.0 by weight) were found in the surface waters in March when both NO_3^- and NH_4^+ were analytically undetectable ($<0.5 \text{ mg N m}^{-3}$). Throughout spring and summer stratification this quotient remained very low ($z = 1.7$, excluding March) in the surface 50 m, but it more than doubled during mixing (z for May-August = 3.6). An unusually high quotient (18.0) was recorded in the deepest strata during early stratification, November 1979. This anomalous quotient was caused by

TABLE 5. Concentrations of nitrate-N (mg m^{-2}) and soluble reactive phosphorus (mg m^{-2}) in selected strata of Lake Taupo, New Zealand. Values are derived from trapezoidal integration of discrete sample analyses at 5-15 m intervals.

Depth (m)	Summer	Autumn		Winter		Spring	
	11 Jan	13 Mar	2 May	21 June	13 Aug	27 Sep	22 Nov
NO₃-N							
0-50	0	0	9.0	29.0	76.1	25.7	28.8
50-100	190	358	507	400	80.5	22.0	388
100-150	495	708	781	937	543	168	1160
SRP							
0-50	28.2	42.2	52.5	42.1	63.4	45.4	23.9
50-100	65.0	161	143	72.9	90.5	46.0	32.0
100-150	102	173	252	138	148	41.8	76.6

TABLE 6. Quotients of concentrations of inorganic nitrogen and soluble reactive phosphorus (N/P by weight) in selected strata of Lake Taupo, New Zealand. Original values were derived from trapezoidal integration of discrete sample analyses at 5-15 m intervals.

Stratum (m)	11 Jan	13 Mar	2 May	21 June	13 Aug	27 Sep	22 Nov
0-50	1.4	<1.0	3.8	3.8	3.3	1.4	2.2
50-100	3.9	2.2	5.0	8.2	2.4	1.5	17.6
100-150	5.7	4.1	4.1	5.5	4.8	5.0	18.0

TABLE 7. Quotients of concentrations of inorganic nitrogen and soluble reactive phosphorus (N/P by weight) in selected strata of Lake Waikaremoana, New Zealand, during 1979. Original values were derived from trapezoidal integration of discrete sample analyses at 5-15 m intervals. A dash indicates no data.

Stratum (m)	Autumn	Winter	Spring	Summer	Winter
	15 Apr	12 Aug	5 Nov	17 Mar	25 July
0-25	5.0	87.5	39.8	16.6	41.3
25-50	55.5	65.0	58.7	42.4	56.1
50-100	112	81.4	95.3	83.7	69.3
100-150	—	—	46.2	294	94.3
150-250	—	—	48.5	117	56.5

a rapid release of nitrate (Table 5) which began when mixing slowed in September, and it later fell to typical values as SRP steadily accumulated during the rest of the stratification period (e.g. $\text{iN/SRP} = 4.7$ near the sediment surface, 13 May 1980).

A very different pattern was observed in Lake Waikaremoana. Inorganic nitrogen was present in excess of 5 mg m^{-3} throughout the year. There was some accumulation of nitrate in the bottom waters of the lake during stratification (18.8% m^{-2} increase in hypolimnetic $\text{NO}_3\text{-N}$ between November and March), but the rate of increase was low relative to that in Lake Taupo over the same period. Unlike Lake Taupo, Lake Waikaremoana had no hypolimnetic accumulation of SRP and the concentration in the bottom 100 m of the lake remained low and not significantly different from those at the surface throughout stratification mean SRP concentrations for March were 0.5 mg m^{-3} in the 0-25 m layer and 0.7 mg m^{-3} between 150 and 250 m.

Quotients of inorganic N to SRP concentrations in Lake Waikaremoana were higher than in Lake Taupo at all seasons (Table 7). Lowest quotients were recorded in the euphotic zone during April, although for N even on this date about 5 mg m^{-3} or more was recorded at all euphotic depths (cf. $< 1.0 \text{ mg m}^{-3}$ in Lake Taupo at the same time). Much

higher values of iN/SRP were recorded in deeper strata of the lake throughout the year. These were maximal in late summer (March 1981) after accumulation of nitrate, but not phosphate, in the deep hypolimnion. Euphotic iN/SRP quotients rose to a maximum during the winter entrainment of nitrate from deep water into the upper layers of the lake; these surface values gradually decreased during subsequent stratification.

In both lakes silicate was present in high concentration at all depths (Lake Taupo >8.0 g Si m^{-3} ; Lake Waikaremoana > 1.0 g Si m^{-3}). Silicon was not therefore considered a limiting element for algal growth.

Nutrient demand

A range of physiological bioassays was used to assess the nutritional state of the plankton at various times of year in each lake. Ammonium enhancement of carbon uptake, a measure of N-deficiency, was never recorded in Lake Waikaremoana in any season (Table 8). In Lake Taupo, however, strong responses were recorded during autumn and winter mixing. Greatest enhancement was in samples from the late winter phytoplankton maximum. No enhancement has been observed in spring and early summer samples (e.g. 7 December 1981), and in late summer, measured responses have always been weak (Table 8).

Turnover rates of ^{32}P - PO_4 (a measure, when high, of phosphorus deficiency) were low in both lakes. Lowest turnover rates were recorded at the times of minimum phytoplankton densities in each lake (November-December in Lake Taupo; July-August in Lake Waikaremoana). However, at the times of their production maxima the phytoplankton of the two lakes behaved very differently. In Lake Waikaremoana the turnover time was greatly shortened during periods of peak density of biomass; shortest times were recorded in spring (16 min) but even in late summer the turnover was much faster than in July-August (Table 8). In Lake Taupo, on the other hand, ^{32}P -turnover remained slow

TABLE 8. Summary of results of measures of physiological status, related to nitrogen and phosphorus availability, of phytoplankton from near the surface of Lakes Taupo (late winter population maximum) and Waikaremoana (late summer population maximum), New Zealand.

	Late summer		Late winter	
	Lake Taupo	Lake Waikaremoana	Lake Taupo	Lake Waikaremoana
Sampling date	30 Mar 1981	17 Mar 1981	28 Aug 1980	12 Aug 1980
Chlorophyll <i>a</i> concentration ($mg\ m^{-3}$)	0.6	1.1	2.6	0.5
NH_4 -enhancement (% increase over control)	30 ($P < 0.05$)	NS ($P > 0.1$)	110	NS ($P > 0.1$)
Specific accumulation rate of N (see text) V'_N (d^{-1})	5.5	4.7	5.3	NS ($P > 0.1$)
Specific accumulation rate of P (see text) V'_P (d^{-1})	1.6	14.8	NS ($P > 0.1$)	NS ($P > 0.1$)
^{32}P -turnover time (min)	33	29	688	990
Alkaline phosphatase activity as O-MF* produced				
per unit volume ($nmol\ l^{-1}\ h^{-1}$)	—	208	14.3	—
per unit ATP ($nmol\ \mu g^{-1}\ h^{-1}$)	—	3740	76	—

NS, not significant.

—, no data.

* O-MF, O-methylfluorescein produced by enzymatic cleavage of O-methylfluorescein phosphate.

during the period of dense algal populations in winter; greatest rates were recorded in late summer when temperatures were high but planktonic biomass concentration was low.

Other indicators of cellular phosphorus deficiency are increased production of the enzyme, alkaline phosphatase, and ATP content, which is usually low per unit biomass when phosphorus is scarce (Healey 1979). The quotient of alkaline phosphatase activity and ATP concentration (both per unit volume of water) therefore combines the two assays and widely separates populations of differing degrees of phosphorus limitation. Healey & Hendzel (1979) recognize a threshold for severe phosphorus deficiency (substrate converted per unit ATP and time) of $100 \text{ nmol } \mu\text{g}^{-1} \text{ h}^{-1}$. Activities in spring in Lake Waikaremoana were well above this limit, indicating severe deficiency, while values for Lake Taupo samples during the period of peak biomass concentration fell below it (Table 8).

Seston N to P quotients give further guides to nutrient status of the plankton (Table 9). In Lake Waikaremoana the quotients were high in both November and March and, upon enrichment of plankton samples with nitrogen (as ammonium chloride) and phosphorus (as sodium dihydrogen phosphate), they fell significantly as phosphorus was accumulated selectively by the plankton at high specific rates of uptake (Table 8). In winter the seston-N concentration (and biomass concentration in general, Table 2) had fallen and N to P quotients did not suggest a severe deficiency of either nutrient, nor was there any significant response by the seston to enrichment with these nutrients.

Much lower seston N to P quotients were recorded in Lake Taupo throughout the year (except during early summer when there was no uptake-demand for either N or P, Table 9). Upon enrichment with N and P in autumn and late winter, these quotients increased owing to selective accumulation of nitrogen not phosphorus as in Lake Waikaremoana. There was, however, some demand for phosphorus in late summer and autumn although specific uptake rates (VP) for this element were much lower than for nitrogen (VN, Table 8).

During autumn and winter mixing in Lake Taupo then, the controlling nutrient for algal growth appears to have been nitrogen. The phytoplankton community demonstrated no physiological signs of P-deficiency, but it maintained a high uptake-capacity for inorganic N (relative to that for P) and responded strongly to nitrogen enrichment. The *in situ*

TABLE 9. Seston N and P concentrations in two New Zealand lakes relative to controls (no addition), measured 2 h after addition of $\text{NH}_4\text{-N}$ (100 mg m^{-3}) and $\text{PO}_4\text{-P}$ (10 mg m^{-3}). Each value is the mean of duplicate samples \pm range.

Date	Treatment	Seston-N (mg m^{-3})	Seston-P (mg m^{-3})	Seston N:P (wt/wt)
Lake Taupo				
Late winter 1980 (28 Aug)	control	13.3 ± 0.4	2.1 ± 0.1	7.1
	+ N & P	20.7 ± 2.2	2.1 ± 0.2	9.9
Autumn 1981 (1 April)	control	8.4 ± 1.2	1.4 ± 0.1	6.0
	+ N & P	13.3 ± 1.0	1.6 ± 0.0	8.3
Early summer 1981 (7 Dec)	control	13.2 ± 3.5	1.3 ± 0.2	10.3
	+ N & P	16.7 ± 1.8	1.4 ± 0.2	12.7
Lake Waikaremoana				
Spring 1980 (6 Nov)	control	24.2 ± 1.7	0.9 ± 0.1	25.8
	+ N & P	29.8 ± 0.9	2.0 ± 0.1	15.0
Late summer 1981 (18 Mar)	control	13.6 ± 2.4	0.7 ± 0.2	19.4
	+ N & P	20.3 ± 2.3	2.4 ± 0.1	8.3
Midwinter 1981 (27 July)	control	10.1 ± 2.0	1.1 ± 0.1	9.2
	+ N & P	9.7 ± 1.2	1.2 ± 0.1	8.1

nutrient data also confirm this effect; when water from the deep hypolimnion was entrained into Lake Taupo's euphotic zone the dissolved inorganic N to P quotient fell as nitrate, and not SRP, was selectively accumulated by the plankton (Tables 5, 6). Between June and August 1979 both nitrate removal and net algal growth were maximal for the year (rate of increase in chlorophyll a concentration in the 0-100 m layer was 0.023 d^{-1} compared with 0.006 d^{-1} in May-June).

In contrast with that of Lake Taupo, the Lake Waikaremoana plankton demonstrated little demand for N or P during winter, but during the rest of the year the community appeared to be severely deficient in phosphorus.

DISCUSSION

Lakes Taupo and Waikaremoana share a similar stratification and mixing cycle but the behaviour of their primary producers is markedly different. Lake Waikaremoana follows the classic pattern winter is a time of greatly reduced algal biomass concentration and minimum photosynthetic production rates. In winter, the supply of nitrogen to the euphotic zone is enhanced, but for the algae of this lake phosphorus appears to be the growth-controlling nutrient. Winter circulation does not increase the availability of this more important element in the euphotic surface waters of the lake. In fact, rates of phosphorus regeneration, which may exert an overall control on P-supply and the metabolic activity of the phytoplankton, are probably dampened by the low water temperatures of winter. Growth conditions during circulation are further worsened by a greatly diminished light regime. The effects of reduced irradiance are seen in low CFC values, low rate of photosynthesis per unit chlorophyll a and considerable photoinhibition by surface light intensities.

During winter in Lake Waikaremoana the plankton community is metabolically depressed by low temperature and low light. The latter appears to exert a greater influence, for at the onset of stratification when average temperatures had risen only marginally ($<3^\circ\text{C}$) but when light availability had increased thirteen-fold, there was a dramatic increase in values of all photosynthetic and biomass variables, including $\Sigma P/\Sigma B$.

The controlling effects of light on algal seasonality have been well documented for a wide range of marine and fresh waters. This work was pioneered in lakes by Lund (1950) who found that winter diatom populations from Lake Windermere (U.K.), grew rapidly without added nutrients if they were artificially exposed to higher irradiances. Physiological studies on these 'optically deep' communities of algae were subsequently extended by Talling (1957) who developed an empirical model relating phytoplankton production to photosynthesis, respiration and depth of mixing. With this model (equations 8 and 9 in Talling 1957) the quotient of total respiration (ΣR) to total photosynthesis (ΣP) in the water column during late winter was calculated as 0.72 for Lake Taupo and 1.14 for Lake Waikaremoana. For these calculations I_k values were obtained from the photosynthesis-irradiance curves in Fig. 7, the average respiration loss was approximated as 5% (Talling 1957) and the other variables were taken from Table 4. The water column average depth was not corrected to 'effective depth' as suggested (Talling 1957) since both basins are steep-sided and large in area; therefore the area of lake margin where the euphotic zone is truncated by the bottom of the lake is proportionately small in each. These calculations indicate that in both lakes water column respiration may account for a very high percentage of gross production in late winter, although more so in Lake Waikaremoana. Both quotients lie close to that which defines the column compensation

depth where $\Sigma P = \Sigma R$ (equivalent to D_c), suggesting that once mixing is complete the low availability of light may prevent further population development.

In Lake Taupo these inhibitory effects of low light availability, as well as low temperature, appear to be of secondary importance to winter production. Algal biomass concentration and photosynthetic rates rise to their maxima for the year when lakewater temperatures have fallen to their annual minimum and when circulation extends to the bottom of the lake. Light availability is then also minimal, although it is reduced to a much lesser extent than in Lake Waikaremoana. However, winter in Lake Taupo is also a time of greatly increased supply of the controlling nutrient, nitrogen, and to a lesser extent of phosphorus, as the deepwater accumulations of NO_3 and SRP are entrained into the surface euphotic zone. As in Lake Waikaremoana, the low light regime reduces production per unit biomass to values well below those in summer, but the enhanced nutrient supply during winter mixing appears to override this effect and allows phytoplankton biomass to grow slowly to its maximum for the year.

The dominant alga during winter mixing in Lake Taupo was the large-celled diatom, *Melosira baikalensis*. Biomass losses to grazing for this species are probably minimal because of its size; the steady rise in *Melosira* cell concentration may be as much favoured by low rates of loss as by the production response to enhanced nutrient availability. When mixing slowed down, however, the heavy *Melosira* cells rapidly sediment out and in the process removed nutrients from the euphotic zone. During stratification the nutrient impoverished water appears to limit phytoplankton to a very low biomass concentration, although metabolic activity (photosynthesis, N and P uptake) per unit biomass is maximal for the year, presumably as a consequence of higher irradiance and temperatures. During mid- to late summer there is a high uptake-demand for both N and P by this small algal population density, but as the mixed layer extends deeper into the original hypolimnion and the community begins to grow, N-deficiency becomes increasingly dominant. A similar pattern of nutrient deficiency has been observed by White & Payne (1977) in batch culture bioassays on Lake Taupo water.

Lake Taupo, and perhaps other nearby waters which behave similarly, might be considered ecologically intermediate between temperate lakes with classic winter minima in production, and tropical lakes which experience production maxima during periods of seasonal cooling and circulation. In the tropical Lake Victoria, for example, a striking increase in diatom populations takes place in both the inshore (Fish 1957) and offshore waters (Talling 1966) coincident with mid-year mixing. Wind-induced upwelling of nutrient-rich waters in Lake Tanganyika appears to induce a series of diatom maxima which characterize the period of peak algal production each year (Coulter 1963). Irregular storms on Lake Lanao (Philippines) which mix deepwater nutrients into the euphotic zone exert an overall control on its primary production cycle (Lewis 1974). Highest productivities in this tropical lake were recorded when nutrients were recently brought to the surface by storm-induced circulation, but only when the mixed layer was restricted to the uppermost 25 m. When the mixed layer was deepened below this level, light limitation offset the stimulatory effects of increased nutrient availability, and plankton populations declined to their minimum for the year. In lakes of central North Island (New Zealand) minimum water temperatures in winter (typically 8-11 °C) are well below those experienced in the tropics during mixing (e.g. 24 °C in Lake Tanganyika, Coulter (1969)). These lower temperatures may reduce respiratory losses which, in warm tropical lakes, are typically very high (e.g. an average of 34% of gross photosynthetic production in the euphotic zone of Lake Lanao, (Lewis 1974)). This may thereby permit new production

under much lower light availability than could be sustained during the same mixing regime in the tropics.

New Zealand's North Island lakes, with production cycles similar to that of Lake Taupo form an ecologically distinct group. They are characterized by algal biomass and production maxima when light and temperature limitation are at their most severe, but when winter mixing entrains hypolimnetic nutrients into the euphotic zone. The midway position of these unusual aquatic ecosystems between typical monomictic waters and tropical lakes offers a useful test case for limnological theory.

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