TURBULENCE AND ITS CONSEQUENCES FOR PHYTOPLANKTON DEVELOPMENT IN TWO ICE COVERED ANTARCTIC LAKES

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ABSTRACT. The development of physical and chemical profiles in two Antarctic lakes during late winter and spring are described. In oligotrophic Sombre Lake, gradients of temperature, oxygen, chloride and phosphate concentrations evolved during the winter period and persisted until the break-up of ice cover. In response to these gradients, a stratified algal population developed, with maximum biomass near the base of the water column where nutrients were most readily available, despite low radiation levels. In eutrophic Heywood Lake, a different pattern was observed, with vertical mixing apparently breaking down winter gradients and maintaining a near homogenous distribution of all measured parameters from the start of growth in spring. This circulation enhanced the supply of both nutrients and radiation to the suspended phytoplankton and enabled a dense population to develop throughout the 5-m water column. Density currents and/or turbulent inflow of meltwater may be responsible for the observed mixing.

Although a certain amount of vertical water exchange has been observed in ice-covered lakes (Rigler, 1978), it is usually assumed that a relatively stable water column develops as a result of temperature-induced density gradients (Hutchinson, 1957). Data are available from Arctic, Antarctic and Alpine lakes where such gradients have resulted in considerable vertical variation in both water chemistry and biology (e.g. Pechlaner, 1971; Weller, 1977; Vincent, 1981). However, studies of Heywood Lake, Signy Island, (60° 43′ S, 45° 38′ W), South Orkney Islands, indicate a considerable degree of vertical mixing under a substantial ice cover which had persisted for 5–6 months. Evidence for this phenomenon is presented and compared with similar data from nearby Sombre Lake, where mixing is not apparent and important consequences for the developing phytoplankton communities are discussed.

MATERIALS AND METHODS

The locations of the two lakes with respect to their catchments and permanent ice cover are shown in Fig. 1. Sombre Lake lies at the end of a chain of three lakes, all of which receive much of their water from the ice-cap. Major inflows to Sombre Lake are via an ice tunnel from Changing Lake and directly from snowfields to the west. Heywood Lake receives most of its water from shallow Knob Lake (max depth 3.5 m) and there are no areas of permanent snow cover within its drainage basin. The bathymetry of the two lakes is shown in Fig. 2 and important differences summarized in Table I. Though the two lakes have similar volumes, Sombre Lake is relatively deep and roughly circular in outline while Heywood Lake is longer, narrower and considerably shallower. Further details are given in Heywood and others (1979).

Throughout this study, water samples were collected by pumping water from the required depth through rigid plastic tubing into light-proof polythene bottles using

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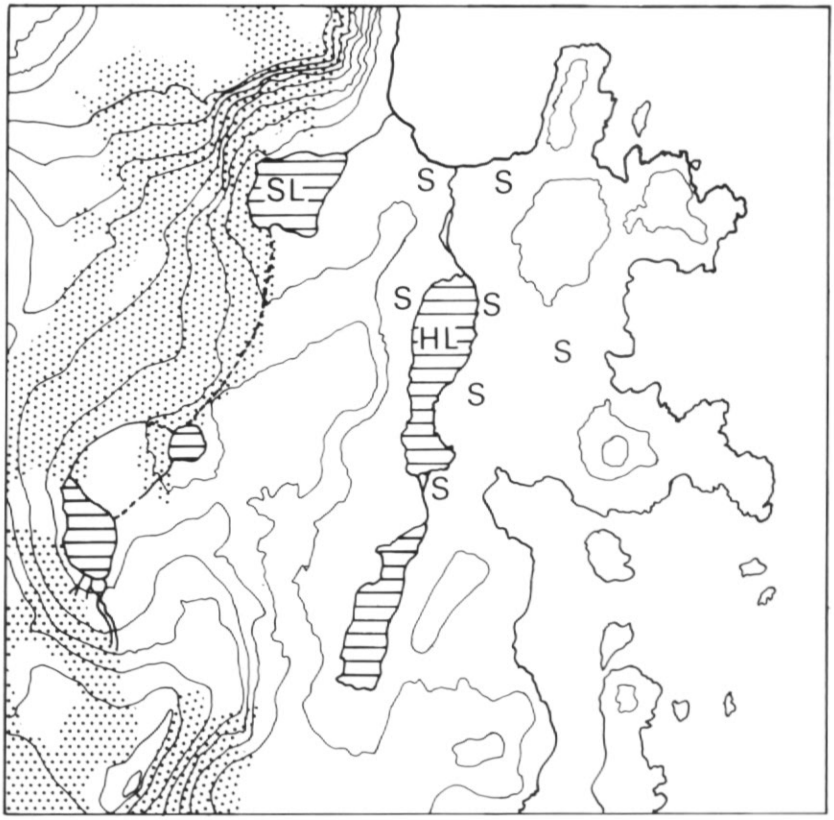


Fig. 1. Location of Sombre Lake (SL) and Heywood Lake (HL) in the north-east corner of Signy Island. Permanent snow and ice cover is shown stippled. S represents areas of moss carpet frequented by elephant seals. Contours are at 20-m intervals.

a hand-operated diaphragm pump. Samples were filtered (Whatman GF/C), with the filters subsequently being used for chlorophyll-*a* determinations and the filtrates for chemical analyses.

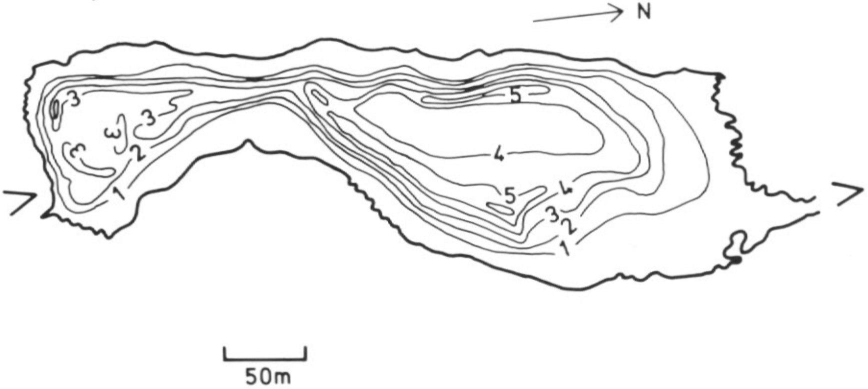
Chlorophyll-*a* was determined spectrophotometrically at 665 nm after extraction of the filters into hot, 95% methanol (pre-1980) or cold 95% acetone (1980). Where acetone was used as solvent, a 24-h extraction was necessary, bu[illegible] concentration of phaeopigments (chlorophyll breakdown products) could also be determined after acidification to 0.003 N with hydrochloric acid. The equations contained in Vollenweider (1969) were used throughout.

Soluble reactive phosphate was determined by the method of Strickland and Parsons (1972) and chloride as described by Golterman (1969). Oxygen concentra-

Table I. Bathymetric characteristics of Heywood and Sombre Lakes

	Length (m)	*Breadth (m)*	*Depth(m)*		*Area (ha)*	*Volume (m^3)*	*Catchment Area (ha)*
			max	*mean*			
Sombre Lake	210	150	11.2	5.0	2.66	132600	48
Heywood Lake	427	137	6.4	2.0	4.50	96200	41

a. Heywood Lake



b. Sombre Lake

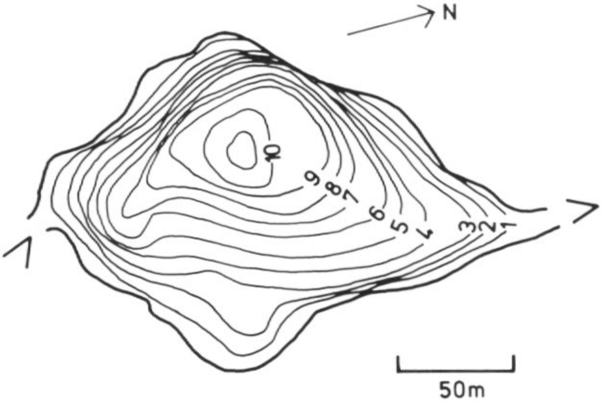


Fig. 2. Bathymetric maps of a. Heywood Lake and b. Sombre Lake. Contours are at 1-m intervals.

tion and temperature were measured *in situ* with a Mackereth oxygen probe. Total inorganic carbon in unfiltered water samples was determined by Gran titration (Talling, 1973). Under-ice radiation was measured with a Quantum sensor (Llambda Instruments) mounted on a cantilever arm (Light and others, 1981), which enabled the sensor to be positioned away from the atypical light regime close to the sampling hole.

The ^{14}C technique described in Vollenweider (1969) was used to estimate rates of photosynthesis. Duplicate 125-ml subsamples were incubated at each depth sampled, for 6 h around midday, in acrylic plastic chambers. Approximately 5 μCi of activity were added to each. Dark controls were run on top and bottom water samples only, and the ^{14}C uptake of these was subtracted from that of the light bottles. At the end of each incubation, the chamber contents were filtered (Sartorius 0.45 μm membrane filters) and the filters fumed over concentrated hydrochloric acid to remove any remaining inorganic ^{14}C before being stored at −40° C. Radioactivity was determined by liquid scintillation counting up to 18 months later.

RESULTS AND DISCUSSION

Winter conditions

During winter 1976, temperature profiles characteristic of ice-covered lakes (Hutchinson, 1957) developed in both Heywood and Sombre Lakes (Figs. 3 and 4), creating gradients of increasing density with depth. A density gradient of more than 0.02 (kg m^{-3}) m^{-1} is usually considered to confer sufficient stability to prevent randomization of suspended material when eddy diffusivity is low (Reynolds, 1982). At the beginning of October 1976, the gradient was only 0.006–0.007 (kg m^{-3}) m^{-1} throughout Heywood Lake, indicating considerable susceptibility to turbulence-inducing forces. Surface temperatures were lower and bottom temperatures were higher in Sombre Lake and the density gradient was consequently more substantial, increasing from 0.01–0.02 (kg m^{-3}) m^{-1} at the end of September to 0.02–0.04 (kg m^{-3}) m^{-1} by 29 November 1976. Both lakes were isothermal when ice formed in 1976, lowest temperatures observed prior to and immediately after ice cover became complete being 1.4° C in Sombre Lake and 0.6° C in Heywood Lake. It is apparent from Figs. 3 and 4 that over the course of winter, temperatures rose very slightly at the bottom of each lake and tended to decrease towards the surface. Hutchinson (1957, p. 454) describes the process of heat conduction from the sediments, which is responsible for bottom heating, though loss of heat energy from the lake surfaces was the most significant process in the development of the density gradients (Heywood, 1967). A similar loss of heat from the surface waters

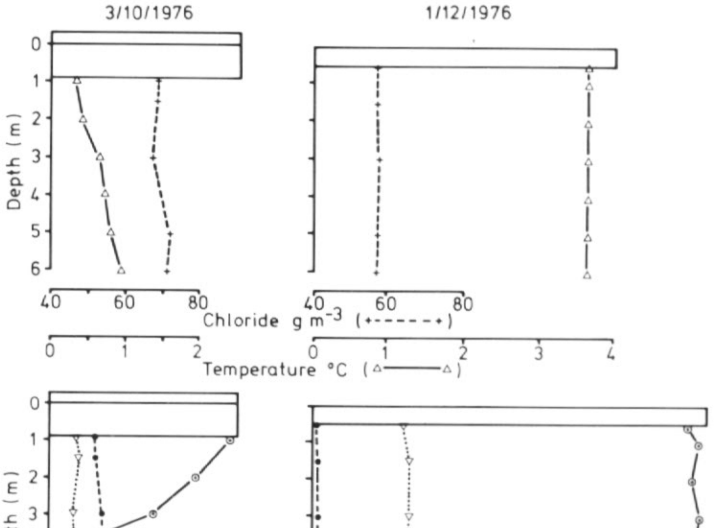


Fig. 3. Development of vertical profiles in Heywood Lake from late winter to spring 1976.

of ice-covered lakes in the Canadian Arctic was reported by Schindler and others (1974*a*, *b*). The two lakes they studied, Char and Meretta lakes, experience a thermal regime similar to that found on Signy Island, with summer temperatures rarely exceeding 5° C. These low summer temperatures, coupled with short duration of the ice-free period (typically 2–4 months), may explain the lack of substantial winter heating (Hobbie, 1973). The contribution of major ions to density differences (represented in Figs. 3–6 by chloride) was negligible compared to temperature effects and any persisting vertical differences may be best regarded as an indication of continuing water column integrity.

Algal biomass and productivity were low throughout the winter and much of the chlorophyll was in the form of phaeopigments (Figs. 3–6). This permitted considerable accumulation of the inorganic nutrients released from lake sediments as a consequence of the continuing microbial activity demonstrated by Ellis-Evans (1982). Accumulation was more extensive in the more productive Heywood Lake than in oligotrophic Sombre Lake. Depletion of oxygen at the sediment-water interface (Figs. 3 and 4) resulted in the dissolution of sediment-bound phosphate to the overlying water. Similar release has been widely reported from other lakes undergoing an anoxic period (e.g. Banoub, 1977) and pronounced phosphate maxima at the base of the water columns were observed (Figs. 3–6).

Development of Spring populations

Increasing light levels in Spring following melt-back of snow cover enabled photosynthesis to commence and an increase in algal standing crop ensued (Light

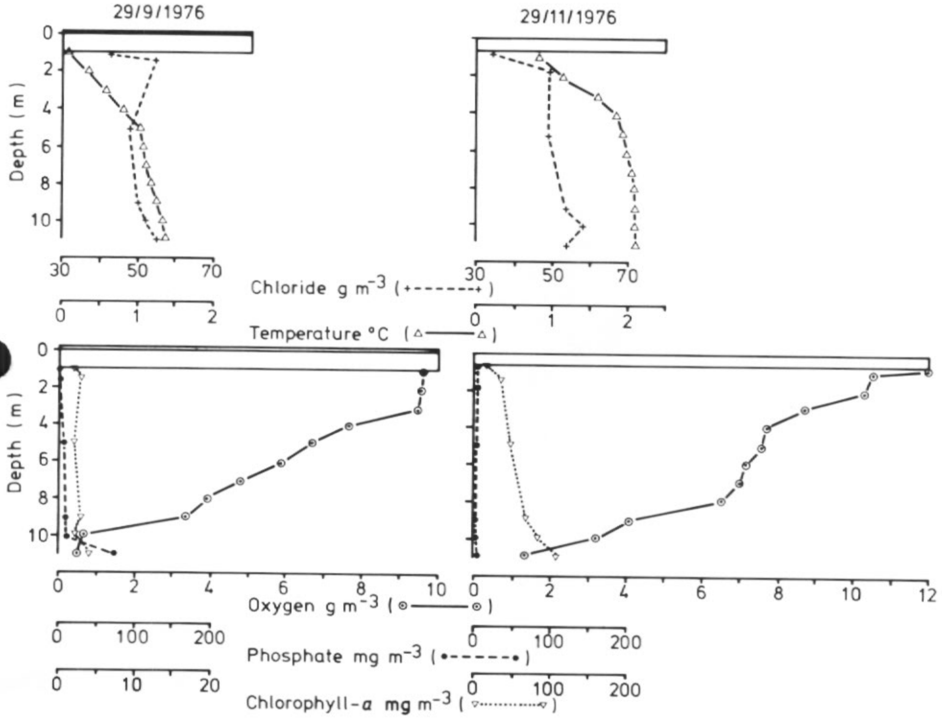


Fig. 4. Development of vertical profiles in Sombre Lake from late winter to spring 1976.

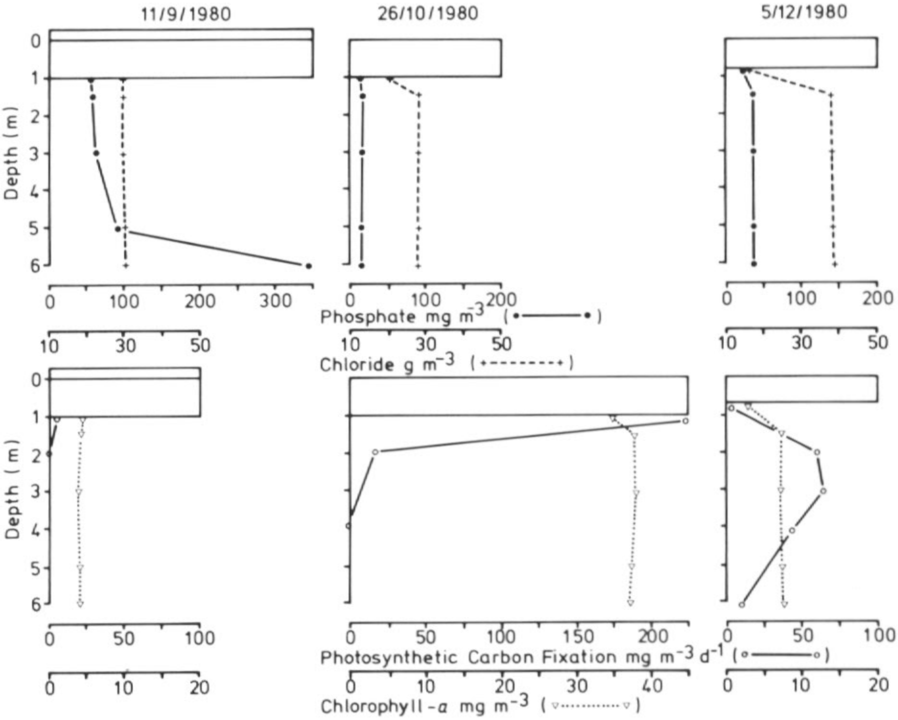


Fig. 5. Development of vertical profiles in Heywood Lake from late winter to spring 1980.

and others, 1981). Attenuation of light with depth was rapid in Heywood Lake (Fig. 7) and during the Spring biomass increase, photosynthesis was confined to the surface waters (Fig. 5). Despite this restriction, in both 1976 and 1980 chlorophyll concentration increased equally throughout the water column, with phaeopigments following a similar pattern. In contrast, the greater water clarity of Sombre Lake (Fig. 7) resulted in a photosynthesis maximum in midwater and the early chlorophyll increase was localized to this region (Fig. 6). The increase in chlorophyll content of water outside the photic zone in Heywood Lake implies that material produced at the surface was redistributed down the water column. If this redistribution were due to sedimentation, less vertical homogeneity might be expected, together with a change in phaeopigment concentration with increasing depth (Yentsch, 1965). Vertical migration of phytoplankton has never been observed at Signy Island (unpublished observations), though it has been reported from another Antarctic lake (Vincent, 1981), but again would be unlikely to produce such an even chlorophyll distribution. As other gradients, which had persisted through the winter, also broke down at this time in Heywood Lake, including the largely abiotic factors temperature and chloride, vertical water mixing is implicated as the distribution mechanism.

Photosynthetic characteristics of the phytoplankton

It is known that the photosynthesis/light relationship in phytoplanktonic algae shows considerable adaptability in response to light climate (Beardall and Morris, 1976) and nutritional state (Senft, 1978). Forms adapted to low radiation levels or

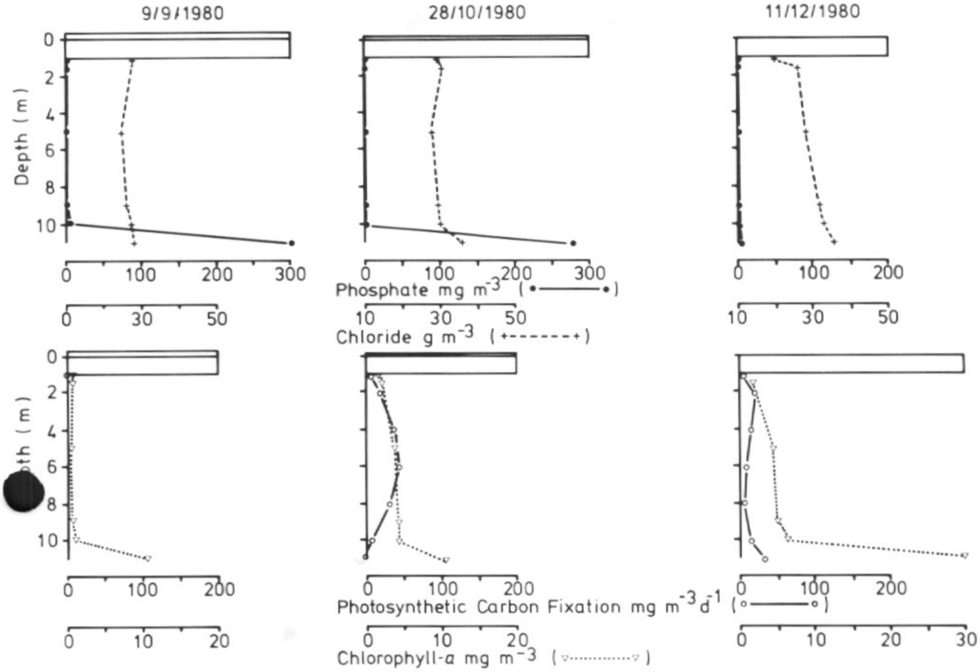


Fig. 6. Development of vertical profiles in Sombre Lake from late winter to spring 1980.

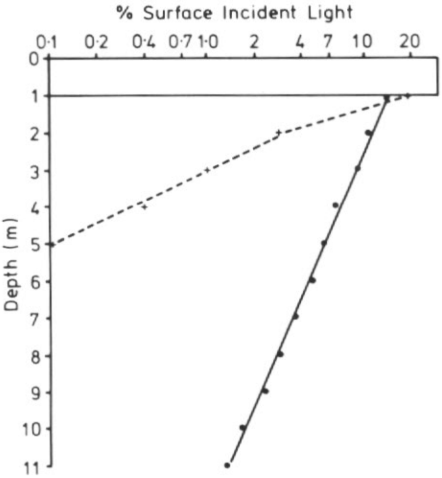


Fig. 7. Penetration of photosynthetically active radiation into Heywood Lake (dashed line – 5/11/1980) and Sombre Lake (solid line – 17/11/1980).

suffering severe nutrient deficiency tend to show lower maximum rates of photosynthesis than cells grown under more favourable conditions. Eppley (1980) suggested that the degree of adaptation of populations at different depths could be used to assess circulation patterns. The widely differing light and nutrient regimes at the top and bottom of Sombre Lake resulted in the development of markedly different photosynthetic characteristics (Fig. 8b). In contrast, samples taken from the top, middle and bottom of the Heywood Lake water column during Spring 1980 showed identical light/photosynthesis relationships (Fig. 8a). Such similarity provides strong evidence that circulation has ensured that all phytoplankton in this lake develop under similar environmental conditions.

Effects of mixing on phytoplankton development

As well as transporting algal material from the trophogenic to the aphotic zone, water circulation ensured that the high concentrations of nutrients present in the bottom water were made available in the euphotic zone of Heywood Lake. Nutrient availability is widely recognized as playing a leading role in determination of algal standing crops, even under ice cover (Vincent, 1981; Wallen, 1979), and nutrient limitation has been observed in both Sombre and Heywood Lakes during spring and summer (Hawes, unpublished data). Consequently, this supply of nutrients from deep water may be of considerable importance to the development of the high concentrations of chlorophyll observed in Heywood Lake. In Sombre Lake, the chlorophyll maximum accumulated at depth, where nutrients were m[illegible] readily available, despite low radiation levels.

The effect of circulation within a light gradient on production rates is difficult to determine. Clearly it increases the vertical extent of growth, until a critical optical depth is reached where insufficient light is received during circulation in the euphotic zone to offset respiration losses in the aphotic. Its effect on growth rates is less clear. A number of simulation studies have suggested that it can increase photosynthetic rates (Harris, 1980) though often only when surface radiation is sufficiently intense to cause photoinhibition (Marra, 1978).

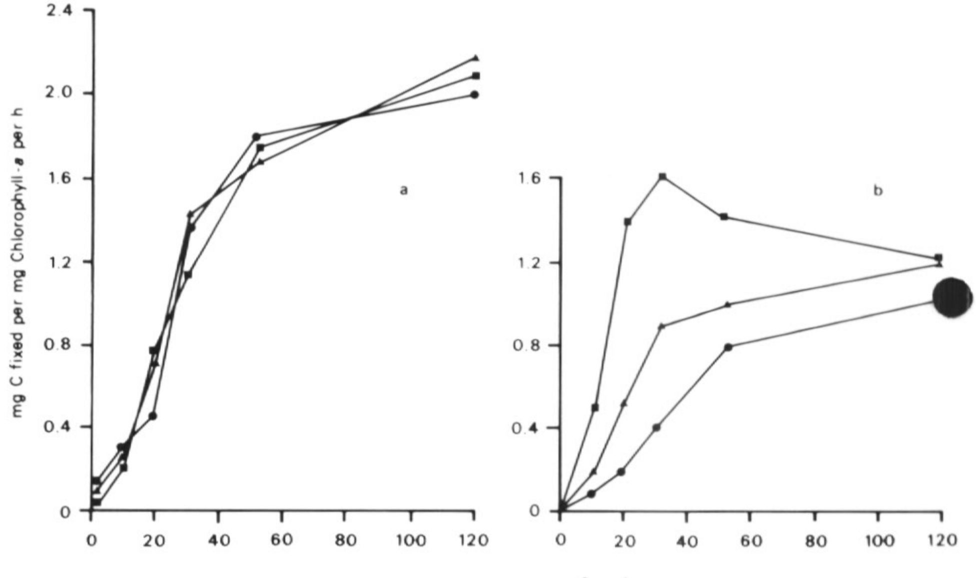


Fig. 8. Photosynthesis/radiation curves for surface (circles), midwater (triangles) and bottom (squares) samples from a, Heywood Lake and b, Sombre Lake on 1 November and 5 November 1980, respectively.

As well as quantitative differences in phytoplankton production qualitative differences were apparent in the species composition of populations developing under the contrasting mixing regimes. Populations in both lakes were characteristically dominated by a small number of species (Light and others, 1981; Weller, 1977). In Heywood Lake an *Ankistrodesmus* sp. comprised a large proportion of the spring bloom throughout the water column with *Ankistrodesmus falcatus* and a *Chlamydomonas* sp. also common. In Sombre Lake, *Ankistrodesmus falcatus* was again common, but confined to the deeper waters, while *Cryptomonas, Chlamydomonas* and *Chlorella*, spp. were more abundant in the midwater zone. The predominance of flagellates in Sombre Lake appears to be typical of non-mixing, ice-covered lakes (Hobbie, 1973; Pechlaner, 1970). The non-flagellated species, which comprise the bulk of the under-ice flora of Heywood Lake, will be maintained in the euphotic zone only by turbulence.

Reoxygenation of the water column

Depletion of oxygen in the lower part of the water-columns of both Heywood and Sombre lakes during winter resulted in pronounced gradients with depth (Figs. 3 and 4). Reoxygenation commenced in spring with the onset of net algal photosynthesis and the influx of low density, oxygen-rich meltwater. Both of these phenomena were largely confined to the surface layers and reoxygenation of deep water in Sombre Lake was a gradual process. The oxygen gradient remained intact until ice cover was lost. Turbulent mixing, however, ensured that the deeper layers of Heywood Lake became as oxygenated as the surface water within a relatively short space of time, with no trace of a depth gradient (Fig. 3).

Spring 1973

Vertical mixing is not apparent every year in Heywood Lake and during the Spring of 1973 a completely different pattern of development was observed, conforming to that which might be expected where the water column remained stable. At the end of winter, vertical profiles were similar to those of 1976 and 1980, but as the chlorophyll concentrations increased, temperature, phosphate and oxygen gradients remained intact (Fig. 9). Consistent with the localization of photosynthesis to surface waters, there was little increase in biomass or oxygen in the deeper, aphotic water, where a substantial amount of phosphate remained unused. The development under what appear to be stable conditions contrasts with that seen in 1976 and 1980 and provides strong support for the view that vertical homogeneity in these years could only be a result of substantial water mixing. Taxonomic data are not available for 1973, though a greater abundance of flagellated forms might be expected. The water temperature of 2.1° C in Heywood Lake immediately prior to freezing in 1973 was considerably greater than the 1976 value. Heat was again lost from the surface over winter, while at 6 m relatively little net change occurred. Consequently, a situation similar to that found in Sombre Lake developed, with a more acute temperature gradient than was evident in Heywood Lake in 1976. This gradient contributed greater stability to the water column and increased resistance to turbulent mixing.

Possible mixing mechanisms

From early October onwards water temperature in the two lakes began to rise, presumably as a result of increased solar energy input associated with increasing daylight and loss of snow cover. Similar solar heating occurs in ice-covered Arctic lakes (Schindler and others, 1974*a*, *b*; Ramberg, 1979). Hutchinson (1957) and

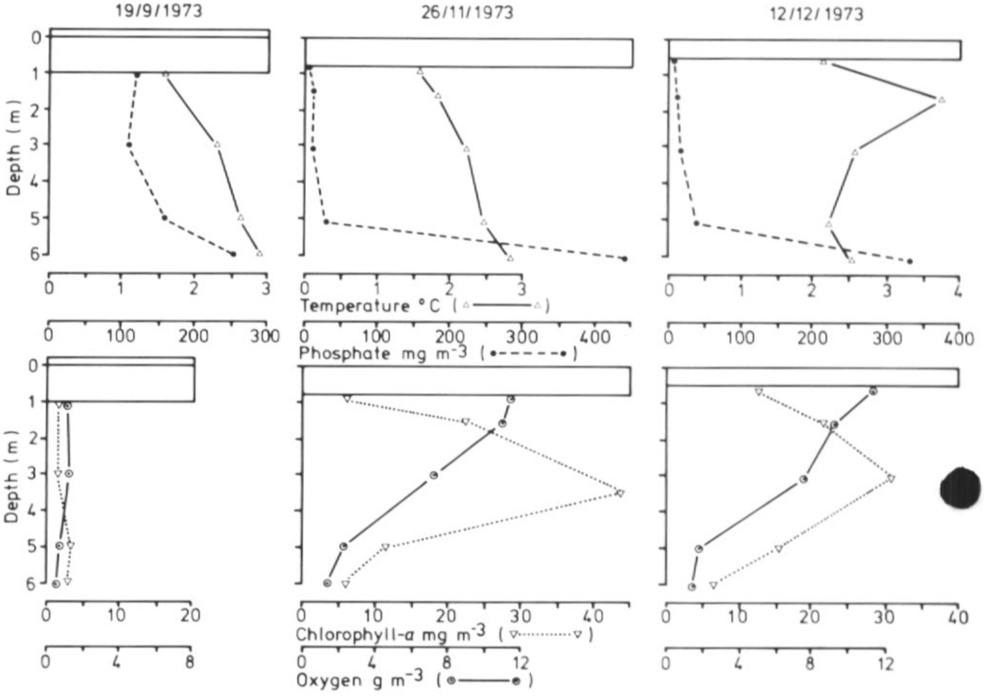


Fig. 9. Development of vertical profiles in Heywood Lake during spring 1973 when mixing was not apparent.

Hobbie (1973) describe how heating of water and sediments by this process at shallow lake margins can create localized pockets of high density water which can then flow down the sides of the lake basin in the form of density gradient currents. In a lake, such as Heywood Lake, where shallows are relatively extensive, this process may be particularly important. Further, it depends on rapid vertical extinction of incoming solar radiation to enable shallow water to warm significantly more than deeper layers and density gradients to form. This is true for Heywood Lake (Fig. 7) and Fig. 9 shows that where mixing does not occur a substantial heat gain ensued at 2 m whereas temperature increase at 6 m was negligible. In contrast the clear water of Sombre Lake permitted an increase throughout the wat[illegible] column.

The relatively high temperatures and greater difference between 1 and 6 m seen in Heywood Lake in Winter 1973, would increase the resistance to density current formation and may explain the lack of mixing. Not only would a greater rise in shallow water temperatures be necessary to exceed that of deep water, but greater temperature disparity is required to constitute a similar density difference as temperatures approach 4° C.

A second mechanism for generating turbulent mixing may be important during the early stages of the spring snow melt. At this time, flow rates through Heywood Lake could be particularly high. Discharges of up to 600 $m^3 h^{-1}$ were recorded at the outflow which would represent a specific dilution rate of 0.24 d^{-1} if the whole lake was mixing. These inflows being colder and more dilute did not appear to mix fully with resident lake water and tended to form a relatively discrete low density layer immediately beneath the ice-cover. This is indicated in Figs. 3 and 5 by low chloride concentrations at the ice/water interface and is analogous to that reported by Schindler and others (1974*a*).

Direct measurements of flow rates under ice cover are not available, but from bathymetric considerations, were the inflowing water to produce a layer 1.0 m thick, average velocity would be of the order of 0.5–1.0 $\mathrm{cm\,s^{-1}}$ during spring. Peak values would rise to over 3.0 $\mathrm{cm\,s^{-1}}$. This compares with a maximum velocity of 0.1 $\mathrm{cm\,s^{-1}}$ calculated for Sombre Lake. These current velocities exceed the critical value of 0.03 $\mathrm{cm\,s^{-1}}$ thought to mark the change from laminar to turbulent flow under such conditions (Hutchinson 1957, p. 252), but stable horizontal flows have been observed at velocities greater than those calculated here (George and Heaney, 1978; Heaney and Talling, 1980). However, although observed in a section of water column with a temperature gradient comparable to that of Heywood Lake, these latter observations were made at 15° C where a 0.5 degree temperature difference has a considerably greater effect on density than at 2° C.

The tendency of turbulent mixing to dominate over stable flow is indicated by the Richardson Number, i.e.

$$g\frac{\mathrm{d}p}{\mathrm{d}z}\Big/\bar{p}\left(\frac{\mathrm{d}u}{\mathrm{d}z}\right)^2$$

where g = acceleration due to gravity, p = density of water, $\bar{p}$ = average density of water over the relevant depth interval, u = mean water velocity and z = depth. Below a critical value of 0.25, turbulence and vertical mixing become dominant over stable horizontal flow (see Smith, 1975). This parameter was calculated for Heywood Lake to be 0.26 between 1 and 3 m depth, assuming a current velocity of 3 $\mathrm{cm\,s^{-1}}$ at 1 m and 0 $\mathrm{cm\,s^{-1}}$ at 3 m. Clearly, the possibility exists for turbulent flow at peak discharge rates in part or all of the Heywood Lake water column. Higher values for $\mathrm{d}p/\mathrm{d}z$ and $1/(\mathrm{d}u/\mathrm{d}z)^2$ preclude this occurrence in Sombre Lake.

This study shows that considerable vertical water mixing can be induced under the spring ice cover of Heywood Lake. As a result, the water column becomes vertically homogeneous and algal development occurs throughout, utilizing the nutrients available from otherwise aphotic depths. Reoxygenation is rapid and the weak winter density gradient is destroyed. Nearby Sombre Lake does not mix until ice cover is lost and under-ice development varies strongly with depth. Features of Heywood Lake which may facilitate mixing are the low water column temperature prior to freezing, low heat gain from sediments over winter, relatively extensive shallow areas, rapid vertical extinction of radiation and the high flow-through rate during spring snow melt. These criteria are likely to be met by a number of other shallow maritime Antarctic and Arctic lakes and the phenomenon of under-ice mixing may be widespread. It offers an explanation for the existance of non-motile algae in a viable state during long periods of ice cover.

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