A general assessment of environmental and biological features of Windermere and their susceptibility to change

K.M. Atkinson
J.M. Elliott
D.G. George
J.G. Jones
E.Y. Haworth
S.I. Heaney
C.A. Mills
C.S. Reynolds
J.F. Talling (editor)

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1. INTRODUCTION (J.F. Talling)

Windermere is the largest natural English lake and of great current interest to those concerned with landscape conservation (it has 5.5.5.1. status), recreation, tourism, and water supply in northwest England. It has also been a principal site of scientific study by the Freshwater Biological Association, whose main laboratory has been situated on its shores since 1931. Such study is briefly summarised below. The main focus is on the liability for change of conditions in the lake, both environmental and biological; that reflects either strong external influence or innate susceptibility.

Time-scales ranging from hours to millenia are involved. Most variables have a seasonal periodicity, which must be taken into account before interpreting irregular shorter episodes (some weather-related), year-to-year fluctuations, and long-term trends. The account draws upon information from over 50 years, but most intensively from regular (often weekly) sampling operations since 1945. Some though not all of this information has appeared in specialist publications here cited, but more general interpretation and interrelation is opportune. To this end a final section treats the relative sensitivity to change of various major components.

Accounts of individual components and topics are given by nine contributors. The range is wide, from primarily environmental to primarily biological aspects. The references are a source of further, more detailed information. Of particular note for present purposes are: the book on the English Lakes by Macan (1970); the bibliography on Windermere by Horne & Horne (1985); the detailed one-year account of events in the water mass by Lund, Mackereth & Mortimer (1963); and the discussions of long-term trends and 'eutrophication' by Lund (1972a) and Sutcliffe et al. (1982).

The following geographical features are important. The lake is in a region of oceanic climate, such that mean rainfall is high (c. 2.2 m year-I), winters are mild, and the seasonal range of temperature small considering the latitude of 54 °N. The water-mass is divided into a deeper (64 m) north and a shallower (42 m) south basin by shoals and islands; bathymetric information, from Ramsbottom (1976), is given in

Fig. 1 and Table 1. The total area is 14.8 km^2, and volume 314.5 x 10^6 m^3. Some published bathymetric information, in Mortimer & Worthington (1942) and a commercially circulating map, contains an overestimate of depth by 4% due to the calibration of an echo-sounder for sea water.

2. MAN-MADE IMPACTS ON THE CATCHMENT (C.S. Reynolds)

The catchment area of Windermere, estimated to be 230.5 km^2 (Ramsbottom 1976), extends well into the Cumbrian mountain massif (Figs 2,3). The northern perimeter of the watershed describes an irregular arc, linking such well-kno~~ Lakeland peaks as Bowfell, the Langdale Pikes, High Raise, Steel Fell, Fairfield, Red Screes and the High Street range, and encompasses a substantial wedge of the glacially dissected plateau: altitude ranges from 902 m to 39 m a.s.l. Geologically, much of the upper catchment is based on the hard volcanic ,rocks of the Lower Borrowdale series but, further south, the lower foothills are largely comprised of Silurian slates, grits, and flags of the Bannisdale series; a thin bed of Coniston Limestone traverses the area and outcrops locally (Moseley 1978). The lower slopes are covered with glacial tills to varying Thicknesses, while the valley floors of the Rothay, Brathay and its tributary, Great Langdale Beck, are of alluvial and pot-ash deposits. Except on steeper or denuded rock surfaces, the catchment is mostly clothed in poor soils which in the past supported woodlands dominated by Quercus Detraea, Fraxinus excelsior and Taxus baccata. Much of this forest has been cleared within historical times but its former extent is thought to coincide with the modern distribution of bracken (Pteridium aauilinum), the upper limits of which are often clearly delimited by a zone of Juninerus scrub. Beyond, the acidic podsols continue to support moorland vegetation, with a tendency towards bog development wherever impeded drainage will allow.

The present-day vegetation is dominated by grasslands of varying quality, consequent upon man's increasing impact upon the landscape since neolithic times (around 5500 B.P.). Numerous artefacts point to there having been a long period of human occupation with the major activity agricultural (Nillward & Robinson 1972). This long stage in shaping the present-day landscape took many centuries and was probably not substantially complete until about the twelfth century A.D. Despite successive invasions of Romans, Norsemen and a gradual post-Norman conquest integration into Medieval Britain, the human population remained sparse.

It was not until the last two hundred years or so, when the Lake District began to be "opened up (Bragg 1983) to inhabitants seeking more than merely land to farm, that the resident population began to expand. The development of other industries (quarrying, mining, forestry) and, most particularly, the coming of the railways encouraged the considerable growth of urban settlements, around Ambleside and Bowness-on-Windermere. This process has accelerated during the present century, which has seen the human population of the Windermere catchment more than double. The trend is still upward, as is shown by successive population censuses of the civil parishes roughly coinciding with the Windermere catchment (Table 2).

In addition, the Lake District National Park now plays host to a vastly increased population of visitors and tourists. The estimated visitor capacity of the National Park is upwards of 50 000 (LDSPB 1978). Because the Windermere catchment makes up nearly a half of the area of southern Lakeland, the more readily accessible side for the majority of visitors, and also contains many of its visitor attractions, as well as the greatest number of hotels and camping sites. it is not unreasonable to suppose that it offers around 50% of the tourist capacity. It may be roughly estimated that, at times, the human population of the Windermere catchment is effectively doubled with respect to the registered residents, *i.e.* to between 30 000 and 40 000.

To the inevitable impact of the increased human population on the biology of Windermere must be added the effects of improved living standards and public health requirements, as well as advancing techniques for maximising the agricultural productivity of the land. Specifically, one can cite the introduction of a mains water supply to a majority of homes; the provision of sewers and effluent treatment plant and the simultaneous improvement of grasslands by better drainage coupled with the increased application of inorganic fertilizers; and the advent of phosphate-rich detergents in the 1950's. Each has been clearly implicated in the significant rise in plant nutrients eventually reaching Windermere (Lund 1972a,b, 1978; see also Section 4e). Between 1962 and 1973, new sewage treatment plants were commissioned at Tower Wood, Windermere, at Ambleside, Grasmere, Hawkshead and Elter Water (Fig. 3). Extensive palaeolimnological work on lake sediments (Section 9), carried out at the

F.B.A., together with the series of direct long-term observations (Sections 4, 5) commenced, inter alia, by Pearsall (1921, 1932) and expanded by Lund, strongly indicate that the effects of these changes on the ecology of Windermere have been significant.

3. PHYSICAL FEATURES; HYDROLOGY, STRATIFICATION, AND WATER MOVEMENTS

3(a) HYDROLOGICAL WATER BALANCE (C.S. Reynolds)

The relationship between rainfall, runoff from the catchment and storage in the lake has been explored in detail by McClean (1940). His assessment of the seasonal rainfall at each of 21 gauging stations in the catchment remains one of the most thorough surveys undertaken. However his level-discharge relationship for the Windermere outflow is probably with appreciable error (C.H. Mortimer, priv. comm. to J.F. Talling).

From the annual average rainfall data at each of the 21 stations (varying between 3.32 m in Mickleden, Upper Langdale, and 1.42 m at Newby Bridge), and the fraction of the total catchment that each gauged subarea represented, McClean calculated the "general rainfall" to be c. 2.2 m annually. Net of annual evapotranspiration losses, on average, equivalent to c. 0.33 m (Penman 1950, Sutcliffe & Carrick 1983b), the run-off generated by the catchment (230.5 km $)^2$ amounts to a mean annual volume (= area x run-off) of 431 x 10^6 m^3, to be discharged through Windermere.

Discharges from Windermere have been continuously gauged at the Newby Bridge Weir by North West Water and its predecessors since 1938. NWW data, for the years 1939-84 inclusive, indicate that annual discharges from the lake have fluctuated in the range 110 x 10^6 to 689 x 10^6 m^3, with a 46-year mean of 427 x 10^6 m^3• In the last decade there has been some additional abstraction by pumping station into a Manchester aquaduct. There is considerable temporal variation in precipitation, run-off and discharge into the lake, both with season and, especially, over much shorter periods of heavy rainfall. In consequence sporadic increases of lake level occur (examples in Mortimer 1938a, Lund 1949, Talling 1971), but flooding of littoral areas is limited. The converse, of exceptionally low level after drought, is exemplified by the summers of 1976 and 1984. HcClean (1940) supported his calculation that the range in surface level of Windermere between the extreme low (pre-1971 weir construction) level of 38.92 m O.D. and the highest recorded flood (November 1898) of 41.0 m represented a difference in lake volume ('storage') equivalent to c. 0.13 m of rainwater on the catchment area, with a detailed analysis of the sharp changes in inflow, outflow and storage volumes through a significant storm event.

Changes in water level are thus sensitive short-term indicators of the hydrological balance of the lake and of its hydraulic retention time (calculated as lake volume/discharge). From the mean volume of Windermere (314.5×10^6 m^3: Ramsbottom 1976),the nominal mean retention time of the lake may be estimated to be about 270 d (Sutcliffe & Carrick 1983a), or about nine months. Instantaneous retention time varies with mean monthly discharge (16.7×10^6 to 54.7×10^6 m^3) between 19 and 6 months, and is subject to substantial between-year differences (recorded extremes of monthly discharge: 1.4×10^6 m^3 in May 1978, 134.3×10^6 m^3 in October 1967; equivalent instantaneous retention times are 18.7 years and 2.3 months respectively). Retention times of the North and South Basins also differ significantly, owing partly to the differences in their mean storage capacities (North Basin 201.8×10^6 m^3, South Basin 112.7×10^6 m^3) and partly to the fact that the South Basin receives an additional water supply from the Cunsey Beck catchment. The nominal mean retention time of the South Basin is about 100 days.

3(b). VARIABILITY IN TIME OF TEMPERATURE/DENSITY STRATIFICATION

(J.F. TaIling)

As in all deep temperate lakes, the water mass of Windermere is seasonally subdivided into layers that differ in density and between which mixing is restricted. In this density stratification differences due to solute increments (assessed from electrical conductivity - Section 4(a)) and particulate contents are probably negligible. The density-basis of stratification is therefore mainly determined by water temperature, and consequently by components of the energy balance. Szumiee (1978) illustrates the overall temperature-radiation relationships for the two lake basins. The net annual heat storage per unit area in Windermere by winter to summer warming (the so-called annual heat budget) has been estimated as 17500 cal cm^{-2} (North Basin) and 13230 cal cm^{-2} (South Basin) by Jenkin (1942), but the balance between components that include net back radiation, evaporative loss, and water-air transfer of sensible heat has not been evaluated. Estimates exist for the nearby lake Esthwaite Water during near-cloudless summer conditions (Frempong 1983).

A particularly influential component, by its magnitude and seasonal variability, is the short-wave flux of solar radiation incident upon the lake surface. It has been measured continuously since 1951, with a typical seasonal variation between winter solstice minima and summer solstice maxima (relative range c. 10:1) shown in Fig. 27. From its seasonal changes those of lake surface temperature (e.g. Figs 4, 5) are separated by a time lag, quantified by Szumiec (1978), expressive of the energy-accumulant basis of temperature. In deep water the lag is much increased from considerations of a variable vertical transmission of heat by turbulence. Thus at a depth of 60 m in Windermere North Basin the highest seasonal temperature is typically reached during NovemberDecember.

Figures 4 and 5 show the main features of seasonal change in the temperature/density stratification. These are further illustrated in the publications of Jenkin (1942), Lund et al. (1963) and Talling (1965) for the North Basin, and of George (1981a) and Reynolds et al. (1982a) for the South Basin. Temperatures are lowest during January-February, although in many years 4°C - the point of maximum density for water - is not reached in offshore regions and the lake is near-isothermal with depth. At lower temperatures (as in winter 1947, Fig. 4) an inverse stratification is developed, with colder water above. An extensive ice-cover offshore is infrequent, at circa 20-year intervals (e.g. 1947, 1963, 1986). There is a net gain of heat during March-May, at first with sufficient vertical turbulence to warm the entire water-column, later with restriction to upper layers and formation of a thermocline as major temperature-density discontinuity (Fig. 6a). In this way there are delimited an upper epilimnion or (relatively) mixed layer, a metalimnion of strong temperature/density gradients, and a lower cold hypolimnion. The thermocline tends to be driven deeper during the summer and especially during the autumn when surface cooling reduces the vertical temperature/density difference. Further reduction, especially in combination with episodes of windy weather, leads to complete vertical mixing or 'overturn' marked by isothermy. Overturn occurs earlier (usually October) in the shallower South Basin and later (November-December) in the deeper North Basin. In the latter its detailed dynamics were studied by Mortimer (1955).

As the above seasonal changes depend upon transfers of heat and kinetic (wind) energy, they are susceptible to pronounced variants of weather. Among the modifications that can result are: presence or absence of winter ice cover and of inverse thermal stratification; the time and temperature for onset of thermal stratification in spring; the depth of the upper mixed layer during summer stratification, often subject (with lake-surface temperature) to cycles of about 1 month period associated with alternating episodes of anticyclonic and cyclonic weather; and the time and temperature for the onset of the autumnal overturn.

Two forms of cyclic variation of shorter period deserve mention. Day-night (diel, diurnal) cycles of near-surface temperature and density stratification are widespread during sunny calm weather, with an amplitude of up to several degrees C. Examples in the North Basin appear in Fig. 7b, showing warming and accentuated stratification by day. However detailed analysis and correlation with phytoplankton biology exist only for the neighbouring Esthwaite Water (Frempong 1981a,b, 1984).
Temperature oscillations of still shorter period - often about 15 h in the North Basin, 23 h in the South Basin - develop after windy episodes by periodic displacement of the thermocline about a central node. Such internal waves, studied by Mortimer (e.g. 1952, 1953), are illustrated in Fig. 7b and Section 3c, Fig. 11. They, and direct displacements of stratified layers under wind stress (Figs 6b, 9b), probably account for the short-term changes of stratification at a North Basin station noted by Ullyott & Holmes (1936).

Between-year differences in the surface temoerature can be considerable, especially near the seasonal minima and maxima. They have been systematically analysed by Kipling & Roscoe (1977) for the period 1933-1975. This work includes a graphical comparison between two years with cool and hot summers (Fig. 8), of monthly mean temperature in successive years (Table 3), and the frequency distribution of mean monthly temperature in various months (Table 4).

3(c). WIND-INDUCED WATER MOVEMENTS (D.G. George)

Two rather distinct types of water movement have been studied in Windermere. These are the periodic movements of the thermocline which develop when the wind drops (Mortimer 1951, 1952, 1953, 1954, 1955), and the aDeriodic movements or currents which are always present when the wind blows (George 1981a, 1986). In practice it is difficult to separate the two processes, but the distinction is theoretically and historically quite convenient.

(i) Thermocline movements

Saunders and U1lyott (1937) designed a thermo-electric thermometer that could be used for the rapid measurement of underwater temperature. Between 1947 and 1951 C.H. Mortimer used instruments of comparable design to study thermocline movements in the North and South basins of Windermere. It had long been recognised that strong winds could cause a thermocline to tilt and oscillate, but Mortimer's investigations were the first to demonstrate how important these movements were to the dynamics of stratified lakes. Most of the information contained in the published papers is primarily of theoretical interest, but there are important practical consequences:-

(a) Mortimer's observations in the North Basin showed that very strong winds could tilt the isotherms to such an extent that hypolimnetic water was brought to the surface (Figs 6c, 9b). In 1949 this would have had no deleterious effect on water quality in either basin. Today, however, the deepest water in the South Basin often becomes anaerobic about October (see section 4b) so a comparable tilt of the thermocline might then bring de-oxygenated water close to the surface.

(b) Mortimer's analysis of the data from Windermere and other lakes showed that the tilting movements of the thermocline were largely responsible for generating currents in the hypolimnion. Fig. 10 shows how such currents develop in the hypolimnion of a two-layered lake. When the thermocline is at equilibrium with the wind stress (Fig. lOa) there is relatively little movement in the hypolimnion. When the wind drops (Fig. lOb) the thermocline begins to oscillate and quite strong currents begin to flow in the hypolimnion (Fig. 10c-i). Mortimer calculated that current speeds of up to 4 cm s-l could be generated by such periodic motions. The turbulence generated by these currents is now known to greatly increase the rate at which nutrients are dispersed in the hypolimnion.

(c) Hydraulic engineers frequently use models to predict mixing in natural bodies of water. Mortimer used his observations on Windermere to develop a theoretical model of thermocline movements in a stratified lake. Some of the results obtained from a simple three-layered model with an arbitrary damping coefficient are shown in Fig. 11. The deflections of the 11.0° sotherm in the model are very similar to those in the lake but the model does not predict the movements of the 6.7 ° isotherm with the same degree of precision. In a subsequent theoretical study Heaps (1961) showed that a simple three-layered model cannot satisfactorily simulate the movements that occur in deep water.

(ii) The wind-driven circulation in Windermere

The first direct current measurements in Windermere were taken by George (1981a). In these studies drift-bottles (Fig. 12a) and depth specific drogues (Fig. 12b) were used to investigate the general pattern of circulation in the South Basin. More recently the same techniques were used to examine the flow patterns around a proposed storm water discharge near Bowness Bay (George 1986).

In deep valley lakes the circulation pattern can most simply be visualised as a 'conveyor belt' running along the wind axis. In the North and South basins of Windermere this simple axial transport is distorted by the Coriolis force which is directed 90 ° to the right of motion in the northern hemisphere. The overall effect is a progressive rotation of the wind drift current with depth (Fig. 12c) which drives deep reverse currents transversely across the lake. The strong cross-wind component of flow is particularly obvious when we plot the velocity-depth profiles as resultant current vectors (Fig. 13). This pattern of transport balance is typical of most open water locations and is only modified when the currents enter an enclosed bay (see George 1986). Fig. 14a shows schematically the imagined flow in the stratified South Basin when a moderate wind blows from the south. The general form of circulation is that of a distorted conveyor-belt with the deep counter-currents flowing to the left of the wind. This helical pattern of movement has an important effect on the dispersion of effluents in the South Basin. George (1981b) has shown that any effluent discharged into the lake from either shore will tend to move across the lake rather than disperse along the long axis. Measurements near the Tower Wood sewage works (Fig. 14b) clearly show how a cool effluent can sink towards the thermocline before being carried away from the shore by the deep counter-currents.

3(d). LIGHT ATTENUATION (J.F. Talling)

In light attenuation, as in nutrient status, Windermere occupies an intermediate position among the Cumbrian lakes. Here the illuminated euphotic zone for appreciable photosynthesis, to a depth where available sunlight is 1% of that at the surface, is typically c. 10 m deep (e.g. TaIling 1957, 1971). This compares with corresponding depths of c. 30 m in Wastwater and Ennerdale and c. 5 m in Esthwaite Water.

The 1% light limit will vary in depth inversely with attenuance per metre (the vertical attenuation or extinction coefficient) of the water above, which is raised by additional silt or algal particles. Examples from seasonal change in Windermere North Basin are given by Pearsall & Hewitt (1933) and Talling (1960). A relatively well-defined algal source is the spring diatom (and chlorophyll a) maximum, which in Windermere raises attenuation coefficients for red, green, and blue light and so introduces an appreciable element of 'self-shading' into the diatom population (Talling 1960). Even more is developed in the denser summer phytoplankton, but - excluding local water blooms - the euphotic zone is rarely less than c. 4 m. Silt resuspended after gales is another source, here rarely conspicuous (as it is in the shallow Bassenthwaite Lake), at least in the absence of dredging operations.

The attenuation of underwater light varies with wavelength and hence colour. Over the spectrum there is a minimum of attenuation (or maximum of transmission), which in Windermere lies in the green region. Historically, light attenuation in Windermere has been measured with a variety of sensors with varying spectral sensitivity. It is therefore difficult to compare measurements in the 1920's-1930's (Pearsall & Hewitt 1933, Pearsall & Ullyott 1933, Pearsall & Ullyott 1934) and 1950 onwards (TaIling 1957, 1960, 1971, and unpublished) From use of two blue-sensitive sensors, Pearsall & Hewitt (1933) believed that there had been some decrease in the summer light penetration from 1920 to 1932, affecting the depth-distribution of submerged macrophytes (apparently only temporarily: Section 8d) and related to higher planktonic production.

From 1933 onwards however, there is no well-established evidence of major progressive change, at least in the North Basin. An additional source of information is the visual transparency measured by See chi disc (of diameter 30 cm since 1952, but 15 or 20 cm earlier), typically about 4 m in Windermere but liable to fluctuate (c. 2.5-9 m) with the content of suspended particles.

4. CHEMICAL LEVELS AND DYNAMICS

4(a). MAJOR IONIC CONTENT (J.F. Ta11ing)

The total ionic content of Windermere water is low by British or world standards, but is somewhat above median levels for the Cumbrian lakes as a whole (Table 5). The latter position is influenced by areas of non-igneous rocks in the drainage basin (Section 2), some alluvial valley terrain, and human inputs - from sewage, agricultural liming, and road salt. The content of the South Basin is appreciably higher than that of the North Basin. due mainly to inflow from the relatively productive western drainage sub-basin that includes Esthwaite Water. The boundary between the two water masses can be easily traced from measurements of electrical conductivity. It generally lies in the shallow central island region, but can be somewhat displaced north or south by wind-driven movements of surface water.

About 95% of the total ionic content is accounted by the cations Na^+, K^+, Ca^+, Mg^{2+} and the anions HCO_3^-, Cl^-, and SO_4^{2-}. Their seasonal variability (detailed data in Carrick & Stcliffe 1982) is well under a factor of 2, which contrasts wi that of the more variable remaining principal anion, $N0_3$- (Section 4c).

Average recent concentrations for the two Basins are given in Table 5. The relative proportions of major ions generally conform to the trend w~th rising total ionic content of Cumbrian lakes, first delimited by Mackereth (1957) and amplified by Sutcliffe et ale (1982), towards a greater representation of the ions Ca^{2}+ and $HC0_3$- Most of this trend can be ascribed to increasing inputs from soil leachate; the weathering of limestone masses is not a major factor in central Cumbria, although a thin band of impure limestone (Coniston Limestone) crosses the North Basin.

The ionic content of Windermere predominantly derives from sea-salt carried via rainwater, atmospheric chemical derivatives (especially N and S compounds), and from chemical denudation. These sources are combined in the inflows, for which there is detailed published information (Sutcliffe & Carrick 1983b, Carrick & Sutcliffe 1983) including the R. Brathay (Fig. 15). Chloride is a component derived largely from seasalt (not entirely: Sutcliffe & Carrick 1983b), and can give information on the quantities of other ions with this derivation. Estimates have also been made (Table 6) of the annual inputs of the various major ions from atmospheric precipitation in comparison with their annual outputs in the lake discharge. For many ions ($Ca^{2}+$, $Mg^{2}+$, $HOO_{3}-$) a larger contribution is made by surface weathering, although precipitation is estimated to account for 48-68% of the output quantities of Na+, K+, Cl and $S0^{4}$ The lake acts as a net sink for $N0_{3}^{-}$ as also demonstrated for nitrogen in the 1930's by Mortimer (1939b). Anthropogenic effects are exemplified by the estimate (Sutcliffe & Carrick 1983a) that de-icing salt used on highways in winter has accounted for a 27% increase of Cl- in the South Basin over a 20-year period (Table 7). Further, effects of sewage inputs to the inflowing R. Rothay appear in increased concentrations of Na+, $Ca^{2}+$ + $Mg^{2}+$, and K+ below a main sewage outfall (Sutcliffe & Carrick 1983b).

Like several other moderately to highly productive Cumbrian lakes, Windermere has shown marked increases in alkalinity (largely $HC0_{3}^{-}$) and conductivity (an index of total ionic concentration) during the past 50 years (Sutcliffe et 81. 1982). The alkalinity increment is probably largely a consequence of increased biological production, although some part may be attributable to agricultural liming. Accurate measurements of these variables can be used as a guide to seasonal differentiation in the water-mass over depth and time (Lund, Mackereth.& Mortimer 1963; Talling unpublished).

Information on some inorganic chemical concentrations found in suspended particulate material, and their seasonal variation in the North Basin, is given by Sholkovitz & Copland (1982).

4(b). DISSOLVED GASES (0_{2}, $C0_{2}$) AND pH (J.F. Talling)

Dissolved oxygen undergoes considerable seasonal changes of concentration that are strongly depth-related and predominantly biological in origin. Figure 16 shows the most detailed published example, for the North Basin in 1947 (from Lund et al. 1963). Concentrations above air-saturation can arise in near-surface water for physical reasons during summer warming, and by photosynthesis at times of higher phytoplankton production. Values above 130% are uncommon. More important for general water quality are the depletions in deeper water, either in the thermocline region (metalimnetic oxygen minima) or below (hypolimnetic minima). Thus, in Fig. 16, a metalimnetic minimum <8.6 mg 1-1 appears in the depth-range of 8-20 m during August-October 1947. Similarly low, or lower, concentrations appear elsewhere only in the deepest water at 50-60 m during October-November, the final phase of stratification.

These two regions of stronger oxygen depletion can be recognised in both basins in most years. Before 1968, when regular weekly measurements by an electrochemical oxygen probe (Mackereth 1964) were begun, records were intermittent but showed minimum concentrations of c. 70% saturation in deep water of the North Basin and c. 30% in that of the South Basin. The greater depletion in the South Basin can be related to the smaller depth-extent and volume of its hypolimnion and to its more productive status. By the 1980's the minimum concentrations in the North Basin had decreased only a little further, to c. 50%. By contrast, in the South Basin anoxia was observed for ·the first time in September-October 1981 and recurred in 1982 and 1985. Its depth extent is illustrated in Fig. 17. A relationship with phytoplankton quality is discussed in Section 5(d), which promises to be of predictive value. In turn, the wider implications of such anoxia include enhanced mobilization of Fe^{2}+ and Mn^{2}+ (Section 4d) and probably of $P0_4$-P and NH_4-N (Section 4c), qualitative modification of the animal benthos (Section 8c), and a restriction of fish (e.g. charr) occurrence at depth (Section 7).

Depletion and accumulation of carbon dioxide occur in opposite senses to those of oxygen, and are conditioned by the processes of photosynthesis and respiration. Accumulation is roughly in equimolar proportions to oxygen depletion (anoxia excluded), but CO_2-depletion has special quantitative characteristics related to shifts in the ionic species $H0_3$- and 0_3^{2}- and to possibilities for gaseous exchange at the air~water interface. During the period 1966 - 1986 potentiometric Gran titrations have been used to follow seasonal changes in surface water of total CO_2 (i.e. free 002 + bicarbonate-$C0_2$ + carbonate-$C0_2$) and of CO_2-deviations from the free CO_2 end-point. However most information on CO_2-status must be deduced more indirectly from pH (method in Mackereth et a1. 1978), which is elevated by CO_2-depletion and depressed by CO_2-accumulation. Thus extremes of pH 9.9 and 6.5 have been recorded in surface and bottom water respectively. Over most of this range a shift of 1 pH unit corresponds to a roughly 10-fold change in free CO_2 concentration. The pH value of Windermere water at air-equilibrium is approx. 7.3.

Both CO_2 concentrations and pH values vary in an annually cyclic manner, which is mainly conditioned by the activity of plankton in the upper layers. During winter there is usually a minimal variation with depth, with pH values (6.8 - 7.2) slightly below the air-equilibrium state. The spring growth of phytoplankton depletes 00_2 in surface water and typically raises pH there to between 8.0 and 9.5. The summer growth has usually a still more marked effect, with pH values of 9.0+ being more frequently encountered in the surface layer. Some episodes are described by Talling (1976). Below the summer thermocline, however, CO_2 accumulation depresses pH below 7.0, to minima of 6.5-6.7 before vertical mixing intervenes in October-December.

4(c). MAJOR PLANT NUTRIENTS (S.I. Heaney)

The major nutrient elements in Windermere are carbon, nitrogen and phosphorus. Certain algal groups, particularly the diatoms, also have a large requirements for silicon. Early (1928 and 1932) seasonal analyses including N, P and Si are given by Pearsall (1932) and Jenkin & Davison (1979), and others were made during 1936-1940 by Mortimer (1939a,b, 1941-2, and unpublished notebooks at The Ferry House). From 1945 until present, largely weekly (or in recent winters bi-weekly) analyses have been made for soluble reactive silicon expressed as SiO_2, soluble reactive phosphorus (SRP) expressed as PO_4-P, and nitrate nitrogen (NO_3-N) from integrated samples over the O-7 m layers of both basins(e.g. Fig.17; During this period there have been changes in methods (details in Mackereth 1963 and Mackereth et 81. 1978). The most important are:

a) Change of the Si method from a non-reductive 'yellow' colorimetric determination used up to May 1956 to the more sensitive spectrophotometric determination by reduction of silicomolybdate to molybdenum blue using metol. Before 1956 concentrations below c. 0.5 mg SiO_2 l^{-1} may be overestimated.

b) Change of the PO_4-P method from a colorimetric determination used up to December 1955 to two spectrophotometric methods for determining molybdenum blue after formation of phosphomolybdate and extraction into hexanol. The hexanol was omitted during 1981 and 1982, which resulted in unrealistically high values during the late spring-summer period for these two years (Figs 19, 22).

c) A number of changes in the determination of NO_3-N using a phenol disulphonic acid (PDS) method to May 1956 (colorimetric) and then to June 1965 and April to December 1971 (spectrophotometric), and later variations on the cadmium/copper hydrazine reduction techniques. The former method gives values (x) which are appreciably less than those by the latter (y). This disparity has been corrected for in Figs 20, 23 and 24 by increasing the PDS values according to the relationship

Y = 1.2x + 30 (y and x in ug N 1-^{1})

derived from a year-long series of samples analysed by both methods. Figs 18 - 23 show long-term plots of seasonal change in Si (as Si0$_2$), P0$_4$-P and N0$_3$-N from 1964-1985. Although the contour lines are set at quite large intervals of concentration, the general pattern of the seasonal and between-year variability is shown. Si and P0$_4$-P are regularly depleted to below the levels of detection during late-spring as a result of diatom growth. Si then shows various rates of recovery but P0$_4$-P usually remains very low (<1 ug P0$_4$-P I^{-1}) throughout the summer as diatoms come to be replaced by algae not requiring silicon (Section 5b). Summer depletions of N0$_3$-N are highly variable and appear to depend mainly on the types of algae which make up the main summer growth. The presence of dense populations of 'large' Oscillatoria and species of Ceratium are strongly correlated with the exhaustion of nitrate during summer (Section 5d).

Concentrations of nutrients increase to their annual maxima during winter when algal growth is least. Sutcliffe et al. (1982) calculated mean values : 95% confidence limits from 1945 - 1980 for P0$_4$-P and N0$_3$-N (uncorrected) in the autumn-winter-spring period when these variables reached their highest concentrations. Their values, extended to 1985 and with method-correction for N0$_3$-N, are shown in Fig. 24 together with similarly determined ones for Si. There has been a very slight increase in the mean winter concentrations of Si *in* both basins. The larger change about the mid-fifties may be real or a result of the less sensitive analytical method used up to that time. More pronounced long-term increases in mean winter concentrations are shown for P0$_4$-P and N0$_3$-N.

There were small between-basin differences in P0$_4$-P until the mid-sixties, after which there was a large rise in the South Basin winter values to c. 20 ~ P0$_4$-P I^{-1} compared to less than 10 ~g 1 in the^{-1} North Basin. These increases in winter phosphate values are most likely to be caused by an increase in phosphorus loadings from the sewage treatment works, as a result of polyphosphate builders in detergents and increased tourism. Also of note is the much greater variance of winter phosphate concentrations in recent years.

Remarkably, the long-term increase in P0$_4$-P since 1970 has been accompanied by either no (N. Basin) or very little (S. Basin) increase in total (i.e. dissolved + particulate) P, a quantity measured regularly in surface (0-7 m) water only since 1970. The South Basin concentrations of total P in 1970 averaged 19 ug 1^{-1} and in 1985 23 ug 1^{-1} Lund (1972a) records earlier values for the South Basin in 1945-46 as c. 21 ug 1^{-1}. Seasonal variation is small.

Nitrate-nitrogen differs from $P0_4$-P in that estimated mean winter concentrations remained relatively constant at around 400 ug $N0_3$-N 1^{-1} until 1970. Thereafter there has been a small gradual and oscillating increase to present levels of c. 600 ug N 1^{-1}. The reason for the

timing of the increase is not clear. Lund (1972a) attributed the first (uncorrected) increase in winter nitrate in the early seventies to the large increase in the use of nitrogenous fertilizers, and Sutcliffe et al. (1982) suggest that climatic factors might be important without specifying which. A superficial comparison with winter rainfall values does not indicate a relationship between them and winter nitrate levels. However any such relationship is probably compounded by carry-over from the variable nitrate minimum of the previous summer - a subject which requires further investigation.

All of the regular samples described here were from samples collected at single stations in both basins. George (1981b) found large horizontal variations in $P0_4$-P and NH_4-N in the South Basin which were particularly pronounced close to the discharge of the treated sewage effluent. Such horizontal differences in nutrient concentrations have implications for local and short-term plankton dynamics. Nevertheless, George concluded that samples collected from single open-water stations are sufficient for comparisons of gross (long-term) patterns of change.

Ammonium nitrogen (NH_4-N) has only been determined regularly from samples collected from the 0-7 m layer of both basins since 1971. Values are generally low throughout the year, often below the limit of detection (5 ~g N 1-1), except around the time of the autumnal overturn when they may increase by upward transfer - to concentrations of over 50 or 100 ug N 1^{-1} in the North and South Basins respectively. This autumnal increase in NH_4-N has become more pronounced since 1975, which may reflect year-to-year variation and a trend to increased accumulation in the summer hypolimnion.

Depth-profiles of total phosphorus, $P0_4$-P, $N0_3$-N, and NH_4-N for the period of stratification in the South Basin during 1979 are given by George (1981b). These indicate a general seasonal increase in hypolimnetic concentrations of $P0_4$-P and to a lesser extent of $N0_3$-N. There was an early summer increase of NH_4-N to yield high deep-water concentrations through regenerative processes. These subsequently disappeared, presumably due to oxidation by denitrifying bacteria, leaving a late-season maximum in the poorly mixed middle layers (metalimnion). Vertical profiles of these nutrients in the South Basin during 1985 and 1986 show large between-year differences in their hypolimnetic concentrations, as would be expected from the large changes in algal composition and deoxygenation in these years (Section 5c). Hypolimnetic concentrations of PO_4-P and NH_4-N were much larger during 1985 when a large population of Oscillatoria bourrellyi dominated the summer phytoplankton (Fig. 35a).

4(d). HEAVY METALS (C.S. Reynolds)

The concentrations of several heavy metals (e.g. Cu, Pb, Zn, Cd, 0.1 - 2.1 ug l^{-1}) in Windermere water appear low, as measured by Davison (1980) and by Laxen & Chandler (1983). Recent measurements of the metal content of suspended particles have been given in Sholkovitz and Copland (1982). The studies by Aston et al. (1973) and Gardner (1978) of mercury levels in waters reaching the lake showed them to be typical of unpolluted waters, being little increased with respect to rainwater concentrations, but to be elevated locally by the leachate from former copper mine working on the Tilberthwaite Fells or by treated sewage effluent.

In a preliminary study of the South Basin of Windermere, Hamilton-Taylor (1979) found that the sediments deposited during the previous 130 years were heavily contaminated with zinc, lead and copper. He suggested a variety of likely sources of these enhanced metallic loadings, all related to increased human activities in the lake catchment. On the basis of earlier studies of local precipitation chemistry (Peirson et al. 1973) and of the metal content of Windermere phytoplankton (Lund 1957), it has been further suggested that the sedimentation of planktonic algae (and diatoms in particular) was a major factor in the depositional flux of metals in Windermere (Hamilton-Taylor 1979; Reynolds, Morison & Butterwick 1982a).

The work of Sholkovitz & Copland (1982) indicated that certain elements do become enriched in the seston but are nevertheless liable to rapid recycling within the water column. Elucidation of the processes effecting metal deposition to the sediment and the extent of elemental recycling has related (i) circumstantial evidence from the phasing of metal fluxes into sediment traps placed near the bottom of South Basin and the nature and scale of the sedimenting material to (ii) information on recruitment of materials to the sediment itself (e.g. Hamilton-Taylor, Willis & Reynolds 1984). At the time of writing the study remains incomplete, pending the results of analyses of metal absorption by potentially sedimentary material. Until such time as these details become available, the following remarks must be regarded as tentative.

Table 8 compares the annual elemental fluxes into deep-water sediment traps with the annual accrual estimated from analysis of the most recent deposits (Pennington 1978, Hamilton-Taylor 1979). The ratio (1 relative error) is given in each instance.

For several of the elements (Fe, Zn, Pb), the trap fluxes do not differ significantly from the previously determined annual accrual in the sediments. If allowance is made for underestimation of the particulate A1 recovered in traps, as explained in Hamilton-Taylor et a1. (1984), then the ratio of trap accrual to sediment accrual is also close to unity.

They suggest that any biogeochemical recycling of this element occurs on a relatively small scale and that local sediment resuspension does not contribute significantly to the sensible fluxes of these metals. The ratios for C and N are significantly >1, supporting independent evidence of the biogeochemical recycling of organic matter at the sediment surface in Windermere and other lakes of Cumbria (Jones, Orlandi and Simon 1979) and elsewhere (Wright et al. 1980). The greater ratio for N than for C is indicative of the preferential loss of N during organic matter degradation and the rapid destruction of proteinaceous material (Price 1976).

Such ratio-based evidence points to relatively large-scale recycling of Mn and Cu. For manganese such transformations are already well-known, involving the reprecipitation of oxyhydroxides mobilized through reduction in deep, micro-aerophilous layers during the summer stratification. It seems likely, therefore, that the Mn redox cycle extends well into the overlying water column at such times (see also Sholkovitz & Copland 1982). A comparable mechanism involving copper is unknown but, as the hypolimnion of South Basin has become increasingly anoxic in recent years, so the mobilization and reprecipitation of Fe has become more evident.

Pearson correlation coefficients among the monthly fluxes of Fe, Pb and Al and the relative composition of trapped particulates were all very high (> 0.9; $p < 0.05$). The main period of deposition of these elements occurred in the winter period (November-January), coinciding with the major period of visible deposition of 'silt'. This is generated by the seasonally-high fluvial discharges into the lake and by resuspension and 'focussing' into deeper layers of detrital material following the breakdown of thermal stratification. Adsorption of metals (especially Pb) onto detrital material generated in the lake itself cannot be discounted, though it seems more likely that such sorption occurs before this, possibly within catchment podsols (Hamilton-Taylor et ale 1984).

The maximum deposition of manganese occurs during the summer stratification, supporting the view that redox cycling of the element provides the main explanation for the exaggerated trap flux. At other times the behaviour of manganese resembles that of iron, and may be interpreted as evidence of processes similar to those shown to operate in Esthwaite Water by Davison et ale (1980, 1982), namely a combination of inputs of particulate material associated with high winter discharges and subsequent resuspension during full mixing.

The apparent sediment-water recycling of copper was found to be phased differently, the peaks occurring in March-April and September-October. These more or less coincide with the seasonal flux of live cells of the diatom Asterionella formosa into the traps during its spring and autumn bloom maxima. Hamilton-Taylor et al (1984) attributed this behaviour to scavenging by the phytoplankton, in the manner envisaged at the start of the trapping work. Peaks were greatest when live cell recruitment was also greatest; to complete the overall recycling process, copper is apparently remobilized as a consequence of microbial deposition. The existence of both mechanisms is also supported by the simple mass balance equations developed by Hamilton-Taylor et al (1984). It is substantially in agreement with Rowlatt's (1980) proposal of a dominant, organically based transport pathway for copper in Windermere.

This was the only clear case of algal involvement in metal cycling in Windermere. Only zinc showed any correlation with particular algae (Cyclotella) but this relationship is arguably fortuitous. Present indications are that the mechanisms of transport by algae and bacteria in sedimenting floes are insignificant in comparison to the direct geochemical processes involving the input and deposition, with some intermediate resuspension and redeposition of particles.

4(e). NUTRIENT INPUTS (S.L. Heaney)

Phosphorus

There is evidence (Section 5e) that the growth rate of large algal populations in summer in both basins of Windermere is regulated by phosphorus availability. Rough estimates are given in Table 9 for the inputs of this element into the two basins, based upon:

(a) Calculated inputs from Cunsey Beck draining Esthwaite Water, the River Rothay draining Grasmere and Rydal Water, and the outflow from Blelham Tarn. These inputs were obtained by multiplying the mean winter concentrations of soluble reactive phosphorus from Esthwaite Water, Grasmere and Blelham Tarn respectively by their outflow discharge over this period (c. November - March). The summer contributions from the lakes are considered negligible as PO_4-P is then usually below the limit of detection(<0.6 ug l^{-1}). No recent analyses of phosphorus are available from Elterwater. The input from the River Brathay is therefore estimated as one half of that of the Grasmere-Rydal-Rothay catchment. The small Trout Beck is ignored as it contains no sewage treatment plant.

(b) Calculated contributions from the resident populations of Windermere and Ambleside connected to sewage treatment plants (North West water) and an estimate of 1.8 g phosphorus per person-day (Alexander & Stevens 1976) into the sewage system. Estimates for holiday residents and day visitors are based on numbers obtained from NWW with the daily phosphorus contribution per capita reduced to 50% of that for a normal resident. No account is taken of phosphorus loading from other sources in the drainage basin.

Table 9 gives a loading of PO_4-P to the North Basin of 0.28 g m^{-2} Yr^{-1} and to the South Basin of 0.91 g m^{-2} yr^{-1}. These values can be compared with 0.48 g P m^{-2} yr^{-1} calculated in a similar manner for nearby Esthwaite Water (Talling & Heaney 1983), generally regarded as the most productive lake in the Lake District. By far the largest sources of phosphorus to the North and South Basins are the sewage works at Ambleside and Tower Wood respectively. Although-the contribution by visitors is minor compared to that of the resident population, this additional load from tourism is greatest over the summer period when the lake is stratified and nutrient demand by phytoplankton is greatest.

For comparison with phosphorus loading to other northern temperate lakes, the values for the two basins of Windermere are placed on the graphical relationship of Vollenweider (1968) (Fig. 25). This indicates that the North Basin is slightly eutrophic whereas the South Basin compares with lakes which are considered highly productive. Vollenweider & Kerekes (1980) provided a preliminary classification of lakes in the OECD eutrophication programme based on a number of variables, into which the two basins of Windermere are inserted using information for 1983-1985 (Table 10). On the basis of maximum chlorophyll concentration the South Basin would be considered eutrophic, and on the basis of total phosphorus the North Basin would be thought oligotrophic. In some other respects both basins would be considered mesotrophic.

Nitrogen

Inputs of nitrogen to Windermere are more difficult to assess. A nitrogen budget for 1937-8 was made by Mortimer (1938a,b, 1939b), who estimated that the total N output, including organic N, was 318 tonnes year^{-1} and that this was similar to the input via streams and sewage effluent. Sutcliffe & Carrick (1983a) found a net balance between NO_3-N output and input in precipitation. They concluded that, as there were also other appreciable human inputs and NH^{4+} in rainfall, Mortimer had correctly proposed that the nitrogen input suffers a net loss in traversing the lake ecosystem. Nevertheless, there is likely to be considerable between-year variation in the extent of annual accumulation of nitrogen within the lake, depending upon the nature of the summer phytoplankton and the rainfall (Section 5d). In the absence of sufficient information on nitrogen input from the sewage works, whose effects are spatially detectable offshore (George 1981b), it is not possible to consider in greater detail the N inputs to the lake. Nevertheless, nitrogen dynamics within the lake are important to the understanding of possible major shifts of trophic pathways (Section 5d), and point to the need for a better understanding of nutrient mass balance within the system.

5. PHYTOPLANKTON LEVELS AND DYNAMICS

5(a). TOTAL BIOMASS (J.F. Talling)

The total quantity of phytoplankton and its changes are here outlined using estimations of chlorophyll a, based on extraction by hot methanol and without correction for degradation products. Records of mean concentrations in the surface layer (usually 0-7 m) are available since 1964. The accompanying depth-distribution is known only for a few years or seasonal episodes. Dry weight and cell volume are two further indices of algal quantity to which chlorophyll a is very roughly related by order-of-magnitude factors of c. 100 ug-dry weight and c. 0.2 mm^3 cell volume per ug chlorophyll a.

Seasonal change of concentrations in the upper (0-7 m) layer and at other depths is illustrated in Fig. 26. The occurrence of two maxima, shorter in spring and longer in summer-autumn, is a pattern broadly characteristic of both North and South Basins in most years. Similarly characteristic are the low concentrations of winter. The downward extension of the spring maximum is typically greater than that of the summer maximum which is generally delimited by the stronger summer thermocline. However the low concentrations in deep water, far below the euphotic limit of about 10 m are evidence of algal transfer by turbulence or sedimentation. The two seasonal maxima differ considerably in species composition (Section 5b). Their absolute magnitude, usually 10-35 ug chlorophyll a l^{-1}, is typical of moderately productive lakes.

There are some systematic differences between the North and South Basins related to their differing depth and nutrient status. Spring increase begins some weeks earlier in the shallower South Basin with better light conditions for the average circulating algal cell (Talling 1971). The summer maximum is typically larger in the South Basin and there usually exceeds the spring maximum in concentration. Different nutrient limitations between the two seasonal maxima can be expected (Section 5e). Both the preceeding winter reservoirs and the summer inputs are greater in the South Basin (Section *4e).*

Year-to-year variability in the seasonal pattern is illustrated in Figs 27 and 28. Although the winter minimum is probably the least variable feature, its level can vary appreciably in the range 0.3-1.0 ug 1^{-1} in the North Basin and 0.7-1.8 ug 1-^{1} in the South Basin. The spring and summer maxima are typically separated by a single deep minimum, but this is occasionally indistinct (e.g. 1966, 1970, South Basin) or accompanied by other summer minima (e.g. 1978, South Basin). Subordinate maxima may develop as late as October in the South Basin (e.g. 1966).

Long-term variability of the major features of spring and summer maxima is further shown in Figs 29 and 30 for the period 1964-86. In both basins there is an appreciable increase with time in the incidence of higher concentrations, above 10 and 20 ug 1^{-1}. At the 2 and 5 ug 1^{-1} levels the beginning and end of the annual growth period are relatively stable, conditioned by the transition in light-availability after and before winter. Least regular are the occasional depressions of concentrations within the broad summer phase, often related to species successions.

5(b). SPECIES: SEASONAL DEVELOPMENT AND SUCCESSION (C.S. Reynolds)

Although some indication of the algal species represented in the plankton of Windermere, as well as their changing relative abundances with season, had emerged from the pioneer studies of West & West (1909), the Pearsalls (especially Pearsall 1932) and Wailes (1939), the main advances in understanding phytoplankton periodicity in the lake were initiated by J.W.G. Lund (Macan 1970). Lund resolved many or the remaining taxonomic difficulties and commenced a programme of regular weekly collection of phytoplankton, supporte4 by physical and chemical measurements, that has been maintained, with little modification, for over forty years to the present. Moreover, Lund made uniquely prolonged and detailed studies of several of the more conspicuous species.

It is perhaps surprising, therefore, that there have been few attempts to provide an overall picture of the seasonal periodicity of the Windermere phytoplankton. Possibly the most complete published overview was that presented in Macan (1970, Fig. 32) based on data for the South Basin in a single year (1965), supplied by Lund. Even so, the sequence of relative species abundance and dominance of the phytoplankton has been shown to apply to more recent descriptions of the periodicity in the North (1978) and South basins (1979-1980) (Reynolds 1980; Reynolds et al. 1982a). Taken in conjunction with Lund's published work on key species, especially the diatoms Asterionella (Lund 1949, 1950, 1966) and Melosira (Lund 1954, 1955), desmids of the genera Cosmarium and Staurastrum (Lund 1971), and very small algae (Rhodomonas sp., Lund 1962; 'u-algae', Lund

1961), as well as with the unpublished information, these synopses provide a basis for the following characterization of seasonal phytoplankton periodicity in the lake.

Macan's (1970) summary is redrawn in Fig. 31 on a single revised scale of approximate aggregate cell volume (note: 10^9 um^3 = 1 mm^3 ~ 1 mg fresh weight) for each species to permit more direct comparison of the changing species dominance of the plankton with season. The salient features include: the early predominance of diatoms, notably of *Asterionella* and *Melosira*, which increase through March and April, reaching maximum levels in May; a late spring pulse of motile, colonial Chrysophytes (typified by *Dinobrvon*) and various colonial green algae (notably *Sphaerocvstis* and *Coenococcus*); a summer phase in which diatoms (e.g. *Tabellaria*), desmids (e.g. *Staurastrum*) and dinoflagellates (especially *Ceratium*) are conspicuous; and an autumnal period in which diatoms (*Fragilaria*, *Tabellaria* and *Melosira*) are the most abundant forms. Cryptomonads and, at least in 1965, *Oscillatoria* spp. represented significant fractions of the phytoplankton biomass throughout the year.

Overall, the sequence is probably typical of many mesotrophic lakes in the temperate region (Reynolds 1984a,b). The seasonal changes in dominance broadly reflect the gross variations in the physical-chemical environment of the lake and the differing responses of individual species thereto. They are influenced by events in other lakes in the Windermere catchment (most notably Esthwaite Water), the plankton of which may be 'seeded' in to Windermere: the biomass of the South-Basin populations of *Ceratium*, for example, is superficially correlated with their abundance in Esthwaite Water, particularly in those wetter summers when there has been an increased rate of inwash of cells to the South Basin of large standing crops.

In the winter months, low water temperatures and especially low light income exacerbated by long periods of full column-mixing, provide the main limitations on phytoplankton growth (TaIling 1971). The superior growth capacity of diatoms, such as *Asterionella* and *Melosira*, at these times is favoured by their relative insensitivity to low temperature (Q10 of maximal growth at <10-G: c. 2.3), and a high ratio of maximal photosynthetic rate: respiration rate ($P_{max}:R > 15$). Certainly, the rate of cell increase represents an efficient assimilation of photosynthetically fixed carbon (Talling 1955) and suggests that the requirements for inorganic nutrients, which coincidentally reach their seasonal maximum at about this time, are saturated by the available pool.

Eventually, the spring diatom bloom is terminated, usually in May through the combination of a number of factors. Above all, there is the depletion of nutrients. Lund's classic work on *Asterionella* in Windermere (see, especially, Lund 1950, 1964, 1966) indicated that effective exhaustion of the supply of soluble reactive silicon usually imposes the most severe constraint on further diatom growth. Other factors may include: the onset of thermal stratification (Lund 1954; Lund et al. 1963) following increasing insolation and surface warming, and which has been shown elsewhere (Reynolds et al. 1982b) to bring about a sharply increased rate of sinking loss from the suspended population of non-motile organisms: increased grazing by a more abundant and active zooplankton (George and Harris 1985): and epidemics of parasitic fungi (e.g. Canter & Lund 1953). The decline in the mixed depth (generally to < 4 m) is insufficient by itself for the sinking loss rate to overtake the *in situ* growth rate of *Asterionella* prior to Si limitation. The last cell divisions occur after the lake has stratified, while sufficient dissolved silicon remains to support it (Reynolds 1986). Nevertheless, sedimentation is the dominant 'sink' for the vernally produced diatom populations in both the North Basin (Lund et al. 1963) and South Basin or Windermere (Reynolds et al. 1982a: Hamilton-Taylor et al. 1984).

Often (as exemplified by the 1965 sequence), diatom growth is resumed later in summer, particularly if the depth of wind-mixing exceeds 4 m or so and that fresh or recycled supplies of silicon are maintained in the epilimnion. The prominent species are generally *Tabellaria flocculosa* and *FraRilaria crotonensis*, rather than *Asterionelle formosa*. Both species possibly have higher light thresholds than *Asterionella* and both maintain colonies sufficiently large to be virtually immune to grazing by filter-feeders. The algal assemblages of summer mixed-layers also include species of non-motile desmids and of the blue-green genus *Oscillatoria*. Neither grow as rapidly as diatoms during spring, owing in part to their greater sensitivity to low temperatures (Heaney & Butterwick 1985, Butterwick unpubl.), although many *Oscillatoria* spp. are apparently tolerant of optically-deep mixing.

Between the main phases of spring and summer mixing, the environmental conditions created in the newly-formed epilimnion (warm, upper water of increasing clarity but of diminished nutrient resources) are exploited by a mixture of motile or slow-sinking algal species (the chrysomonad *Dinobrvon* and gelatinous, colonial Chlorophyceae). Experience from Windermere and other lakes (e.g. Reynolds 1984b; Harris 1986) is that these are often joined and eventually replaced by larger algae, whose slower rates of growth are offset by an enhanced capacity to regulate their own vertical distribution in relation to the availability of light and nutrients and by a resistance to losses through sedimentation and grazing. The bloom-forming species of Anabaena (potential hazards to water quality: Section 9c) and the dinoflagellates Ceratium hirundinella and C. furcoides are prime examples of such species. Although also favoured by a "seeding-in" effect from other lakes upstream (notably Esthwaite Water: see above), the occasional dominance of the summer plankton of Windermere by Ceratium is consistent with this hypothesis.

5(c). LONG-TERM ALGAL CHANGES: NORTH BASIN (C.S. Reynolds)

Macan's (1970) summary of phytoplankton periodicity in Windermere holds, at least qualitatively, for a majority of years since 1945. Apart from lower average biomass levels and a slight time-lapse in the seasonal phases in the North Basin, it applies equally to both basins. Later summaries for subsequent years (Reynolds 1980, Hamilton-Taylor et ale 1984), during which markedly increased loadings of phosphorus (especially) and nitrate have been observed (see Section 2 above), indicate that the primary response of the phytoplankton community has been to produce 'more of the same'. Nevertheless, some relatively minor modifications have been detected. These are important in making objective assessments of trends and future extrapolations about the likely consequences of the continued man-made enrichment of Windermere.

The spring maxima of the Asterionella formosa have continued to be a major feature of phytoplankton cycles to the present time, and the populations attained in most years still fall in the range 5×10^3 - 8×10^3 cells ml^{-1} Of the diatoms that have increased in mean abundance over the forty years or so, Stephanodiscus hantzschii (a common indicator of eutrophication) and Fragilaria crotonensis merit particular mention. Populations of the latter still rarely exceed 1000 cells ml^{-1} but more recently the maxima develop earlier in the year, between May and August rather than in the early autumn, yet may persist until the final breakdown of thermal stratification in November or December. The relative increase in this species in Windermere resembles its response in other lakes of the Windermere catchment to increased nutrient enrichment (see, for instance, Lund 1972b, 1978).

Increases in the populations of surface bloom-forming bluegreens (*Anabaena*, *Aphanizomenon*, *Microcystis*) are common compositional responses to phosphorus enrichment in lakes (Reynolds & Walsby 1975). The standard sampling and counting techniques followed at the FBA have certainly recorded the presence of these organisms but, to date, have scarcely shown up as contributing a significant proportion of the planktonic biomass of Windermere. Nevertheless;' occasional surface blooms of *Anabaena* spp. have formed more frequently since the early 1970s during June-August, in quiet weather following episodes of wind-mixing.

5(d). LONG-TERM ALGAL CHANGES: SOUTH BASIN (S.I.Heaney)

It is in the South Basin that the greatest phytoplankton-related changes have occurred. The present purpose is to quantify annual changes of maximum population density for major algal species from 1945-1985 and to illustrate relationships 'between-species composition and large interannual changes of nutrient concentrations.

The annual maximum population densities of a selection of major algae are shown in Fig. 32 for the diatoms *Asterionella formosa*, *Melosira italica* subsp. *subarctica*, *Fragilaria crotonensis*, *Tabellaria flocculosa* var. *asterionelloides*, and in Fig. 33 for the blue-green algae *Oscillatoria bourrellvi*, *O. agardhii* var. *isothrix* and *Anabaena flos-aQuae* + *A. spiroides* + *A. circinalis*, the small ubiquitous flagellate *Rhodomonas lacustris* and the small green algae *Chlorella* spp. Lund (1972a) presented these values for *Asterionella* up to 1970 and concluded there had been a general decline in this species, the alga being replaced by other species of diatoms (Section 5b). However, when observations for a further 15 years are added there is little evidence of significant change in the size of the spring *Asterionella* maximum over the 40-year period to 1985. Thus there are dangers of making long-term prognostications even from 25 years of information. Of the other diatoms only *Tabellaria* shows any indication of change, the populations of this 'summer' algae being appreciably lower since 1969. The reason for this decline may in part reflect the relatively drier (Sutcliffe et ale 1982) and more stable summers of the last 15 years.

Rhodomonas lacustris and *Chlorella* spp. represent small, readily grazed algae. These show no obvious patterns of change in abundance between 1955 and 1985.

More evidence of change is shown by the major species of blue-green algae. Except for 1975 there would appear to be a decline in the abundance of Oscillatoria agardhii var. isothrix after 1955, even taking into account the alteration in counting procedure. On the other hand, there is an apparent increase in annual population size of Anabaena spp., although these species are always present-at low biomass and do not become dominant members of the plankton.

It is remarkable that these surface-bloom forming species of Anabaena, which can fix nitr~gen, do not come to dominance during those summers when inorganic nitrogen becomes depleted in the epilimnion. The reason for this apparent paradox possibly lies with the success of Oscillatoria bourrellyi. This unusual planktonic blue-green alga, lacking gas vacuoles, has become more prominent in both basins of the lake in recent years. The role of this alga in the general metabolism of the South Basin is the subject of present study and speculation, as outlined below.

The maximum population size of O. bourrellyi from 1945-85 is shown in Fig. 34. During this time two methods of counting were used and together indicate that appreciable populations were present in the South Basin as long ago as 1948. However, serious attention was not given to its presence until 1981 when a large population preceded the first record of anoxia in the hypolimnion. Since 1981, large populations of the alga (> 300 mm filament length $m1^{-1}$) have occurred in 3 of the 5 summers and, when present, have preceded appreciable lake anoxia (> 10% lake volume). Such large populations are also strongly correlated with exhaustion of nitrate-nitrogen in the epilimnion. These relationships are clearly seen in Fig. 35, which also shows the abrupt decline of the alga in June 1986. This unusually sudden collapse of the population for reason(s) unknown was followed by an equally unusual abrupt rise in soluble reactive phosphorus, presumably as a result of mineralization in situ of the population in the epilimnion.

A possible hypothesis for these between-year changes of lake anoxia and epilimnetic depletions of nitrate nitrogen is that they are governed by (a) the presence of particular species of algae or algal types and (b) the sensitivity of the South Basin to change as a result of its sensitive ratio of epilimnetic volume/hypolimnetic volume of 0.79. O. bourrellyi normally grows long filaments unsuitable for crustacean grazing. These filaments do not have gas vacuoles and, as a result, behave more like diatoms than the more common gas-vacuolate blue-green algae. Thus O.

bourrellyi is denser than water, requires a degree of turbulence to keep it in suspension, and ultimately will settle out of the euphotic zone. Also, it has no known microbial diseases, although the abrupt decline in 1986 may have been so mediated. When established the alga has the potential for becoming the dominant phytoplankter and producing large populations. In doing so it acts as a sink for nitrate-nitrogen which becomes exhausted. At the same time it accumulates other essential nutrients (P, Fe, etc.), hence depriving species of Anabaena of the resources to enable them to exploit their nitrogen-fixing advantage. Ultimately the filaments sink into the hypolimnion. The South Basin has a volume such that the sedimenting mass of 0. bourrellvi during 'bloom' years is sufficient to cause anoxia through respiration and decomposition.

In years when 0. bourrellyi is absent or does not produce large populations, its place is usually taken by small flagellates, green algae, desmids, diatoms and only rarely by the large dinoflagellates Ceratium spp. Small flagellates and green algae are not collected in sedimentation traps in numbers which relate to their abundance in the plankton, although desmids and diatoms are (Reynolds et al. 1982a, Hamilton-Taylor et al. 1984; Section 4d). Members of all these groups are liable to mineralization in the upper layers of the lake as a result of mortality by grazing or diseases. This mineralization leads to a recycling of nutrients which includes the conversion of cellular nitrogen to NH_4-N; The latter is then taken up as N-source preferentially to $N0_3$-N by the next phase of algal growth. A result of appreciable mineralisation in the upper layers is that a smaller proportion of biomass passes into the hypolimnion, reducing the oxygen demand in this region. Ceratium spp. form a taxonomically complex group of large ungrazed algae, and until 1983 were not known to suffer from epidemics of disease in the South Basin. At the end of population growth cysts are usually formed (Heaney et al. 1983) that rapidly settle to the sediment. The cellulosic structural cell wall of the vegetative cell is shed during encystment but is mineralized, with associated oxygen demand, before reaching the deeper waters (Reynolds et al. 1982).

A schematic representation of the above account is given in Fig. 36 for three summer situations in the South Basin with different algal assemblages, amplified in Fig. 37 by oxygen profiles from example-years. Further support for these relationships is given in Fig. 34, which depicts changes of epilimnetic $N0_3$-N, hypolimnetic deoxygenation, and the maximum size of populations of the 'large' algae *0.bourre11yi* and *Ceratium* spp. for 1964-1985 against a background of increasing winter concentrations of soluble reactive phosphorus. It is unfortunate that oxygen was not measured during 1964 as the size of the *O. bourrel1yi* population would suggest a severe deoxygenation of the hypolimnion, as in 1974.

Depletion of $N0_3$-N at times of large biomass of *O. bourre1lyi* has been observed in the North Basin in 1981 and 1984. However no anoxia was observed, probably because of the smaller ratio of epilimnetic to hypolimnetic volume (0.45) in this basin.

The long-term records show that once there is a sufficient nutrient input to the lake to support large standing biomass, as is now the case for both basins, major changes in the direction and form of lake metabolism are largely influenced by the form (size) and biological characteristics of the species present. The species assemblages will largely determine whether the major algal mineralisation, nutrient recycling and respiration is in the epilimnion, metalimnion or hypolimnion. This can also have implications for energy transfer along food-chains.

5(e). CHEMICAL CONTENTS AND LIMITING FACTORS (S.L Heaney)

Important as they are, measurements of dissolved plant nutrients in the suspending water do not necessarily indicate the factors which regulate production at a particular time. About 45% of the dry weight of non-siliceous phytoplankters is carbon, 4-10% nitrogen and 0.1-2% phosphorus; for diatoms 30-50% of the dry weight can be contained in the silica frustules. It is clear, therefore, that when cells exhaust external supplies of carbon or silicon growth must soon cease as the capacity for cellular storage of these elements relative to requirements is small. For nitrogen, and particularly for phosphorus, the capacity for 'luxury' storage within cells is much greater and for phosphorus can be sufficient to support several cell divisions although at the expense of *growth rate*.

In classic studies of the growth of *Asterionella formosa* in Windermere, Lund (1950) showed that the decline of the spring diatom maximum was associated with depletion of 5i. In another classic study Hackereth (1953) elegantly demonstrated that although $P0_4$-P declined together with Si, phosphorus deficiency was unlikely to provide a limit to the growth of Asterionella in Windermere despite the very low initial concentration of PO_4-P. He showed (Fig. 38) that in 1950 and 1951 there was significant growth of Asterionella in the lake at the expense of cellular phosphorus reserves, and where in 1951 the alga approached the limiting low content of cell phosphorus found in culture.

In the following 35 years the situation with respect to the spring diatom population seems to have changed little. The mean winter levels of Si are largely unchanged (Section 4c) as is the maximum biomass of Asterionella (Section 5c,d), suggesting a close relationship between the two. What has changed markedly is the mean winter concentration of PO_4-P (Section 4c). It is instructive to consider the extent, if any, to which phosphorus influences phytoplankton production in the lake. Evidence for phosphorus-limitation in autumnal phytoplankton was provided by growth and photosynthesis responses to phosphate added to plastic enclosures suspended in the lake (Komarkova 1974).

As another approach to this problem integrated samples from the 0-7 m layer were collected from both basins during 1983-4 and analysed for particulate carbon, nitrogen and phosphorus. The values for particulate carbon can be considered an index of phytoplankton biomass, and the atomic ratios of *PIC, PIN,* and *NIC* taken as possible indicators of P or N limitation of growth (Figs. 39, 40). In these Figures periods of cellular phosphorus depletion are indicated by deviations (shaded) below the *PIN* and *PIC* proportions to be expected from the generalized 'Redfield ratios' for phytoplankton.

During 1984 there were decreases in the ratio of *PIC* during development of the spring Asterionella formosa and summer Oscillatoria bourrellyi populations, these decreases being greater and more extended in time in the North Basin. By contrast, depletions of P relative to C were relatively small during the summer of 1983 when Oscillatoria bourrellyi was not a major component of the then less dense phytoplankton. These results (Tett et ale 1985) show that phosphorus may control the growth rate, but not necessarily the maximum biomass of spring and summer growths, and that cellular depletions are greatest in the North Basin where the initial concentration of PO_4-P is least. Moreover, there are marked between-year differences which appear to be related to particular species or groups of species compromising the phytoplankton.

Although these results indicate that during 1984 phosphorus was likely to be the main growth rate-controlling element during summer, the prolonged period of nitrogen depletion in the epilimnion in several years, including 1984, suggests that this element is also in short supply. Precisely which element is controlling growth at any time depends on the flux of nutrients to the population relative to need. The flux of limiting nutrients will be from recycling *in situ*, which will not lead to greater biomass production, and from external (to the epilimnion) inputs which will. River inputs of inorganic nitrogen are likely to be much greater than for phosphorus. Another potential source of both elements is from the nutrient-rich hypolimnion as a result of entrainment following weather-induced depressions of the thermocline.

Besides the limitation of the spring diatom population by silicon and the evidence for possible control of *growth rate* by phosphorus during spring and summer, there have been in recent years indications of severe carbon limitation. In June 1985 the pH of the South Basin reached 9.9 (Section 4b) with the strong depletion of carbon dioxide from the poorly buffered water. This potential 00_2 limitation was relieved the following week when the weather deteriorated and mixing ensued. Further examples are described by Talling (1976).

Other related factors influencing -growth are temperature and light. Some species only grow within restricted temperature ranges. For example, the blue-green alga *O. bourrellyi* grows poorly below 8-C (Heaney & Butterwick 1985), the large dinoflagellate *Ceratium* will not grow below 10 °C (Heanev*et al*. 1983), whereas *Asterionella* will grow at temperatures as low as 2°C (Butterwick unpublished). Similar interspecific differences of growth have been shown at temperatures above 20°C. Light-limitation of growth also occurs in Windermere, as demonstrated by Lund (1949) and Talling (1971) for the period preceding onset of the spring algal increase (see also Sections Sa, 5b, and Fig. 27), and during summer at times of dense, sedimenting populations of *O. bourrellyi* (Tett *et al*. 1985).

6. ZOOPLANKTON

6(a). INTRODUCTION (D.G. George)

The phytoplankton of Windermere has been studied in detail since the turn of the century but relatively little work has been done on the zooplankton. Qualitative accounts have, however, been published periodically (Gurney 1923, Wailes 1939, Smyly 1968) and there have been more specialised studies of the animals' vertical and horizontal distribution (Ullyott 1939, Colebrook 1960, George 1976). The two main components are the Rotifera (rotifers) and Crustacea; the latter comprises the Cladocera (water fleas) and the Copepoda.

Quantitative samples of crustacean zooplankton have been collected, as vertical net hauls, from the North Basin at fortnightly intervals since 1938. Until recently very few of these samples had been examined systematically but an account of the long-term changes in biomass has now been published (George & Harris 1985). No comparable samples have been collected from the South Basin, but J.F. Talling has recorded the number of the larger crustacea caught in the phytoplankton samples (see 6(c) below).

6(b). QUALITATIVE STUDIES (D.G. George)

Most of the early collectors treated Windermere as a single site so it is not possible to compare conditions in the North and South Basins.
Table 11 lists the species of planktonic rotifers found in Windermere; it is based on the Table in Wailes (1939) which incorporates some unpublished records from Bryce as well as notes from Galliford (1948, 1949). Most of the species listed are rare and occur in the plankton only as occasional migrants. The four most abundant species in the lake are Keratella ouadrata, Keratella cochlearis, Polvarthra vulgaris and Kellicottia longispina. K. Quadrata is generally regarded as a eutrophic species but is quite commonly found in high mountain lakes (Pejler 1964). The other three species are more typical of oligotrophic lakes but all are polymorphic and may show adaptations to local conditions. Recent unpublished observations by D.P. Hewitt suggest that the rotifer fauna of Windermere has undergone little change during the last forty years. Population densities in the North Basin have increased somewhat in recent years but the same dominant species appear from year to year.

Table 12 lists the planktonic crustacea recorded in Windermere during the past sixty years. The species list is fairly typical of large northern waters and has changed little over the years. Some components of the Windermere plankton have been present in the lake for over 10 000 years. Scour field (1943) examined entomostracan remains in the bottom deposits of Windermere and concluded that the cladaceran fauna of

Windermere had not altered much since the glacial period. In this century there have certainly only been one or two changes. Gurney (1923) did not collect any D. laticeps but this species tends to remain in deep water and could have been missed by his sampling methods. The only well documented change is the loss of Holopedium gibberum sometime in the late sixties (Smyly 1968). This species was never very abundant and was almost certainly washed into the North Basin from Grasmere. The numbers of H. gibberum in Grasmere appear to have been in decline before the sewage treatment plant was commissioned in 1971. The subsequent enrichment of Grasmere by sewage effluent has, however, ensured the virtual extinction of H. gibberum in that lake.

6(c). ROUGH NUMERICAL CHANGES . (J.F. Talling)

Since 1967 a series of rough estimates of the larger crustacean zooplankton (excluding nauplii and early copepodite stages) has been available for both basins. Animals recognisable to the naked eye were counted on the glass fibre GF/C filters used to separate phytoplankton for analysis of chlorophyll a. Sample volumes of 0.5-2 1 were generally used, as aliquots of integrated samples over an upper (generally 0-7 m) water layer. The results are expressed as seasonal contour diagrams (Figs 41, 42), and can be compared with the corresponding diagrams for chlorophyll a (Figs 29, 30). They differ from the zooplankton estimates based on vertical net hauls (Section 6d) in that the deeper water layers were not sampled.

These rough counts show little evidence of strong long-term trends, above a factor of 2, either in mean weekly numbers or maximum seasonal numbers. There is possibly some significant increase about 1970 in both basins (cf. 6d below). Most prominent in Figs 41 and 42 is the major numerical development during May-June. This, lagging slightly behind the spring phytoplankton maximum, was also depicted for 1936 by Mortimer (1939a). Although Copepoda preponderate in its initial phase, the later maximum is strongly dominated by Cladocera - especially Daphnia hyalina var. galeata.In both basins the highest numbers are generally between 50 and 100 animals (2 1)-1, although - as for phytoplankton - there is an appreciably greater development in the South Basin. From experience elsewhere (Thompson et al. 1982) the higher numbers are likely to involve a strong grazing pressure on the smaller phytoplankters.

6(d). QUANTITATIVE STUDIES (D.G. George)

In 1965 Edmondson published an account of factors influencing the reproductive rate of rotifers in the North and South Basins of Windermere. The rotifers were Keratella cochlearis, Kellicottia longispina and Polyarthra vulgaris. Since the sampling method was rather unsatisfactory Edmondson did not provide any estimates of population density so we cannot use this study for any quantitative comparisons. His graphical analysis of the egg production data never~heless showed that the reproductive rate of the rotifers varied in relation to both food and temperature (Fig.43.)

In 1985 George & White developed a simple volumetric method for estimating the biomass of zooplankton in preserved samples. This method was later used to analyse long-term trends in the crustacean biomass of the North Basin of Windermere (George & Harris 1985). The contour diagram in Fig. 44 shows the annual and seasonal variations in biomass that have occurred in this basin between 1940 and 1980. About 1970 there was a sustained increase in zooplankton biomass that almost certainly reflects the documented changes in water chemical composition (Sutcliffe et al 1982). In earlier years, however, there appears to have been a cyclical pattern of change with a periodicity of approximately 10 years. George & Harris showed that these cyclical changes are not related to variations in the year-class strength of perch (Perca fluviatilis) but are correlated with the timing of thermal stratification. Fig. 45 compares smoothed estimates of mean summer biomass with similar smoothed estimates of water temperature. There is a clear pattern of low zooplankton biomass in the summers following warm Junes (early stratification) and high zooplankton biomass in the summers following cool Junes (late stratification). The timing of thermal stratification appears to influence the dynamics of the herbivorous zooplankton by regulating the periodicities of their preferred algal food. The critical reproductive period for the crustacean zooplankton is more likely to coincide with the period of maximum food availability in 'cool' rather than 'warm' Junes. In warm Junes the preferred food species tend to appear earlier and may be in decline by the time the Daphnia are ready to increase their rate of reproduction.

7. FISH (C.A. Mills)

Six salmonid taxa are found in Windermere: resident and migratory trout (Salmo trutta), migrating salmon (Salmo salar), spring and autumn spawning populations of charr (Salvelinus alpinus), and occasional rainbow trout (Salmo gairdneri) which have escaped from Esthwaite trout farm. Perch (Perca fluviatilis), pike (Esox lucius) and eel (Anguilla anguilla) are also abundant. Small species, largely confined to shallow areas, comprise three-spined sticklebacks (Gasterosteus aculeates), bullhead (Cottus gobio) and the only common cyprinid in the lake, the minnow (Phoxinus phoxinus). The stone loach appears to inhabit inflow streams rather than the lake itself. The lampreys Lampetra planeri and P. fluviatilis are also present but infrequently recorded. Three cyprinid species are thought to have been introduced this century, probably as discarded live-bait. These are tench (Tinca tinca), rudd (Scardinius ervthrophthalmus) and roach (Rutilus rutilus) but only the latter species is encountered with any regularity.

Historical evidence indicates that trout, pike, perch, charr and eels have been the common species of the lake for at least the past 200 years and that all these species have been exploited by man for food (Table 13 Le Cren, Kipling & McCormack 1972). At times the charr have been seriously over-exploited. However by 1940 there had been no large-scale removal of fish from Windermere for nearly 20 years. The lake contained a large number of small, slow-growing perch and a moderate population of pike which tended to be both large and old. Information on the feeding of perch and pike in the lake (Frost 1954, Craig 1978) indicates that in addition to predation by pike on perch, cannibalism by both species probably acted to stabilise the populations. By 1940 anglers were having poor success at charr fishing (Le Cren, Kipling & McCormack 1972) and this is reflected in the low catch per unit effort (CPUE) values for the FBA’s annual net catches in Low Wray Bay (Fig. 46).

During the war the perch were intensively trapped, canned and sold as "Perchines" for human consumption. This war effort reduced perch numbers six-fold (Fig. 47) and at the same time the pike, as their main predator, were gill-netted by the FBA. The estimated number of pike in Windermere aged two years or more fell from 2300 to 1400 with few of the remaining fish over six years old (Fig. 48). Perch numbers stayed low for a number of years but pike numbers recovered quickly to around 2500. Very successful hatchings of perch in 1955 and 1959 brought numbers back to pre-war levels but with much higher mean weights. Pike numbers responded, rising to over 4000 in the early 1960's (Fig. 48). However, the high numbers of adult fish of both species and a series of cool summers had a dampening effect on the survival of young fish and pike growth fell, though not to pre-war levels. The mid-1960's to mid-1970's saw some warm summers and successful spawnings of perch (Craig 1982a) yet, though pike growth was excellent, the spawnings produced few fish. It has been suggested that the young-of-the-year perch were now growing so rapidly that the young-of-the-year pike were deprived of suitable prey at a crucial period and turned instead to increased cannibalism (Kipling 1984a). Thus whilst pike growth and recruitment are influenced by temperature the relationship is complex, depending also on the biomass of adult pike and the availability of prey. Similarly Craig (1979) found that the relationship between the various factors affecting perch recruitment could be modelled by formulae of the form:

$$\ln \underline{y} = \underline{b}_0 + \underline{b}_1 x_1 + \underline{b}_2 x_2 + \underline{b}_3 x_3$$

Where $\underline{v}$ = cohort strength at age 2 years, $\underline{X_1}$ is a measure of temperature in year of hatch, $\underline{x_2}$ is biomass of adult stock in year of hatch, $\underline{x_3}$ is ln (perch cohort strength/pike cohort strength) and $\underline{b_0}$, $\underline{b_1}$, $\underline{b_2}$ and $\underline{b_3}$ are constants. The model was round to be an excellent fit to the data collected from 1959 to 1974 for both the North Basin (the multiple correlation coefficient, $\underline{r}$ = 0.9882) and the South Basin ($\underline{r}$ = 0.9844). Fig. 49 illustrates this model for the North Basin of Windermere. It shows how increase in temperature (a density-independent factor) increases cohort numbers, but an increase in predation, both by cannibalism of adult perch and predation by pike (density-dependent factors), decreases the number of perch reaching age 2 years.

However in 1976 some 98% of the adult perch in the lake were killed by perch disease (Bucke et al. 1979). The adult pike retreated from their normal shallow summer habitat to deep water to feed on charr. Normally the larger pike only concentrate on this food source during the October to March period when the charr gather to spawn. Between 1976 and the early 1980's the number of pike aged two years or more fell steadily to under 1000 in 1980 but by 1985 the number had reached 1500. Whilst many adult pike weigh 2 to 4 kg there are still few pike over 5 kg.

Since the initial gill-netting the FBA has continued to remove some pike each winter, mainly from charr spawning grounds. The opercular bones are used to obtain accurate age data and measurements are taken of gonad size and fecundity. For a given size of pike fecundity has doubled over the period of the study (Craig & Kipling 1983). Between the war and the onset of the perch disease the FBA usually took about 300 pike with a mean weight of about 3 kg each year. Catches were higher in the early 1960's reflecting the very large numbers of pike in the lake (Fig. 48). The effect of these removals was complex but generally they kept the pike population younger and faster-growing than it would otherwise have been, though many other changes in the pike population have occurred for quite different reasons (Kipling 1983a, 1983b, 1984a).

In recent years both our fishing effort and our annual catches have been greatly reduced, averaging only 100 fish between 1981 and 1985. This represents less than 10% of the adult population of pike in the lake. Few of these fish exceeded 5 kg in weight and in recent years only one large pike (12 kg) has been netted. Future trends in the pike population will depend largely on the state of the perch population and on summer temperatures. If these are favourable and given the low level of our fishing effort, there could be a substantial increase in the pike population. Tne perch population recovered up to 1982 and though the numbers have subsequently fallen back (Fig. 47) the summer of 1984 produced an extremely strong year-class which has shown up in the 1986 trapping exercise. A small proportion of adult perch continue to display the characteristic lesions associated with the perch disease.

Our annual charr catches show an eight-fold increase in catch per unit effort (CPUE) since the war (Fig. 46). The most likely explanation is that the pre-war population of large pike had a more severe impact on the charr population than that in subsequent years. Even though there have at times been larger numbers of adult pike in the lake (Fig. 48), their mean size has been considerably smaller than in 1940.

In comparison with the detailed information on pike and perch from both basins of the lake, data on charr is sparse, mainly restricted to the North Basin (Kipling 1984b) and much more limited in its scope. Some information on feeding is available (Frost 1977) but previous growth data, based on scale reading, may not be very accurate. Preliminary comparisons with ages from otoliths indicate that some older fish have been underaged by one or more years. Information on the location of spawning sites is quite good (Frost 1965) but much less is known about the behaviour of the charr during the rest of the year. This is particularly so for juvenile charr. The two spawning groups of charr do display small differences in meristic characters such as gill raker number and spawning sites and times (Frost 1965), but no differences in other ecological characteristics such as feeding or preferred depth have been demonstrated.

Charr are typically fish of cold deep waters. There is some evidence from Ireland and Scotland (Maitland, Greer, Campbell & Friend 1984) that charr populations in more productive and shallower waters are liable to extinction. The recent trend towards lower oxygen levels in the hypolimnion of the South Basin is a cause for some concern. If oxygen levels were ever to fall during spring, when the spring-spawned eggs are developing at a considerable depth (Frost 1965), this group of charr could be lost from the South Basin. There would only be a very gradual restocking from the North Basin-if conditions improved, as charr shows a strong tendency to return repeatedly to the same spawning site (Kipling & Le Cren 1984). The existing levels of summer deoxygenation could already be affecting juvenile charr from both spring and autumn stocks, but due to our lack of knowledge about the requirements of these early stages this would first show up as reduced catches of adults by anglers over the next few years. It is also possible that in hot summers South Basin charr may be excluded from the upper water layers by high temperatures and from the lower layers by low oxygen levels. Charr in the North Basin are unlikely to face any comparable threats but the FBA's routine monitoring would pick up any decline in the North Basin stocks.

The most comprehensive account of trout in Windermere was published by Allen (1938). Craig (1982b) gives information on growth and mortality of trout sampled in six inflow streams of Windermere during the spawning season. Data have also been collected from trout inadvertently caught in nets set for pike or charr. Due to the small numbers caught in most years these data have not been fully analysed. If this were done it might show any trends in growth rates in the lake and possibly changes in survival. It would be unlikely to give any indication of the relative abundance of trout in the lake and how this compares with that in earlier times. Information on eels is largely restricted to age and growth studies (Frost 1945a, 1945b) and no recent information has been collected.

Future Trends

1. The pike'population is now relatively young and fast-growing and is increasing in size.
2. Whether this continues depends partly on the number which are removed and partly on the size of the perch population.

3. The perch population is now extremely fast-growing but numbers have remained relatively low since the perch disease in 1976. However the 1984 year class is an extremely strong one resulting in large trap catches in spring 1986, and should lead to an increased number of large perch in subsequent years.
4. Relatively little is known about the charr populations in the lake and especially those of the South Basin, but-any substantial increase in the number of large pike would probably reduce charr numbers. Either an increase in FBA pike fishing or removal for restocking by NWWA might be considered desirable.

S. Low oxygen levels in the South Basin pose a number of potential threats to the charr populations but lack of information on their tolerances prevents any realistic predictions.

6. If increasing nutrient levels in the lake result in increased zooplankton abundance both charr and perch will benefit. However if blooms of the filamentous alga *Oscillatoria* caused reduction in zooplankton abundance then the fishes' food supply will actually be lessened by increased nutrient inputs.
7. It is also evident that *Oscillatoria* filaments physically interfere with the gear of charr anglers. This or course w~ll increase charr survival, though there is no evidence that charr catches are undesirably high.
8. Little scientific information is readily available on the current status of the trout or eel populations of the lake.
9. If the shallow littoral areas of the South Basin continue to become more eutrophic it is likely that the larger cyprinids, especially roach, will become more numerous.

8. OTHER BIOTA

8(a). BACTERIA (J.G. Jones)

It is not possible to comment on long-term changes or trends in the bacterial population of Windermere because reliable methods of counting bacteria in water have only recently been developed. Direct counts of the total bacterial population are now generally performed by epifluorescence microscopy. Almost all earlier records of the bacterial population were based on the 'viable' or plate count technique. This results in a gross underestimate of the population size since only c. 0.25% of the population will grow readily on agar media. An example of the difference between plate counts and direct counts of bacterial populations in Windermere (North Basin) and the more eutrophic Esthwaite Water is given in Fig. 50.

Some recent bacteriological and related data from the North and South basins of Windermere are shown in Table 14. The few differences that exist indicate a higher microbiological activity in the South Basin. Results obtained by Mortimer in the early 1940's indicated that sediment from the North Basin possessed a greater capacity to consume oxygen than that from the South Basin, although the work has not been repeated. The few results obtained since then suggest an increasing oxygen demand in isolated sediment cores and marked depletion of oxygen in the South Basin (see Section 4b).

If the major lakes in Cumbria are placed in increasing degree of eutrophication on a scale from 1 to 16 (1 corresponding to Wastwater and 16 to Blelham Tarn) then a combination of important planktonic variables would place Windermere North Basin at 9 and the South Basin at 12. Some benthic variables would place them at 7.5 and 11 respectively (Jones, Orlandi & Simon 1979). The placing of the South Basin higher up the scale of trophic status is, however, based on single-station observations which do not take into account spatial variability within the lake itself. Multivariate analysis (Jones 1977) indicates that only 20% of the temporal variability in the bacterial population in the North Basin and 10% in the South Basin could be associated with changes in conventional physicochemical variables such as temperature, pH, phosphate concentration etc. This suggests that other factors including spatial variability and point sources of pollution may be important.

Although stratification of a lake often accounts for the major component of vertical and temporal bacterial variability, this is not always the case. In the South Basin of Windermere samples taken on the same day can show a coefficient of variation of 70% in the vertical plane and up to 240% in the horizontal. Thus, in a transect across the South Basin (Jones 1977) total bacterial counts have ranged from 0.6 to 1.35 x 10^9 1^{-1}, viable bacteria from 5 to 29 x 10^6 1^{-1} and coli forms from 1 to 119 x 10^3 1^{-1}. (Please note that all counts are given per litre of water and not in the 100 ml unit volume used in water testing). These results show that the narrower the range of organisms counted the greater (and better) the expression of variability. This illustrates the value of “indicator” organisms.

With regard to such bacteria the following counts have been obtained in Windermere during 1983-5. Numbers of faecal streptococci range from 5 to 140 l^{-1}, the highest values being recorded in Bowness Bay and offshore at the sewage treatment plant in the South Basin. The effluent at this plant discharges at c. 6.8 x 10^{5} faecal streptococci 1-1. As with all counts of indicator bacteria, numbers of *E. coli* vary considerably from day to day and from site to site. Counts on surface water at one site on the west shore fluctuated as follows over a two-week period at the end of August 1985: 22, 98, 157, 365, 22, 76 *E. coli* l^{-1} ; the highest counts (apart from those near the sewage effluent) were found in Bowness Bay. The sewage outlet discharges between 4 x 10^{5} and 4 x 10^{6} *E. coli* 1^{-1}. Coliform counts are, on average, an order of magnitude higher, and might be expected to be between 10 and 5 x 10^{3} 1^{-1} in the open water of the lake. In contrast water in an oligotrophic lake such as Wastwater might yield 10 coliforms 1^{-1}.

The values given above do not imply that the same populations are being sampled. Indicator organisms (e.g. *E. coli*) in the lake may not have originated from the nearest point source of pollution. Some measure of the heterogeneity of the communities may be obtained from a more detailed analysis of their taxonomy and-their patterns of antibiotic resistance (Jones et al. 1986). If the incidence of single and multiple resistance is examined very little difference is observed between isolates from the lake water and those from the sewage effluent (Table 15).

However there are considerable differences between the responses of the various bacterial taxa. When the responses to individual antibiotics are analysed, the differences between the taxa remain and, in addition, resistance to many individual antibiotics is seen to be more widespread in isolates from the lake (Table 16). The multiple resistance patterns are shown in Table 17, and the approximate sizes of the populations and the incidence of resistance in Table 18. These results were obtained from lake water samples taken from the main offshore body of the lake.

However, when several sites were surveyed, further differences in antibiotic resistance patterns emerged related to human activity. There was, for example, a significantly higher overall resistance to cotrimoxazole and tetracycline (55% and 20% respectively) in Bowness Bay than in the open water (28% and 5%). Similarly the incidence of ampicillin resistance in sheltered bays containing large numbers of boat moorings was also much higher (42%) than in open water on the same day (15%).

It is this information, coupled with that on the distribution and potential longevity of *Salmonella* strains in Grasmere, which causes me, probably more than other biologists at Ferry House, to have considerable reservations about the siting of a storage and discharge point for sewage at Cockshot Point and the bay to the south of it.

8(b). BENTHIC ALGAE (J.F. Talling)

Bottom-living or benthic algae are well-developed seasonally in the marginal regions with sufficient illumination. They occur either attached to substrata, such as stones or plants, or unattached (often motile) on the sediment surface. The two major studies were in 1933-5 by Godward (1937) and in 1948-50 by Round (1957a,b,c,d, 1960, 1961a,b). The floristic information is considerable,as is that on relative occurrence with season and depth above 6 m. Quan~itative data on biomass related to unit area are lacking. There are only a few sporadic and largely unpublished observations on deeper regions, where divers have noted the occurrence of the encrusting *Hildenbrandtia* on some rock (and bottle) surfaces (J.W.G. Lund, personal comm.). In one study by Round (1961b), on the depth-distribution of the sediment-surface ('epipelic') forms, numbers fell off abruptly below 6 m and were negligible at 12 m. Both he and Godward (1937) found many species to reach maximum numbers at 2-4 m rather than nearer the surface.

A seasonal development is obvious to the casual observer, who sees a brown or green coloration develop in shallow water during March-April. Both Godward & Round give examples of such early-spring maxima among the many species studied, that include the diatom *Cvmbella ventricosa* and the filamentous green alga *Ulothrix zonata*. Round (1960, 1961a,b) further showed how growth increase after February appeared in the total cell counts of diatoms and blue-green algae, including numbers summed for the 0-6 m layer (Fig. 51). Later, after June, numbers of diatoms were typically much reduced, although some other algae (e.g. the filamentous *Oedogonium* spp.) were most plentiful then.

The causal control of these changes with depth and season, as by light, temperature, nutrient availability, grazing, and water-level fluctuation, is largely unknown. At greater depth, and probably in mid-winter, restrictions by low light conditions are predominant. Several workers (Godward 1937, Allanson unpubl.) observed and measured a dense colonization by algae of artificial submerged materials, such as glass slides.

8(c). BOTTOM FAUNA

(J.M. Elliott)

Between 1932 and 1969, only fifteen publications dealt with the animal benthos of Windermere "and these were summarised in the book by Macan (1970). The following species were classed as "newcomers" by Macan:

Planorbis (Tropidiscus) carinatus (gastropod mollusc, first recorded 1936), *Potamopyr~us ;enkinsi* (gastropod mollusc, probably Australasian, first recorded 1936), *Cran~onyx pse~do~racilis* (amphipod crustacean, North American, first recorded 1960), *Stenelmis canaliculata* (elminthid beetle, first recorded 1961). To-this list should be added the leech *Trocheta bykowski* (first recorded 1957). The spread of *CranRonyx pseudoRracilis* in Windermere has been documented by Garland (1981); it was present at the north end of the South Basin in 1960 but by 1965 it was found everywhere in shallow water. Another species that may have been introduced, and appears to be increasing its range, is the isopod crustacean *Asellus aquaticus* which may be slowly replacing *A. meridianus* (Moon 1957).

The presence of *Stenelmis canaliculata* is notable because Windermere is the only definite locality for this species in the British Isles. Another rare species is the stonefly *Capnia bifrons*, found only at one locality in the lake (Elliott 1986). This species is the only British stonefly which is ovoviviparous (eggs develop within female and hatch as soon as they are laid in the water).

Since Macan's review of 1970, the only additional work on the benthos has been a series of papers from a thesis on flatworms (De Silva 1976a, b, 1978, Macan & De Silva 1979), a paper on feeding and growth of *Asellus* (Marcus *et al*. 1978), a paper on changes in the littoral fauna (Macan 1980), and an unpublished thesis on the oligochaete worms of the profunda 1 benthos (Reynoldson 1983).

Most work on the benthos has been on the invertebrates living on the shore in shallow water (depth < 60 em). Macan concludes from his extensive surveys of 1965-66 and 1979 that the shore fauna is typical of a eutrophic lake such as Esthwaite Water, apart from a stretch on the west side of the North Basin between Belle Grange and Watbarrow Point. The fauna of the latter shore is more typical of less productive lakes such as Ennerdale and includes the rare stonefly _Capnia bifrons_. There are no major differences between the collections made in the two surveys except for an increase in crustaceans and flatworms on the shore between Belle Grange and Watbarrow Point. Macan concludes that this part of the lake shore is slowly becoming more eutrophic and that eventually the "Ennerdale-type" community will disappear.

The profundal benthos has been generally neglected since the general survey in 1934-5 by Humphries (1936), apart from work on worms by Brinkhurst (1964) and Reynoldson (1983). The latter study provided the best quantitative data and showed that the oligochaetes in the mud are most abundant in the South Basin (station means, 1977-79, 1680-2250 animals m^{-2}) and the north end of the North Basin (1270 animals m^{-2}) with much lower numbers inbetween (192 animals m^{-2}) - a distribution pattern suggesting once again that most of the North Basin is the least eutrophic part of the lake. Less information is available about the Chironomidae, the other major component of the profundal benthos (Humphries 1936, Reynoldson 1983).

Little is known about the sub-littoral benthos, i.e. invertebrates living on the shore at water depths between 1 m and 10 m. The general survey by Humphries (1936), catches of emerging aquatic insects and the contents of fish stomachs all suggest that benthos production is greatest in this region.

The general conclusion from this brief survey is that species lists and some qualitative information are available but little quantitative information exists for the bottom fauna of Windermere. There is a paucity of information on the profundal benthos and especially on the sub-littoral benthos, both of which provide large quantities of food for the fish in the lake.

8(d). MACROPHYTES (S.L. Heaney)

Macrophytes, as submerged, floating-leaved, and reed swamp species (species listed by Stokoe 1983), are only well-developed in shallow littoral or sheltered bay areas that are not extensive in Windermere. The three common 'isoetids' - _Isoetes lacustris_, _Littorella uniflora_, and _Lobelia dortmanna_ - are widely distributed, but such larger submerged aquatics as _Ceratophyllurn_, _Myriophyllum_ and _Potamogeton_ spp. are abundant mainly in shallow silted regions with some protection from wind/wave action, and floating-leaved species (e.g. water-lilies) require still more restricted shelter. Wave exposure is also a major factor in limiting hydrosere vegetational successions in Windermere as elsewhere (Tutin 1941).

Unlike nearby Esthwaite Water, there is little detailed description of submerged macrophyte abundance and change in Windermere. What information exists is mainly in the limited surveys of Pearsall in the early part of the century (Pearsall 1920, Macan 1970). These publications give descriptions of macrophyte distributions at Grassholm, between Wray Castle and Watbarrow Point, and at Pull Wyke nearby. Pearsall & Hewitt (1933) recorded that the lower limit of rooted plants in Windermere had risen from 6.5 m in 1920 to 4.3 m in 1932. Later Godward (1937) observed that it was 6 m during 1933-5, and suggested that deep penetration of macrophytes may be related to-fine summers.

The only record of a major change is the invasion of a new form of Canadian pondweed (*Elodea nuttal1ii*?) which during the last decade has replaced *Elodea canadensis* in Mitchell Wyke (Lund 1979). From his long observations of the lake, J.W.G. Lund believes that, except for this unusual invasion, there has been no noticeable change in the presence of macrophytes in Windermere other than the expected between-year variation.

8(e). BIRDS (K.M. Atkinson)

Windermere provides a range of habitats for many birds, and since 1967 regular monitoring of the wildfowl population of Windermere has taken place (Atkinson & Shepherd 1974, Atkinson 1981). The highest number of birds are present during the winter months of October-March, with the mean annual peak-count of wildfowl (excluding coot) for the winters of 1978-9 to 1985-6 being 2647. The four most numerous duck are mallard (*Anas platyrhynchos*), tufted duck (*Aythya fuligula*), pochard (*Aythya ferina*) and golden eye (*Bucephala clangula*) with mean annual maxima for 1978-1986 of 1654, 480, 297, 277 respectively. In addition, for coot the mean maximum is 1168.

The goldeneye numbers, of over 200 from November until March, are particularly significant with Windermere being the third most important site in England for this species (Owen et ale 1986).

In summer wildfowl numbers fall. Changes in the success of the main breeding species, mallard, red-breasted merganser (*Mergus serrator*) , and mute swan (Cygnus olos), have been exhibited since counts began in 1967. Mallard numbers, both in winter and summer, rose markedly in the late 1960's, after the cessation of shooting on the lake in 1966 and the release onto nearby tarns of hand-reared birds. In summer mallard congregate in the main tourist centres such as the Waterhead and Bowness bays, where the duck are regularly fed and the number of young birds seen rose from under 50 in 1968 to approx. 400 in 1980.

The first recorded breeding of red-breasted merganser, which is mainly ,a. ,summer visitor, on Windermere was in 1957 after which the population increased and from 1969 to 1976 about 120 young were reared each summer. In 1977 there was a sudden fall due to a catastrophic decline in one of the merganser's main food sources, the perch. An average of only 22 young merganser were reared between 1977 and 1980. Although perch numbers have recovered the merganser population has not yet attained its pre-1977 numbers.

Mute swan numbers were low during the 1970's but have risen to a maximum of 60 in November 1985, after a succession of successful breeding seasons from 1980 to 1985.

Also common on the lake are several species of gull. Some roost there seasonally in large numbers. Cormorants also occur.

Loss of lakeshore habitats, especially reedbeds, scrub and wetland, has led to a decrease in breeding of other vaterbirds such as coot, moorhen and great crested grebe and also sedge warblers and reed buntings. An increase in recreational use of the lake and the shoreline has caused disturbance to birds, es~ecially during the breeding season, and numbers and breeding success of some birds, such as the common sandpiper, have fallen.

Winter wildfowl are particularly susceptible to disturbance by water-based recreation. The recent increase in winter usage of Windermere is being carefully monitored to determine what effect, if any, it may have on the nationally important goldeneye population of the lake.

9. SEDIMENTS AND HISTORICAL RECORD (E.Y. Haworth)

This section is mainly based upon the publications of Pennington (1943, 1947, 1973a, 1981) and Horne & Horne (1985), which offer far more information than can be presented here.

The several rock basins of Windermere are primarily covered by the rock debris, gravels, silts and clays left by retreating glaciers of the last, Devensian, ice-age. Seismic survey (Howell 1971) suggests that this deposit may be over 50 m thick in places. The Windermere Sand and Gravel Co. (now defunct) did assess the potential for commercial extraction of glacial rather than river gravels, but this would have radically reduced water clarity by resuspending the fine clays that only sedimented slowly under long winter ice-cover.

In the 1930's sediment cores were collected to examine the discontinuity in sediments apparent in early echo-soundings (Jenkin, Mortimer & Pennington 1941). Windermere was thus one of the early sites where the environmental history of a lake, its catchment and the region were assessed from a section through lake mud (Pennington 1943, 1947).
The post-glacial sediment deposits are typically about 5 m thick in offshore areas (e.g. Fig. 52). Glacial clays were gradually replaced by organic silts, which were interrupted about 10 500 B.P. by laminated clays of the final valley glaciers (Fig. 53). Above these the lake mud becomes increasingly organic, as shown by the carbon and mineral proportions (Fig. 52a).

Windermere now provides geologists and palaeolimnologists with the Late-Devensian reference section for the earliest climatic amelioration, the late-glacial organic deposits of the Windermere Interstadial (Coope & Pennington 1977). This section, containing the evidence of succession from pioneer herbs to birch woodland and regression to tundra vegetation during cold phases, ha~ only been found in a small area in Low Wray Bay (Pennington 1973b). As this is a shallow water location, it could be at risk from commercial operations such as alteration of boat-moorings; it includes a small section of diatomite deposited sometime around the end of the Boreal Period (c. 7000 B.P.). Sediment stratigraphy in the southern part of the lake is also used as the 'master curve' for palaeomagnetic studies (Thompson & Turner 1979).
Chemical and microfossil analyses show that the early minerogenic soils were richer in bases such as potassium and sodium (Mackereth 1966), and the lake water supported a more alkaline diatom flora than today (Pennington 1943 and Fig. 53). An increase in acidic indicators, as soil cations were leached and organ~c matter increased, has been clearly demonstrated for Esthwaite Water, Blelham and Blea Tarns as well as Windermere, although the latter study is less detailed (Haworth 1985).

The sedimentary record of forest clearance, begun by Neolithic man and continued more aggressively by subsequent farming groups, is not only that of the changes in pollen indicative of herbs rather than trees, and including cereals, but also appears in the accelerated addition of catchment soils to the lake bed. The last feature was demonstrated for Blelham Tarn (Pennington 1981 Fig. 6) on a lowland part of the Windermere catchment (see Fig. 3). Arable farming began on the coast lands and expanded on to the uplands during Romano-British times (Pearsall & Pennington 1973). Major deforestation also occurred during Norse settlement c. 1000 A.D. - hence the distribution of Scandinavian farming names, such as Grisedale and Grasmere. Mediaeval ploughing, and the drainage and liming of valley fields in the 1800s, also made their impact. Although there is now little ploughed land, many fields were used for cereals prior to 1950.

Unlike those of Coniston and Ullswater, Windermere sediments contain no distinct layers related to mine waste since the 1500's (Mackereth 1966, Pennington 1973). Local mining activity for slate and iron ores was comparatively small and the sediment does not differ markedly from natural minerogenic material. The 1966 floods in Langdale discoloured the main inflow to Windermere with haematite material from Red Tarn yet no traces were found in nearby sediments. From mediaeval times, local industry was based on woodlands which supplied charcoal for the iron works, bobbins for textile mills and bark for tanneries (Kipling 1974), and none of these markedly affected the lake. However there have never been any detailed studies of this section of the sediment record.

A transition, in the early 1800's, from brown to black sediment in Windermere (Fig. 52) is accompanied by increasing predominance of the remains of the diatom Asterionella formosa (Pennington 1973). Stockner (1972) showed how changes in this and other diatoms reflected the pattern of lake enrichment in Windermere. More precise dating of the upper sediments by remanent magnetism (Mackereth 1971) and radio-isotopes (Pennington 1973, Aston et al. 1973) correlates such enrichment with the increase in the local population - both resident and tourist - in the 1850's, when the railway arrived. Table 19 summarizes the present human pressures on our lakes in terms of population referred to unit lake area, and gives estimates of current deposition rates.

A lake is the product of the inputs; the apparent 'good' state of Windermere, as perceived by various lake users, has partly been due to a relatively rapid throughput of water and to sewage treatment but mainly to the relatively low level of chemical waste from modern industry in the area. Even so, an increase in heavy metals has been observed in sediments of the last 150 years (Aston et ale 1973, Hamilton-Taylor 1979) and attributed to atmospheric sources, river pollution, sewage, road run-off and boat traffic (see Section 4d). The radioisotope 137-caesium is the product of nuclear fission (Fig. 52b) and provides both a stratigraphic time-marker and a record of such emissions. The most recent event - the Chernobyl disaster - has now added a new peak in the surface layer (Hilton pers. comm.). Glacial microfossils, evidence of redistribution from recent dredging in and around Bowness Bay, were found in water samples collected near the Beech Hill Hotel.

Since the original analyses of pollen and diatoms (Pennington 1943, 1947), other biological and chemical remains have been recognized as indicative of pollution or disturbance of the environment. The sediments thus continue to provide a valuable record of changes in the state of the lake.

10. RELATIVE SENSITIVITY TO CHANGE

10(a). INTRODUCTION (J.F. TaIling)

Preyious sections have described the changes to which many physical, chemical, and biological variables in Windermere are liable. Most are reversible on time-scales of 1 year or less, although their temporal representation and seasonal excursions between minima and maxima may shift in successive years as long-term trends. Such trends, that can also appear in qualitative aspects (e.g. species presence or absence), are of especial concern for lake management. Six potential sources are: (i) climatic change; (ii) mechanical disturbance or alteration of the lake basin and its outflows; (iii) changing chemical input from the atmosphere plus drainage basin; (iv) changes in the quantity or quality of biological populations; (v) consequent changes in water characteristics; and (vi) biological hazards from introduced toxins, pathogens, predators, or invasive competitors.

Examples from all these sources have affected Windermere over the past 50 years. Effects from (i) and (ii) appear of least general importance; they include probable effects of varying summer rainfall and temperature between the 1950's and 1970's on average solute income

(Sutcliffe et ale 1982) and summer stratification, past dredging of bottom sediments, and some influence of a new outflow weir (1971+) and aquaduct-related abstraction on water storage. Source (iii) is probably of greatest importance for long-term change, especially from increased inputs of phosphorus (Section 4e) with effects on lakewater concentrations (Section 4c) and nutritional response by algae (Section 5e). Effects on lakewater concentrations of some major ions (Ca^{2+}, Cl-) have been detectable (Section 4a) but inconsequential; there is no evidence of acidification via atmospheric precipitation. Regarding source (iv), there appears to have been some-long-term increase «factor of 3) in the average densities of phytoplankton (Section Sa) and possibly zooplankton (Section 6d), but so far the changing representation of species in these major communities has not been large. Consequent changes in water characteristics (source v) include phases of elevated pH, autumnal deep anoxia in the South Basin (Section 4b), and turbid water during local water-blooms. For source-(vi) there have been major alterations in fish (especially perch) populations by disease (Section 7), some enhanced local concentrations of human bacterial pathogens (Section 8a), and invasions by certain animals (Section 8c) and one macrophyte (Section 8d).

Further discussion on the past and present susceptibility to change of some major environmental and biological components appears below.

lO(b). WATER CHARACTERISTICS (J.F. Talling)

Water characteristics respond to input and output fluxes of energy and materials to the lake basin, as well as to internal movements and transformations (e.g. phytoplankton growth) in the water-mass itself. Their relative sensitivity to change depends upon the size and duration of the net input-output flux relative to basin content (e.g. retention time); to differentials between the fluxes of water and of solutes or suspensoids present in variable concentration (e.g. high concentration inputs); to restriction of consequences by variable compartmentation in the water-mass (e.g. epilimnetic warming, hypolimnetic anoxia); to critical thresholds or limiting concentrations for physical, chemical, and biological events (e.g. wind stress, solubility products, nutrient-growth response); to the functional significance of small differences above a large background (e.g. water-density in thermoclines); and possible transformation to more or less active forms (e.g. metal binding, P-species shifts, sedimentary release or burial). Given cross-interactions the possible variants are immense, yet the annual seasonal pattern has a considerable stability impressed - directly or indirectly - by the large-amplitude cycle of solar-radiation.

Regularity in the annual cycle of most variables can be disturbed by irregular events (e.g. floods; droughts, cloud cover), by systematic trends of inputs (e.g. $P0_4$-P), and possible carry-over from year to year (e.g. heavy metals in sediments). From the last two categories long-term trends are conceivable. That established for winter concentrations of $P0_4$-P is liable, from the loading estimates, to develop further (as in the Lake of Constance, Germany) and via plankton biology and food chains is potentially the biggest source of change in the lake ecosystem, including the littoral and profundal interfaces. So far the qualitative and quantitative consequences in community change appear limited, as with deep-water anoxia, but may well develop further in the next few decades. Also significant for water quality are the biological idiosyncrasies of some species with variable interannual representation, such as ·the blue-green Oscillatoria bourrellvi (Section 5d). Although many solute ions are derived in considerable part from atmospheric precipitation (Section 4a), large recent changes in the latter (e.g. 'acid rain') are not locally established.

ID(c). HEAVY METALS (C.S. Reynolds)

In my opinion, little can be readily forecast. If there is accentuated planktonic production and deoxygenation in deep water, the redox cycling of iron and manganese may also increase in magnitude, according to well-established interpretations developed for other lakes. Increased sewage loads may also add to the inputs of heavy metals but this will not, presumably, be large while the sewage is primarily domestic. Events in the catchment, quarrying, or any processes accelerating the removal of metals from the catchment itself could be of greater significance and, in view of the levels of Pb, Zn and Cu already received into Windermere, deserve to be monitored in relation to water quality.

IO(d). PHYTOPLANKTON - ENVIRONMENT RELATIONSHIPS (S.L Heaney, C.S. Reynolds)

Some sensitivity to chemical and biological changes, involving phytoplankton, has its foundations in morphometric characteristics. The ratio of epilimnetic to hypolimnetic volumes is such that the lake undergoes interannual changes dependent upon whether mineralization is larger within the epilimnion or hypolimnion. Increasing levels of hypolimnetic oxygen depletion are largely governed by the nature of the dominant algae. The South Basin, and to a lesser extent the North Basin, already show a tendency to produce large summer populations of a particular blue-green alga. It is uncertain, but possible, that the summer dominance of this or functionally equivalent algae will increase.

There is little available information on the role of the sediments for nutrient exchanges within the lake. These may be crucial if sediments are acting as major accumulators for phosphorus and organic matter. If so, conditions may be favoured to more regular blooms of blue-green algae or large flagellates and to more regular and severe anoxia. Such features in turn will lead to a positive feed-back in the form of greater internal loading of nutrients during summer in both the epilimnion (P release from sediments from raising of pH)-and hypolimnion (P release from redox-driven exchanges). If this was to occur other changes are likely to result along the food chain from algae to fishes.

Increasing enrichment could also give rise to future dominance of surface bloom-forming blue-green algae (e.g. species of Anabaena, Aphanizomenon and Microcystis). So far this has not happened and one might wonder why. The salvation of Windermere from such nuisance algae partly lies in its shape and the oceanic climate. During anticyclonic weather daily afternoon winds are a regular feature as the land warms and draws in 'sea breezes', which cause mixing of the surface layers of the lake. This daily mixing during good or bad weather, together with the general lack of well-defined embayments, do not allow these algae sufficient time either to rise or to accumulate at the surface. Such blooms do occur but, so far, have been confined mainly to Mitchell Wyke. On the other hand, the turbulence induced by the daily mixing event is ideal for the non-buoyant blue-green Oscillatoria bourrellyi which often thrives so well, with consequences chemical (nitrate-depletion, deep anoxia) and biological (fish interferences) that can be unwelcome.

Experiences from other Lake District lakes (Lund 1972b, 1978) indicate that dense and often *prolonged* blue-green blooms would cause other, currently prominent, algal species to become less abundant. This could be by immobilizing nutrient resources, generating a shading effect, and raising the pH of the water to levels which apparently select against some algae (including *Dinobrvon*) characteristic of less strongly productive (mesotrophic) lakes. If there was in Windermere such a major compositional change of phytoplankton communities in response to cultural eutrophication, with immediate causal factors probably only indirectly related to increased nutrient availability, there could be far-reaching effects. These could include the turnover and cycling of nutrient resources and, via dominant trophic pathways, zooplankton occurrence and the success of planktivorous fish, especially in their juvenile stages.

10(e). ZOOPLANKTON (D.G. George)

In qualitative terms the zooplankton populations of Windermere have changed little over the past 60 years and are unlikely to change in the forseeable future. In quantitative terms, however, the zooplankton will respond to any changes in-the composition of the phytoplankton. If large 'inedible' algae such as *Oscillatoria* come to dominate the summer crops the biomass of *Daphnia* will correspondingly decline. Preliminary studies suggest that the zooplankton in Windermere is an important source of food for both charr and young fish. More detailed studies are urgently required to document the links between zooplankton production and the year-class strength of planktivorous fish.

10(f). FISH POPULATIONS (C.A. Mills)

The FBA's long study of the perch and pike populations in Windermere has demonstrated that both growth rates and the number of young fish produced in a given year (the year-class strength) are sensitive to changes in abiotic and biotic factors. The principal abiotic factor is temperature, the principal biotic factors are the biomass and size structure of the adult populations, and possibly the availability of food (e.g. zooplankton: see Section 10e above). Attempts to model these relationships have been successful for at least some periods during the study but the influence of unexpected events, notably the 1976 perch disease, makes prediction more difficult.

The limited evidence that is available indicates that the size of the charr populations are sensitive to the number of large adult pike in the lake. The populations of charr in the south basin may also be sensitive to reductions in hypolimnetic oxygen concentrations, but further study is required before the influence of present or future concentrations could be predicted.

11. SUMMARY (J.F. Talling)

1. Windermere, the largest English lake, is divided into two basins which differ in depth, inflow-outflow and water characteristics. This account describes its main characteristics and components, environmental and biological, chiefly from published and unpublished work over 50 years of the Freshwater Biological Association. Emphasis is on the susceptibility to change, where possible assessed quantitatively, and on time scales from hours to millenia.

2. The catchment area of 230.5 km^2 is predominantly of thin and poor soils in uplands, underlain by either hard volcanic rocks or softer slates, with richer alluvium and more intensive grazing in a few major valleys. Since 1900 the resident population has more than doubled, and in summer periods a similar number of visitors raises totals to c. 30 000 40 000. This increased human occupation, combined with sewerage schemes and other technological developments, has produced a large increase of nutrient input to the lake in recent decades.

3(a). The hydrological water balance is summarized. The estimated run-off over 1939-84 averages 431 x 10^6 m yr- , with a range from 110 x 10^6 to 689 x 10^6 m^3 yr^{-1} Combined with a total lake volume of 314.5 x 10^6 m^3 the nominal mean retention time is about 9 months. However values for the two lake basins differ appreciably (shorter retention in the South Basin), and retention times calculated from instantaneous fluxes are extremely variable. The range of water level is about 2 m, with maxima lagging episodes of heavy rainfall.

3(b). Each lake basin regularly acquires a temperature-density layering from net surface heat income during summer, with differentiation into epilimnion, metalimnion (with thermocline), and hypolimnion. Its onset, in April-May, may be slightly delayed by cold windy weather; its loss, the overturn, is accelerated by storms and typically occurs earlier in the shallower South Basin (late-October) than in the deeper North Basin (November-December). An inverse stratification with surface water below 4^0C occurs regularly in cold winters, but rarely with extensive ice-cover offshore. The summer thermocline typically descends with time, but also experiences wind-induced displacements and subsequent oscillations over shorter time-scales of hours or days. Cycles of epilimnetic warming and cooling plus mixing occur over day-night periods in calm weather, and over monthly periods tend to follow the passage of anticyclonic weather conditions. Between-year variability of surface temperature over the period 1933-1975 is illustrated.

3(c). The transfer of kinetic energy from wind to water movements in Windermere can take several forms. The longitudinal or transverse tilt of stratified layers under direct wind-stress is capable of inducing upwelling of deep water by the upwind shore. -Subsequent oscillations of thermocline depth generate horizontal currents in the hypolimnion, estimated as large as 4 cm s^{-1}. Nearer the surface are direct wind-induced currents with direction rotated at depth. In the common situation of wind along the lake's axis, a helical pattern of progressive movement can result. This can lead to sewage effluent into the South Basin being carried transversely across the lake.

3(d). Light penetration is intermediate among Cumbrian lake waters, with a euphotic and photosynthetic layer usually about 10 m deep. It is sensitive to variation of particulate content, including seasonal changes in phytoplankton abundance. Long-term changes are not clearly established; they may include some increase of attenuation between 1920 and 1932 related to planktonic production.

4(a). Windermere water is of low ionic content, with slight increase in the South Basin that can be used to delimit the two water-masses by conductivity measurements.-Seasonal variability of major ionic concentrations is detectable but small. Atmospheric precipitation (bearing sea-salt) is estimated to be the most important source of Na+, K ,Cl and $S0_4$,but with surface weathering predominant for Ca^{2+} ,Mg^{2+} ,and HCO^{-}_3 Over the last 20 years the concentrations of Cl^- and HCO^{-}_3 have markedly increased, the former increase ascribable to use of road-salt in winter, the latter to agricultural liming and to redox reactions consequent on increased biological production. Sewage inputs may be of significance for several major ions.

4(b). Concentrations of the gases oxygen and carbon dioxide show large seasonal changes of biological origin, very roughly in equimolar proportions but in opposite directions. The changes in CO_2 affect several chemical species (free CO_2, HCO^{-}_3 CO_3^{2-}) and are deducible from pH shifts. The highest concentrations occur in either the epilimnion (O_2, by phytoplankton photosynthesis) or the hypolimnion ($C0_2$, by respiration and decomposition). More generally influential are the depletions resulting from largely biological uptake. Those of CO_2, in the epilimnion at times of abundant phytoplankton, drive pH levels above 9.0 in most years from air-equilibrium values of c. 7.3. Those of $C0_2$ occur, with interannual variation, either in the metalimnetic (thermocline) region or in-the--late summer-autumn hypolimnion. During the period 1950-1986 the deep hypolimnetic minima of the North Basin have accentuated (from roughly 70% to 50% saturation); near to complete anoxia has appeared in the South Basin during September-October of several years since 1981, with other chemical correlates.

4(c). Seasonal and interannual changes in concentrations of the major plant nutrient elements C, Si,P and N have been followed in both Windermere basins for one decade (C) or four decades (Si, P, N). Long-term interpretations require attention to some changes in analytical methods. Depletions of all four elements can result from phases of algal growth (for Si, of diatoms); they are typically most severe and prolonged in summer and least in winter. The period of $P0_4$-P depletion, below 1 ug^{-l}, is especially long. Depletion of Si is regularly near-complete after spring diatom growth, but rates of recovery vary thereafter according to river inputs and further episodes of diatom growth. Summer depletions of $N0_3$-N are highly variable, more marked in the last decade, and associated with algal types prone to mass sedimentation. Concentrations of NH_4-N are low for most of the year, but show a discrete maximum by vertical transfer after autumnal mixing. Episodes of carbon depletion, deducible from pH, are often interrupted by weather and species changes. The winter-spring maxima of Si, $P0_4$-P and $N0_3$-N reflect inputs to the lake and have risen over 1945-1986, least for Si and most for $P0_4$-P, especially in the South Basin (x 20 increase). The corresponding changes in total-P concentration appear to have been insignificant, implying shifts in its fractional composition. Besides differences' between basins, there are some spatial differences of $P0_4$-P and NH_4-N within the South Basin related to sewage input.

4(d). Recorded concentrations of Zn, Pb, Cu, Cd, and Hg in the lake water are low (<3 ug 1-1). Recent sediments (deposition of the last

180 years) are enriched in the heavy metals Zn, Pb and Cu, together with more normal contents of Mn and Fe. Current rates of deposition have been measured directly and by accrual to sediment traps; their ratios for Cu and Mn indicate recycling by biological or redox-sensitive processes, which also govern a considerable hypolimnetic cycling of Fe. Vertical transfer by uptake and sedimentation in phytoplankton is probably significant for Cu, but doubtfully for other metals.

4(e). Rough estimates are made of the annual input of phosphorus to the two basins, by summing $P0_4$-P inputs from rivers with those from sewage works calculated using population and generalized per capita values. The estimated loading of 0.91 g P m^{-2} yr^{-1} to the South Basin is heavy and compares with those of highly productive and eutrophic lakes of similar depth; that of the North Basin, 0.28 g P m^{-2} yr^{-1}, is indicative of slight eutrophy. Corresponding recent estimation for nitrogen ~s not possible, but a study for 1937-8 suggested that the lake was a net sink. Nitrate-nitrogen from atmospheric precipitation is a dominant present-day input, of similar magnitude to that in the river output.

5(a). The total quantity of phytoplankton, assessed by estimations of chlorophyll ~ concentration, is typically minimal in winter when solar radiation is least. It develops two main seasonal maxima in the upper layers during spring and summer-autumn. The usual magnitude of 10-35 ug chl-a 1^{-1} is typical of moderately productive lakes. Maxima in the South Basin are usually larger and more extended in time than in the North Basin. Year-to-year differences particularly affect the summer minima and maxima, and sometimes the vertical extent of the spring maximum. There has been a trend to higher concentrations from 1964-86, especially during summer in the South Basin.

5(b). In species composition the phytoplankton undergoes large seasonal changes; the main features are illustrated by the 1965 (South Basin) sequence. General features are: winter minima of most species, spring diatom growth, a late spring-early summer assemblage, a summer phase of diverse and variable composition, and an autumnal period in which diatoms, dinoflagellates, or blue-greens may produce a final growth maximum.

Wash-in of algae from an upstream lake, Esthwaite Water, can influence the sequence. Controlling factors are numerous and their relative importance changes seasonally; included are low light and temperature (winter), silicon depletion (late spring - summer), other nutrients, sedimentation under shallow summer stratification, parasitism by fungi, and grazing by zooplankton. As elsewhere, the seasonal succession often moves towards slow-growing larger algae that are less readily grazed but with some capacity to regulate depth of occurrence.
S(c). In the North Basin, with less nutrient loading, the gross qualitative composition of the phytoplankton has changed little in recent decades. The spring maximum of *Asterionella formosa* has been especially stable. Some other species (e.g. several diatoms, *Anabaena* spp., *Oscillatoria bourrellvi*) have increased significantly, sometimes with modification of seasonal phasing (*Fragilaria crotonensis*).

Sed). Most comments above also apply to the South Basin, although ~ere certain year-to-year changes of species numbers and their environmental correlates have been more pronounced. A selection of 9 species illustrates increase (*Anabaena* spp.), decrease (*Tabellaria flocculosa* var. *asterionelloides*, *Oscillatoria agardhii* var. *isothrix*) or no systematic change over the past few decades. Between-year differences are especially large for the relatively large forms *Oscillatoria bourrellvi* and *Ceratium* spp. These seem to function as major removers of $N0_3$-N from the summer epilimnion; and by subsequent mass sedimentation and decomposition. 0. *bourrellvi* can produce anoxia and nutrient release in the hypolimnion. By contrast, the dominance of most smaller algae probably favours turnover by grazing and mineralisation in the epilimion.

See). The cellular proportion of P in Windermere phytoplankton is variable, and when low can indicate that the element is a potential limiting factor for growth rate. Reduced proportions have developed during spring growth of the dominant diatom *Asterionella formosa*, where the relatively stable maximum populations are known to be mainly limited by Si depletion, and during large summer growths of the blue-green *Oscillatoria bourrellyi*. Such reduction is generally more marked in the North Basin where the initially available concentrations of $P0_4$-P are least. It also varies between years in some correlation to the species representation. Evidence for other limiting factors involves the occasional depletion of inorganic carbon, of low winter temperature for some species, and low winter light conditions before the spring algal increase. The varying summer depletion of inorganic N is unlikely to be a major limiting factor.

6. Neither the crustacean nor rotifer zooplankton has shown marked change in species representation during the last 60 years. Seasonal change in numbers is large in both basins, and, for Crustacea, dominated by a strong May-June maximum of *Daphnia hvalina* var. *galeate*. At this time there is probably a strong grazing pressure on the smaller phytoplankters. There is evidence of between-year variation in the mean summer numbers of Crustacea in the North Basin, partly related to a climatic cycle of temperature affecting the early or late onset of thermal stratification and consequent availability of eligible food algae. About 1970 there was probably some increase in zooplankton biomass.

7. Of some 18 species and subspecies of fish, the trout, eels, charr, perch and pike have been exploited by man for centuries. Population changes of perch and pike have been estimated since 1940, with manipulation by large-scale removals. The population dynamics of these two species, here summarised from 1940-1985, have been influenced by human removal, predation of pike on perch, temperature-dependent control of year-class success from spawning and growth (favoured by warm summers), some cannibalism by older pike and perch, and a catastrophic disease of perch in 1976 with 98% adult mortality. Pike numbers and feeding habits were also affected. A limited recovery of both populations has now occurred. The population changes have been accompanied by strong changes in age- and weight-structure. There is less detailed quantitative information on the charr population, but the catch per unit effort has increased eightfold since 1940, perhaps mainly due to reduced predation by pike. Charr might also be particularly sensitive to possible development of deep anoxia. There is little recent information on the trout and eel populations.

8(a). Counts of total bacterial concentrations by an adequate method are recent and long-term comparisons cannot be made. Examples of counts and related bacterial activity are given for water and sediment from the two basins; such measures are generally higher for the South Basin. In both basins the bacterial population is variable in time and space, horizontally and vertically, the variance showing limited correlation with conventional physical and chemical factors. There is enhanced 'indicator' value in a finer resolution of bacterial types. Thus concentrations of the faecal E. coli and streptococci are highest in areas (e.g. Bowness Bay) where sewage contamination is known or suspected. Still finer resolution of heterogeneity is provided by patterns of single and multiple resistance to antibiotics, which show some relations to human activity on the lake.

8(b). Bottom-living algae occur attached or free on various substrata in littoral areas that receive sufficient illumination. Detailed studies, all prior to 1950, provide information on relative species distribution with season and depth to 6 m, but not on absolute biomass or long-term changes. Numbers are lowest in winter, after which there is a pronounced spring increase; on sediments there are overall mid-year maxima. Light is a major factor for deep-water and probably winter distribution, but other controls (e.g. nutrients, temperature, grazing) are largely unknown.

8(c). Bottom-living animals, all invertebrates, are broadly differentiated into littoral, sub-littoral, and profundal communities. Six newcomers to the littoral have been recorded since 1930, several spreading widely around the lake. Two rare insects are notable. Some changes in the littoral fauna have been related to eutrophication. The community is generally typical of a productive lake, with an exception (liable to disappear) along a steep north-west shore. The sublittoral community was surveyed in 1934-5 but its present status is unknown; it appears to be highly productive and important as a food source for fish. The profunda 1 is dominated by chironomid insect larvae and oligochaete worms. For the latter a recent quantitative survey showed higher average numbers in the South than in the North Basin.

8(d). Wholly or partially submerged macrophytes grow in a depth-range of the littoral with sufficient illumination, most strongly in bays and shallows protected from wave action and with accumulated sediment. Few surveys have been made, especially since 1932. The lower depth limit for rooted species appears to vary, probably in relation to light penetration. In the last decade there has-been an invasion of a form of *Elodea*, the Canadian pondweed, now locally abundant.

8(e). The wildfowl population has been monitored since 1967. Highest total counts were obtained in the winter months, and for four species of duck averaged 2647 from 1978-9 to 1985-6; coot added a further 1168 birds. Later success of the three main breeding species varied. A strong increase in mallard related in part to the end of shooting in 1966 and feeding by tourists. The red-breasted merganser was reduced by a severe decline in a main food-source, the perch. The mute swan has recovered from low numbers during the 1960's. The conservation of these and other aquatic birds of Windermere is affected by loss of lakeshore habitats and disturbance by recreational use, now extending in winter. For goldeneye duck the lake is a major national site.

9. Over the post-glacial history, a record. of chemical and biological changes with time is preserved in the lake sediments. Among these changes, early land-use in the catchment (deforestation for agriculture) was important. The early soils and sediments were relatively base-rich, after which acidic indicators increased following leaching, together with organic matter associated with more biological production. A more recent transition from brown to black sediment, with a rise in the diatom *Asterionella formosa*, marks enrichment associated with increase of human population in the early 1800's. Mining and the minimal industrial development have made little impact, but the most recent sediments show inputs of heavy metals. and radioactive isotopes. A human disturbance of sediments by dredging is also recognisable.

10. The relative sensitivity to change of various components or behaviour patterns is discussed, with reference to general principles, water characteristics and various biological communities. Distinction is made between reversible short-term changes and long-term trends; among the latter are PO_4-P enrichment, some increase in phytoplankton and possibly zooplankton abundance, accentuation of hypolimnetic deoxygenation, and some changes in species representation.

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TABLE 1. WINDERMERE: AREAS ENCLOSED BY CONTOURS

Depth of contour metres	*North Basin* km²	%	*South Basin* km²	%	*Whole Lake* km²	%
0	8·046	100	6·718	100	14·764	100
2	6·943	86	5·630	84	12·573	85
5	6·027	75	4·779	71	10·806	73
10	5·385	67	3·880	58	9·265	63
20	4·343	54	2·658	40	7·001	47
30	3·288	41	1·696	25	4·984	34
35	2·873	36	0·811	12	3·684	25
40	2·454	30	0·107	1·6	2·561	17
45	1·665	21			1·665	11
50	1·022	13			1·022	6·9
55	0·607	8			0·607	4·1
60	0·147	2			0·147	1·0

Windermere is divided naturally into two basins of roughly equal length; for the purpose of the computations, the division between North and South basins is taken as a line from Cockshot Point on the east shore south of Bowness bay, across Belle Isle and projected midway between the Lilies of the Valley islands on to the west shore. In the region of this intersection the depth of water is less than 5 metres. For Windermere, therefore, data are given for each basin separately, and for the whole lake.

(from Ramsbottom 1976)

TABLE 2

Table 2. Population growth in the Windermere Catchment since 1951. (From Census Reports, for Westmorland, Lancashire and Cumbria, as published by HMSO).

Parish	1951	1971	1981
Claife	400	432	492
Hawkshead	633	684	660
Lakes	5 082	5 498	6 789
Windermere	6 580	8 065	8 636
Total	12 695	14 678	16 577

TABLE 3
TABLE 4

Table 3.

Monthly mean surface temperatures, Windermere 1933 to 1975, in degrees centigrade

Year	1933	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Jan	5.3	5.3	6.5	5.0	6.1	5.4	5.8	2.1	2.7	4.0	5.8	6.1	2.7	5.2	4.5
Feb	5.0	5.2	5.9	2.6	5.5	5.0	5.3	2.6	2.7	1.5	5.8	5.1	4.1	5.0	1.5
Mar	5.4	5.0	6.0	4.4	4.4	6.4	5.9	4.2	3.7	3.0	5.8	4.7	5.6	4.3	1.5
Apr	6.8	5.8	6.9	6.0	6.5	7.9	7.1	6.6	5.4	6.2	7.6	7.0	8.2	7.3	4.7
May	10.8	8.8	11.0	11.2	11.4	10.6	10.8	12.6	8.0	9.3	10.7	10.1	10.8	10.5	9.9
Jun	16.7	15.3	14.9	14.8	15.1	13.7	16.4	18.9	15.1	13.9	14.9	13.1	14.1	13.4	15.8
Jul	19.1	19.2	18.3	17.3	16.8	15.6	16.2	16.5	18.7	16.4	16.8	16.4	17.2	16.4	16.8
Aug	16.2	16.3	17.9	16.4	18.7	17.5	17.9	16.4	16.1	15.8	16.3	18.4	17.8	15.4	20.1
Sep	16.4	14.7	14.3	15.5	15.0	14.7	16.3	13.8	15.5	14.3	13.8	13.7	15.7	13.3	16.9
Oct	12.7	11.2	10.5	11.3	12.3	11.3	11.0	10.6	12.4	11.5	11.3	10.4	12.6	11.0	12.7
Nov	8.0	8.0	8.4	8.3	8.4	9.8	8.8	8.2	7.8	8.0	8.8	7.7	9.6	8.6	9.0
Dec	5.5	7.8	6.0	6.6	5.6	7.5	7.1	6.4	7.1	7.3	6.7	6.1	7.2	6.4	6.5

	1948	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Jan	5.7	6.1	6.0	2.9	3.5	3.1	5.1	3.7	4.6	6.0	4.5	2.5	5.2	4.2	3.7
Feb	5.1	5.5	5.0	2.7	2.6	3.2	2.3	2.9	1.9	5.4	3.9	2.0	3.4	5.0	4.5
Mar	5.8	5.6	5.8	3.4	5.2	5.2	4.6	2.6	4.5	7.3	3.1	6.2	5.3	6.4	2.8
Apr	7.6	7.8	6.8	6.1	7.8	7.6	8.5	8.6	8.0	9.0	6.5	8.1	8.1	8.9	6.7
May	12.1	11.7	10.4	9.9	12.8	13.4	11.5	10.0	11.5	12.0	10.2	13.8	12.9	11.9	11.0
Jun	14.4	16.2	16.8	14.7	15.6	16.1	15.0	14.4	14.7	17.5	15.0	16.9	17.8	14.8	14.6
Jul	15.5	18.6	16.8	18.3	17.7	17.7	15.9	20.5	17.0	19.1	17.4	18.6	17.3	16.7	16.1
Aug	16.3	17.4	16.6	17.2	16.8	17.8	15.7	20.4	15.5	17.6	17.2	18.7	17.5	15.9	15.3
Sep	13.8	17.0	13.3	14.7	13.6	14.9	13.8	16.7	14.7	13.8	16.9	17.1	15.8	15.7	14.1
Oct	11.9	13.9	10.7	12.1	9.7	12.7	12.0	11.9	11.8	11.8	12.3	14.2	11.8	12.0	12.1
Nov	9.2	9.0	7.5	8.9	6.3	9.4	9.3	8.7	8.1	8.7	9.4	9.0	8.1	8.3	8.0
Dec	7.5	6.9	3.6	6.7	2.8	7.9	7.2	6.4	8.4	6.7	6.2	6.8	5.9	4.7	4.2

Year	1963	64	65	66	67	68	69	70	71	72	73	74	75
Jan	0.6	3.9	3.8	3.3	4.2	3.7	4.7	2.4	4.1	5.0	5.0	5.7	6.6
Feb	0.0	4.3	3.6	4.1	5.5	2.8	1.9	2.1	4.4	4.1	4.6	5.9	5.4
Mar	3.2	4.6	3.2	5.8	5.8	4.4	2.5	3.1	4.9	5.6	6.2	5.8	5.3
Apr	6.5	6.6	7.1	6.9	7.1	7.4	6.5	5.4	8.3	7.7	7.5	9.2	7.6
May	9.8	10.8	11.3	11.2	9.9	11.0	10.6	12.4	12.8	10.5	11.3	12.3	11.6
Jun	16.0	14.7	15.1	16.8	16.7	17.6	16.8	18.2	14.6	12.7	16.8	16.2	16.9
Jul	16.7	17.3	16.5	18.0	17.8	17.1	17.8	16.6	18.9	17.5	18.3	17.1	18.9
Aug	17.0	17.7	16.3	16.5	17.3	17.7	18.8	17.6	17.7	17.7	18.2	17.0	20.7
Sep	14.3	15.4	14.0	15.2	15.1	15.6	16.1	14.6	16.3	15.2	16.0	14.2	15.6
Oct	11.8	11.9	12.3	12.7	11.5	12.7	13.1	11.7	12.7	12.2	11.6	9.8	11.2
Nov	9.3	8.8	7.4	8.2	7.7	8.3	8.1	8.2	8.0	8.7	8.0	7.3	8.4
Dec	4.3	5.4	4.6	5.9	5.4	5.9	4.6	6.1	6.7	6.3	5.5	6.7	5.9

Table 4. *Frequency distributions of monthly mean surface water temperatures*

Windermere 1933 to 1975

Degrees centigrade	*Jan*	*Feb*	*Mar*	*Apr*	*May*	*Jun*	*Jul*	*Aug*	*Sept*	*Oct*	*Nov*	*Dec*
20.0–20.9							1	3				
19.0							3	0				
18.0						2	9	6				
17.0						3	13	18	2			
16.0						13	14	10	8			
15.0						8	3	6	12			
14.0						12			12	1		
13.0					2	4			9	2		
12.0					8	1				16		
11.0					13					18		
10.0					13					4		
9.0				2	5					2	10	
8.0				8	2						26	1
7.0			1	15							6	9
6.0	7		5	14							1	17
5.0	13	17	16	3								9
4.0	8	7	10	1								5
3.0	8	4	7									1
2.0	6	10	3									1
1.0	0	4	1									
0.0–0.9	1	1										
	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*	*Jul*	*Aug*	*Sept*	*Oct*	*Nov*	*Dec*

(both Tables from Kipling & Roscoe 1977)

TABLE 5. Mean concentrations (μequiv. l^{-1}) of major ions in surface waters of twenty-four lakes and tarns, 1974–78. *n* is the range of the number of determinations on individual ions (From Sutcliffe et al. 1982).

Lake	Total anions*	Total cations†	pH	Na^+	Cl^-	Ca^{2+}	Mg^{2+}	K^+	Alk	SO_4^{2-} + NO_3^-	SO_4^{2-}‡	NO_3^-‡	Sampling period	*n*
Group 1														
1. Levers Water	275	264	4.7	135	153	43	57	9	−16§	138	101	30	Aug 74–Mar 78	44–64
2. Buttermere	342	336	6.2	160	192	118	51	7	48	102	91	9	Apr 74–Jul 76	25–29
3. Blea Tarn	348	340	6.3	145	154	142	46	7	57	137	123	7	May 74–Jan 78	82–131
4. Thirlmere	356	357	6.5	159	175	148	42	8	50	131	112	13	May 74–Jul 76	24–28
5. Wastwater	357	358	6.7	172	186	114	62	10	50	121	101	18	Apr 74–Jul 76	28–32
6. Ennerdale Water	368	369	6.5	187	208	100	72	10	42	118	102	15	Apr 74–Jul 76	26–30
7. Crummock Water	379	389	6.6	181	215	126	73	9	43	121	106	13	Jan 75–Jul 76	15–17
8. Goats Water	392	383	6.4	167	190	127	78	11	34	168	128	34	May 74–Apr 76	17–19
Group 2														
9. Haweswater	485	487	6.8	148	155	249	78	12	175	155	142	15	May 74–Nov 75	18–21
10. Grasmere	487	487	6.8	184	191	237	56	10	141	155	138	17	Jun 74–Feb 78	77–119
11. Rydal Water	505	505	6.8	193	200	240	60	12	156	149	135	13	Apr 74–Jun 76	47–85
12. Derwentwater	511	520	6.7	220	298	236	55	9	98	115	109	8	Apr 74–Jul 76	25–28
13. Brotherswater	550	548	6.7	195	197	276	68	9	188	165	157	12	Jul 74–Jul 76	22–24
14. Ullswater	555	564	7.0	172	178	293	87	12	231	146	136	11	May 74–Jul 76	26–30
* 15. Windermere (N)∮	608	611	7.0	202	222	314	81	14	204	182	157	24	Apr 74–Mar 78	79–122
16. Coniston Water	640	644	6.9	220	259	318	91	15	178	203	183	22	May 74–Jul 76	27–31
Group 3														
* 17. Windermere (S)∮	677	683	7.1	219	242	355	92	17	236	199	171	25	Apr 74–Feb 78	84–123
18. Bassenthwaite Lake	681	690	6.9	251	309	310	111	18	189	183	147	16	Apr 74–Jul 76	22–25
19. Loweswater	693	708	6.9	266	321	291	130	21	175	197	171	30	Apr 74–Jul 76	25–29
20. Blelham Tarn∮	930	926	7.0	222	248	542	136	26	403	279	242	34	May 74–Mar 78	64–90
21. Esthwaite Water∮	933	923	7.1	249	282	526	123	25	386	265	231	31	May 74–Feb 78	67–93
Tarns on Claife Heights														
22. Hodsons	650	650	6.7	251	295	276	113	10	122	233	—	—	Sep 74–Nov 75	11–15
23. Wise Een	652	641	6.9	210	245	328	91	12	197	210	—	—	Aug 74–Nov 75	12–16
24. Wraymires	654	658	6.8	213	248	337	96	12	202	204	—	—	Aug 74–Nov 75	12–16

* Sum of means for Cl^-, SO_4^{2-} + NO_3^- and Alk.

† Sum of means for Na^+, K^+, Ca^{2+} and Mg^{2+} (and 20 μequiv. l^{-1} H^+ for Levers Water).

‡ Values for *n* are given in Table 17.

§ Positive acidity (mean) determined by Gran titration.

∮ Integrated tube samples (see Methods).

TABLE 5

TABLE 6
TABLE 7

TABLE 6. Estimated annual inputs and outputs of major ions on the Windermere catchment in 1975 and 1976, showing inputs via precipitation and outputs via discharge from Windermere South Basin

	Precipitation at Wraymires		Precipitation on catchment	Windermere S.B. discharge		Total amounts pptn/disch. (%)
Ion	Concentration (μequiv. l^{-1}) (1)	Amount (equiv. 100 m^{-2}) (2)	Total amount (equiv. × 10^6) (3)	Concentration (μequiv. l^{-1}) (4)	Total amount (equiv. × 10^6) (5)	(3)/(5)
Na^+	86	13.8	38	219	80	48
K^+	5–8	0.8–1.3	2–4	17	6	50
Ca^{2+}	30	4.8	13	355	130	10
Mg^{2+}	20	3.2	9	92	34	26
H^+	40	6.4	18	< 0.1	(0.04)	—
NH_4^+	33–36	5.3–5.8	15–16	*c.* 1	0.3	—
Cl^-	100	16.0	44	242	88	50
NO_3^-	22	3.5	10	25	9	110
SO_4^{2-}	95	15.2	42	171	62	68
Alk	nil	—	—	236	86	—
Anions	217	34.7	96	674	245	39

(1) Means for two years (Sutcliffe *et al.*, 1982; Sutcliffe & Carrick, 1983); NH_4^+ estimated to balance the sum of anions.

(2) Estimates for Wraymires Hatchery; average annual rainfall 160 cm (1975–76).

(3) Entire catchment (230 km^2); average annual rainfall from Wraymires × 1.2.

(4) Means from Sutcliffe *et al.* (1982, Table 13).

(5) Average discharge 365 m^3 × 10^6 $year^{-1}$ in 1975–76.

TABLE 7. Estimated inputs of sodium chloride to Windermere from deicing salt and treated sewage effluents and the concentrations expected for the range of discharge from the catchment in 1972–81

	Source		
	Deicing salt		Treated sewage
NaCl inputs (tonnes)	1872	1000	222
Amounts of Na^+ and Cl^- (equiv. × 10^6)	32.0	17.1	3.8*
Discharge from Windermere (m^3 × 10^6 $year^{-1}$)	291–500	291–500	291–500
Lakewater concentrations of Na^+ and Cl^- (μequiv. l^{-1})	110–64	59–34	13–8

*Based on mean concentrations (μequiv. l^{-1}) in Grasmere treated sewage effluent: Na^+, 1078; Cl^-, 765.

(both Tables from Sutcliffe & Carrick 1983a)

Table 8. Annual depositional fluxes of elements in the South Basin of Windermere (in µg cm^{-2}) and the ratios between the amounts recovered in sediment traps and from the bottom deposits. (From Hamilton-Taylor et al. 1984).

Element	A: Sediment Trap (1980-1981)	B: Bottom Deposits	Ratio A:B
Mn	5 300	650	8.6 (± 2.7)
Fe	2 620	2 300	1.1 (± 0.3)
Al	1 540	2 600	0.6 (± 0.2)
Zn	35.9	24.4	1.5 (± 0.5)
Cu	28.6	3.0	9.5 (± 2.9)
Pb	17.7	12.5	1.4 (± 0.4)
C	12 500	7 100	1.8 (± 0.5)
N	1 830	570	3.2 (± 1.6)

TABLE 9

Table 9. Major annual inputs of soluble reactive phosphorus into Windermere.

(a) North Basin

1) Blelham Tarn outflow (Blelham Tarn)

$$\text{mean winter concentration } (\mu g\ l^{-1}) \times \text{number of weeks} \times \frac{\text{volume of tarn } (m^3)}{\text{retention time (weeks)}}$$

$$12.4 \times 20 \times \frac{0.693 \times 20^6}{6.5}\ (\mu g) = 26.5\ kg$$

2) River Rothay (Grasmere)

$$7.18 \times 22 \times \frac{5.0 \times 10^6}{5.3}\ (\mu g) = 149\ kg$$

3) River Brathay (Elterwater)

(as (2) x 0.5) = 75 kg

4) Ambleside sewage works

residents

2800 x 1.8 g x 365 days (g) = 1840 kg

resident visitors

2200 x 0.9 g x 48 days (g) = 95 kg

day visitors

2500 x 0.9 g x 135 days (g) = 306 kg

total = 2241 kg

Assume 88% passes through sewage works;

then input to lake = 1972 kg

Combined annual inputs (1 - 4) into North Basin

= 2223 kg or 0.28 $g\ m^{-2}\ yr^{-1}$

(b) South Basin

1) Cunsey Beck (Esthwaite Water)

$$\text{mean winter concentration } (\mu g\ l^{-1}) \times \text{number of weeks} \times \frac{\text{volume of lake}}{\text{retention time (weeks)}}$$

$$10.4 \times 20 \times \frac{6.4 \times 10^6}{13}\ (\mu g) = 102.4\ kg$$

2) Windermere Tower Wood sewage works

residents

8575 x 1.8 g x 365 days (g) = 5633.8 kg

resident visitors

6425 x 0.9 g x 48 days (g) = 277.6 kg

day visitors

7500 x 0.9 g x 136 days (g) = 918.0 kg

total = 6829 kg

Assume 88% passes through sewage works;
then input to lake = 6010 kg.

Combined annual inputs (1 + 2) into South Basin
= 6112 kg P or 0.91 g m^2 yr^{-1}

TABLE 10

Table 10. Preliminary classification table for the assessment of trophic state in lakes in the OECD eutrophication program. Trophic state is assigned based on the opinion of the investigator of each lake. Linear Averages and Standard Deviations.

From Vollenweider and Kerekes (1980), with categories appropriate to Windermere basins marked † (South Basin) and ‡ (North Basin)

Variable (Annual mean values)	Oligotrophic	Mesotrophic	Eutrophic
Total phosphorus $\mu g\ l^{-1}$	‡ mean = 8.6 ± 3.69 N = 20 range = 3 - 16.1	† 25.1 ± 16.33 N = 18 5.6 - 80	113. ± 89.4 N = 73 8.8 - 386
Total nitrogen $\mu g\ l^{-1}$	775 ± 476 N = 11 306 - 1630	798 ± 364 N = 7 361 - 1387	2367 ± 1536 N = 38 300 - 6100
Chlorophyll a $\mu g\ l^{-1}$	1.8 ± 0.92 N = 21 0.2 - 3.6	†‡ 5.2 ± 2.46 N = 16 2.2 - 11.0	19.1 ± 15.87 N = 72 2 - 78
Chlorophyll a maximum value $\mu g\ l^{-1}$	4.62 ± 1.96 N = 15 1.3 - 8.6	‡ 16.0 ± 6.44 N = 11 5.9 - 24.8	† 63.7 ± 61.34 N = 46 9.5 - 275.
Secchi depth m	11.1 ± 6.95 N = 13 5.4 = 28.0	‡† 4.8 ± 2.25 N = 21 1.9 - 8.1	2.84± 1.64 N = 79 0.8 - 7.0

TABLE 11

TABLE 12

Table 11. The planktonic rotifers of Windermere. Nomenclature after Ruttner-Kolisko (1974).

Ascomorpha ovalis
Asplanchna priodonta
Collotheca libera
Collotheca mutabilis
Collotheca pelagica
Conochilus unicornis
Conochilus hippocrepis
Euchlaris lyra
Filissia longiseta
Gastropus stylifer
Gastropus hyptopus
Kellicottia longispina
Keratella cochlearis
Keratella quadrata
Lecani luna
Lepadella ovalis
Notholca foliacea
Notholca squamula
Ploesoma hudsoni
Polyarthra vulgaris
Synchaeta grandis
Synchaeta pectinata
Synchaeta tremula
Trichocerca capucina
Trichocerca porcellus
Trichocerca pusilla
Trichocerca rousseleti
Trichocerca similis

Table 12. The planktonic crustacea of Windermere.

	Gurney 1923	Wailes 1939	Smyly 1968
Bosmina coregoni var. obtusirostris	*	*	*
Bythotrephes longimanus	*	*	*
Ceriodaphnia pulchella	*	*	*
Daphnia hyalina var. galeata	*	*	*
Diaphanosoma brachyurum	*	*	*
Holopedium gibberum	*	*	-
Leptodora kindti	*	*	*
Cyclops leuckarti	*	*	*
Cyclops strenuus abyssorum	*	*	*
Diaptomus gracilis	*	*	*
Diaptomus laticeps	-	*	*

Table 13. The impact of fishing on Windermere fish populations (adapted from Le Cren, Kipling & McCormack 1972).

Specific activity	Species caught	Quantity removed (tonnes)	Duration of fishery	Impact
Mediaeval food fishery	all	Not more than 5 t $year^{-1}$	up to 1500	Not much
Shore seine fishery	all	5-10 t $year^{-1}$	1500-1920	Mid-19th century charr were overfished. Netting suspended for 5 years and stock recovered.
Semi-commercial angling	charr, trout	2 t $year^{-1}$	after 1830	New fishing techniques used from 1830 contributed to overfishing of charr. These were banned in 1884.
Sport fishery (trout)	trout	less than 1 t $year^{-1}$	Intensified after 1850	Little or none
Sport fishery (coarse fish)	perch, pike	1 t $year^{-1}$	Intensified after 1850	Little or none
Long line fishery	pike, eels	1 t $year^{-1}$	up to 1950	Not much
F.B.A. trapping	perch	100 t between 1941-47	1941-47	Possibly more zooplankton available to charr. Pike predation more intense on smaller population of perch.
F.B.A. trapping	perch	1 t $year^{-1}$ average	1948-76	Little or none
F.B.A. netting	pike	1 t $year^{-1}$ average	1944-76	Reduction in pike longer than 55 cm has reduced predation on spawning charr. North basin charr catches increased eight fold.

TABLE 14

Table 14. Mean values and ranges of bacteriological and related variables from Windermere water and sediment samples, taken during the period 1975-1985.

Variable		North Basin	South Basin
Water column (epilimnion)			
Viable or Plate counts	(l^{-1})	1.5×10^{6}	2.0×10^{6}
Direct counts	(l^{-1})	1.8×10^{9}	2.3×10^{9}
Phosphatase activity			
(µmol PO_4 released l^{-1} d^{-1})		0.64	0.97
Sediment			
Viable or Plate counts	(g^{-1} dry wt)		
Aerobes		5×10^{6}	5×10^{6}
Anaerobes		10×10^{6}	20×10^{6}
Direct counts	(g^{-1} dry wt)	$6-7\times10^{10}$	$5-12\times10^{10}$
Chlorophyll *a*	(µg l^{-1})	55-135	140-240
ATP biomass	(µg g^{-1})	4-14	10-24
Depth of 0.2 V isovolt	(mm)	12-16	10-16
Sediment % C		8	10
% N		0.75	1.0
Electron transport activity			
(equiv. as mg O_2 g^{-1} h^{-1}		2.5-4.0	3.0-6.0

TABLE 15

Table 15. Incidence of antibiotic resistance in bacteria from Windermere (South Basin, 1985) lake water and the sewage effluent (from Jones et al. 1986).

$\%^r$ to n antibiotics

Site/bacterial groups	No. of isolates examined	n						Antibiotic resistance index (ARI)[a]
		0	1	2	3	4	>4	
Windermere lake water								
Faecal streptococci	100	36	52*	10	2	0	0	0.13
Total coliforms[b]	179	42	34	22*	2	1	0	0.14
Citrobacter spp	8	38	50	13	0	0	0	0.13
Enterobacter spp	20	55	25	20	0	0	0	0.11
Klebsiella spp	117	38	34	25	3	1	0	0.16
Other coliforms	37	51	32	16	0	0	0	0.11
Escherichia coli	150	11	57	19*	4	6	3	0.25
Pseudomonas spp.	85	0	5	72	13	11	0	0.38
Other aquatic bacteria	102	33	48*	10	4	4	1	0.17
Sewage effluent								
Faecal streptococci	100	32	37	19	10	2	0	0.19
Total coliforms[b]	167	62	29	8	1	0	0	0.08
Citrobacter spp	10	30	60	10	0	0	0	0.13
Enterobacter spp	24	64	36	0	0	0	0	0.11
Klebsiella spp	96	72	20	8	0	0	0	0.06
Other coliforms	33	58	27	12	3	0	0	0.10
Escherichia coli	100	33	53	7	5	2	0	0.15
Pseudomonas spp	58	0	19*	59	10	12	0	0.35
Other aquatic bacteria	100	72	25	3	0	0	0	0.05

---

* Indicates significant difference between $\%^r$ at the two sites at the 5% level.

[a] ARI is the overall proportion of resistance to the antibiotics in the population. If all isolates were resistant to all antibiotics the value of ARI would be 1.

[b] Excluding *Escherichia coli*.

Table 16. Percentage resistance to selected antibiotics in bacteria from Windermere and the sewage effluent (from Jones et al. 1986).

Site/bacterial groups	No. of isolates examined	$\%^r$					
		Ap	Cm	Cx	Em	Ot	Sm
Windermere lake water							
Faecal streptococci	100	0	0	16	1	6	55*
Total coliforms[a]	179	31***	1	5	42	3	2
Citrobacter spp.	8	0	0	0	50	25	0
Enterobacter spp.	20	15	0	10	35	5	0
Klebsiella spp.	117	41***	1	5	44**	2	3
Other coliforms	37	19	0	3	38	3	3
Escherichia coli	150	11	5	25*	71*	23**	13
Pseudomonas spp.	85	100	20	27	83*	0	0
Other aquatic bacteria	102	54***	10**	14***	10**	1	11**
Sewage effluent							
Faecal streptococci	100	0	1	51***	4	20**	37
Total coliforms[a]	167	10	0	1	32	4	1
Citrobacter spp.	10	0	0	0	60	20	0
Enterobacter spp.	24	4	0	0	63	0	0
Klebsiella spp	96	13	0	0	23	1	0
Other coliforms	33	12	0	6	30	9	3
Escherichia coli	100	7	1	11	57	5	9
Pseudomonas spp.	58	98	17	26	71	0	3
Other aquatic bacteria	100	5	1	1	2	22***	0

---

* ** *** Indicate significant differences between $\%^r$ at the two sites at the 5%, 1% and 0.1% levels, respectively.

Ap, Ampicillin; Cm, chloramphenicol; Cx, Cotrimoxazole; Em, erythromycin; Ot, oxytetracycline; Sm, streptomycin.

[a] Excluding *Escherichia coli*.

TABLE 17

Table 17. Incidence of multiple antibiotic resistance in 1148 bacteria from Windermere lake water (South Basin 1985) and the sewage effluent (from Jones et al. 1986).

Site/bacterial groups	Percentage of the isolates in which the multiple resistance was found
Windermere lake water	
Faecal streptcocci	(CxSm 8%,OtSm 5%)[a]
Total coliforms[b]	ApEm 19%
Citrobacter spp.	EmOt 13%
Enterobacter spp.	CxEm 10% (ApEm 5%,EmOt 5%)
Klebsiella spp	ApEm 25%
Other coliforms	ApEm 14%
Escherichia coli	EmOt 16%, CxOt 11%,EmSm 11%, OtSm10%, CxEm 10% (EmOtSm 9%,CxEmOt 7%,ApEmOt 6%,ApEmSm 6%, ApOtSm 5%)
Pseudomonas spp.	ApEm 82%,ApCx 27%,CxEm 15%,CmCx 15%, CmEm 14% ApCxEm 15%,ApCmCx 15%,ApCmEm 14%,CmCxEm 11%
Other aquatic bacteria	(ApEm 8%,CxSm 8%,ApCm 6%,CxEm 6%, CmEm 6%)
Sewage effluent	
Faecal streptococci	CxSm 25%,OtSm 15%, CxOt 13%,CxOtSm 11%
Total coliforms[b]	(ApEm 6%)
Citrobacter spp.	EmOt 10%
Enterobacter	Incidence < 5%
Klebsiella spp.	(ApEm 7%)
Other coliforms	(ApEm 6%)
Escherichia coli	(CxEm 7%,CxSm 5%)
Pseudomonas spp	ApEm 69%,ApCx 26%,ApCm 17%,CxEm 17%, CmCx 14% CmEm 12%, ApCxEm 17%, ApCmEm 12%,ApCmCx 14%, CmCxEm 10%
Other aquatic bacteria	Incidence < 5%

---

[a] Values in parentheses are > 5% and < 10% incidence.
Ap, ampicillin; Cm, chloramphenicol; Cx, cotrimoxazole; Em, erythromycin; Ot, oxytetracyline; Sm, streptomycin.

[b] Excluding *Excherichia coli*.

TABLE 18

Table 18. The pool of antibiotic resistance in the bacterial population in Windermere lake water (from Jones et al. 1986).

Bacterial group	Population size range (bacteria/l)	Antibiotic resistance index (ARI)
Faecal streptococci	$5 \times 10^0 - 1.5 \times 10^2$	0.13
Total coliforms	$1 \times 10^2 - 5 \times 10^3$	0.14
Escherichia coli	$1 \times 10^0 - 1 \times 10^3$	0.25
Pseudomonas spp.	$1 \times 10^4 - 1 \times 10^5$	0.38
Other aquatic bacteria	$5 \times 10^6 - 5 \times 10^7$	0.17

TABLE 19

Table 19. Summary of present characteristics of Cumbrian lakes, including Windermere South Basin (W'mS.) and North Basin (W'mN.), with reference to human population, current rates of sediment deposition, and oxygen concentration in the summer hypolimnion (from Pennington 1978).

		Variables												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Lakes														
1	Esth.	1.0	15.5	1239	0.9	127	19.9	9.1	1.30	3.7	0.54	16.6	2.8	0
2	Blel.	0.1	15.1	1000	0.7	164	11.4	17.4	1.00	4.1	0.27	14.3	1.2	0
3	Gras.	0.6	21.5	1550	0.5	122	5.8	10.6	0.43	3.4	0.16	16.5	0.8	0
4	Lowe.	0.6	16.0	156	0.5	70	3.2	6.1	0.31	3.0	0.28	21.6	1.0	0
5	W'mS.	6.7	42.0	1197	0.4	87	7.1	6.2	0.57	3.1	0.20	13.3	1.0	22
6	W'mN.	8.1	64.0	651	0.6	73	8.7	8.6	0.79	2.2	0.23	20.0	1.3	62
7	Ulls.	8.9	62.5	87	0.4	77	6.1	5.4	0.46	2.6	0.17	17.4	2.1	65
8	Enn.	3.0	45.1	11	0.1	87	1.6	6.0	0.12	1.6	0.03	18.5	0.3	85
9	Wast.	2.9	78.6	17	0.2	89	2.7	5.5	0.20	1.8	0.06	19.5	0.6	90

Variables: 1 = lake area, km^2; 2 = max. depth, m; 3 = population, per km^2 lake area; 4 = sediment, cm/yr; 5 = mg/g C; 6 = mg C/cm^2/yr; 7 = mg/g N; 8 = mg N/cm^2/yr; 9 = mg/g P; 10 = mg P/cm^2/yr; 11 = mg/g K; 12 = mg K/cm^2/yr; 13 = min. oxygen saturation, %.

FIG. 1

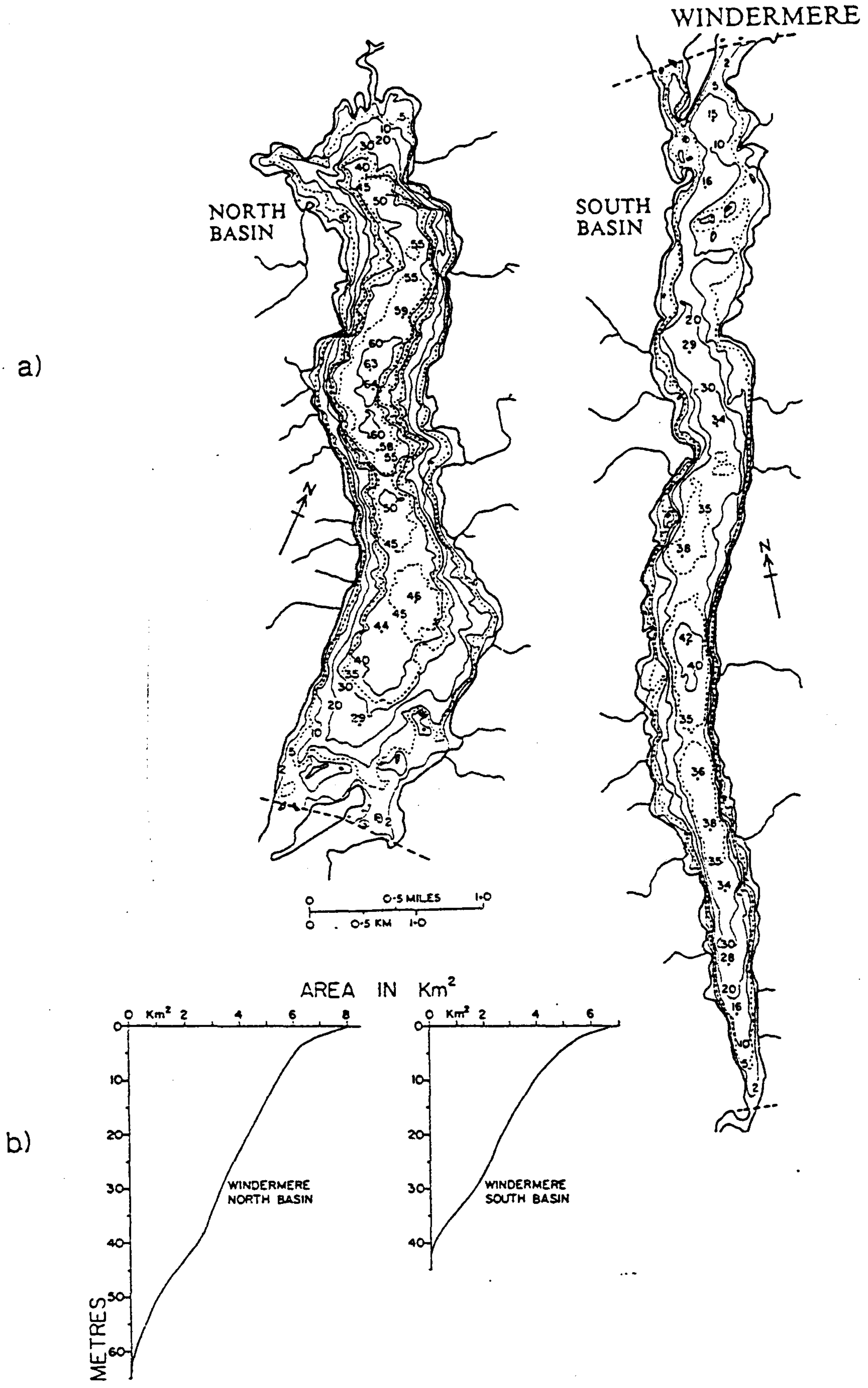


Fig. 1. Bathymetry of the two Windermere basins: (a) depth contours(m), with some additional median soundings (b) hypsographic (area-depth) profiles. From Ramsbottom (1976).

FIG. 2

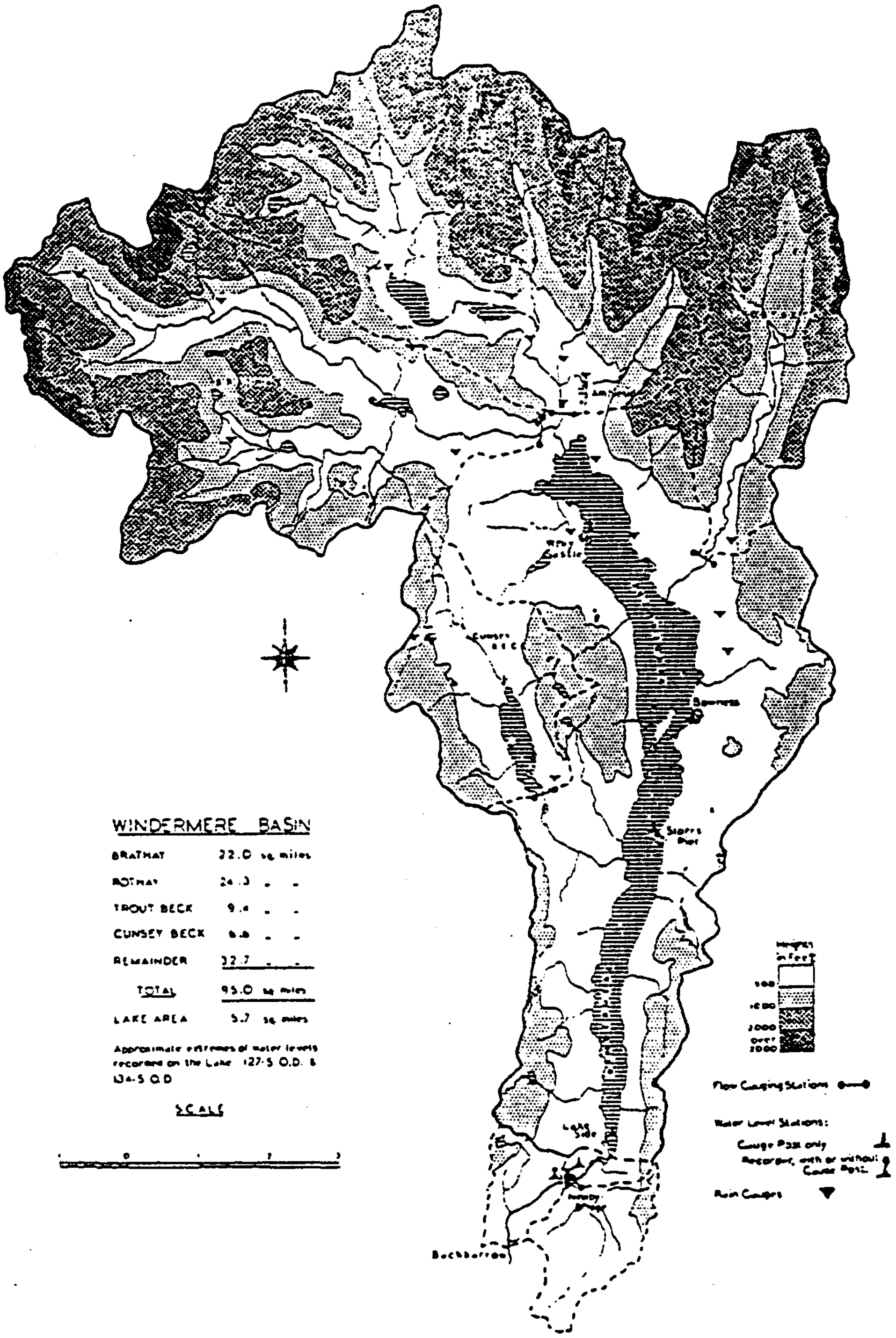


Fig. 2. The Windermere catchment, showing drainage sectors and surroundin uplands. From McClean (1940).

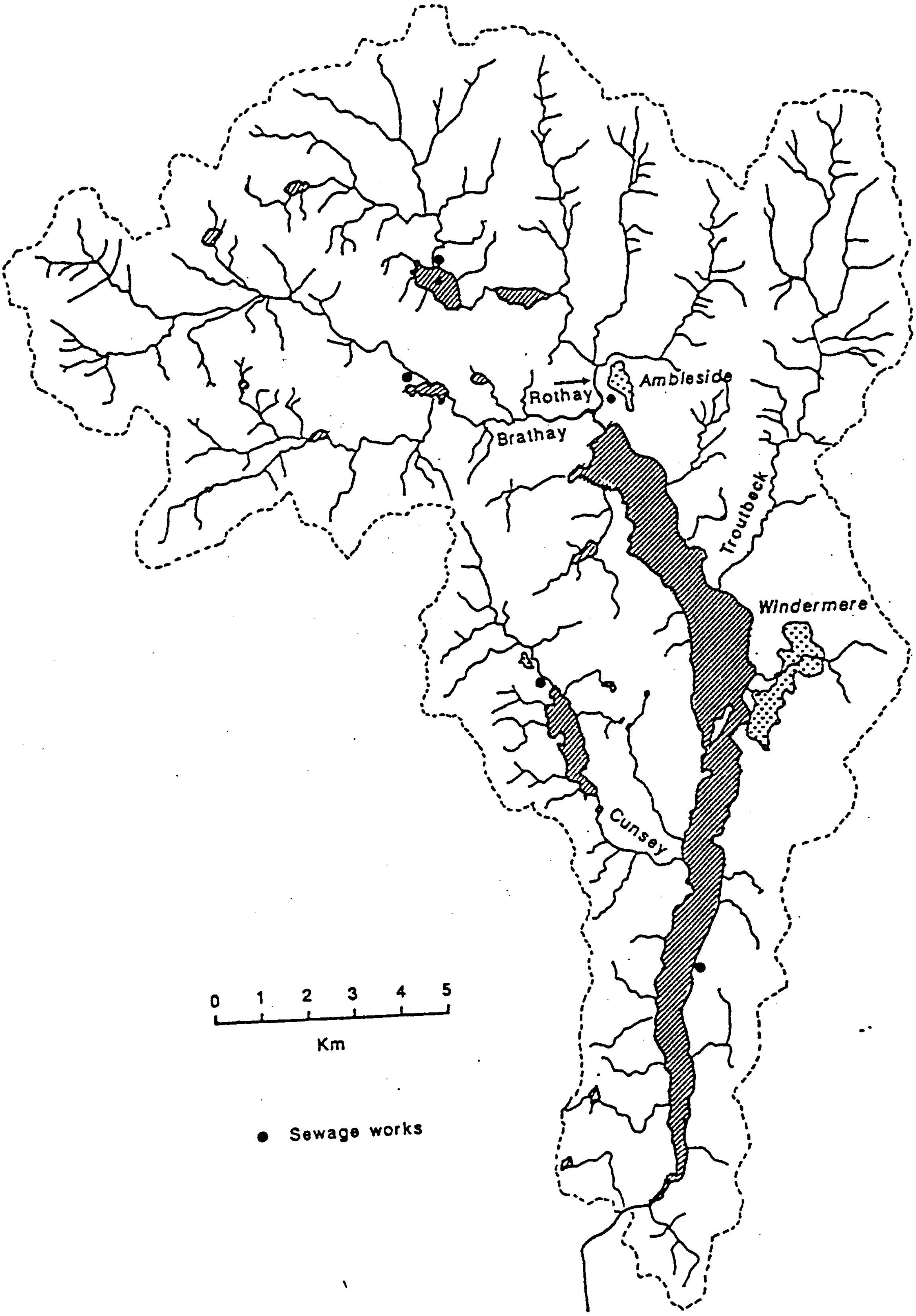


Fig. 3. River and stream drainage in the Windermere catchment, with locations of sewage works.

FIG. 4

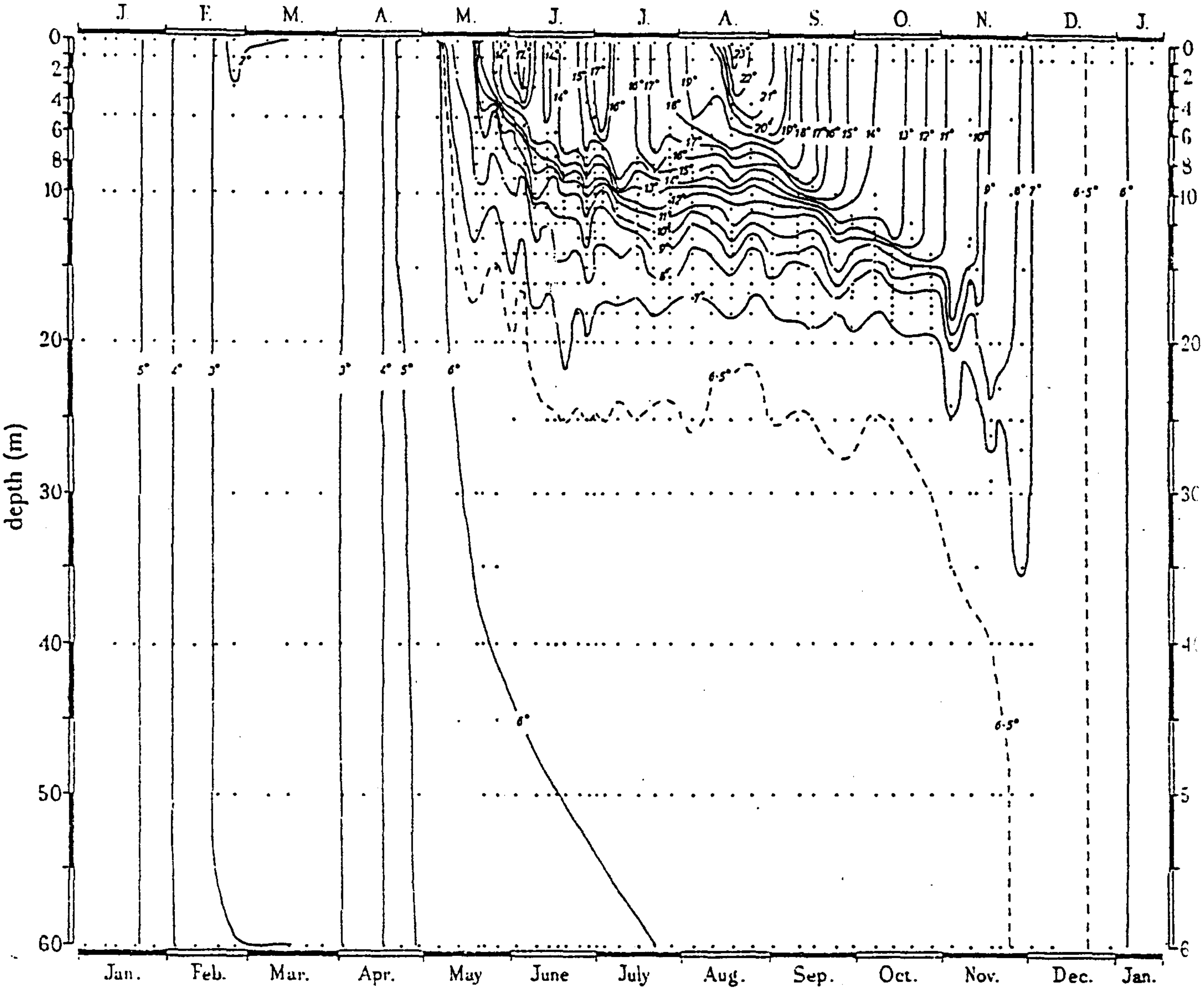


Fig. 4. North Basin: distribution of temperature, shown by isotherms in °C, with depth and season during 1947. From Lund et al. (1963).

FIG. 5

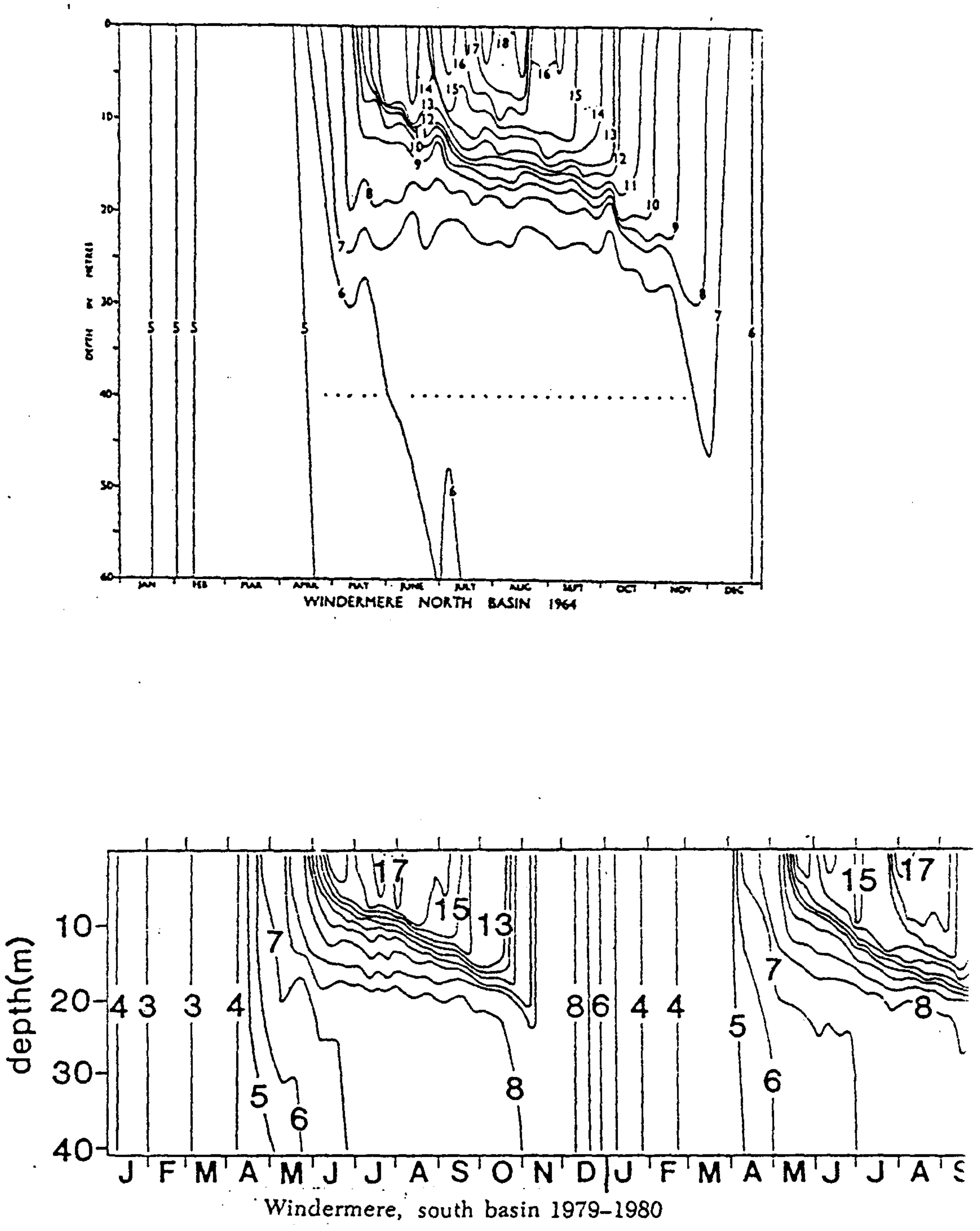


Fig. 5. Comparative depth-time distributions of temperature (isotherms in °C) in the two Windermere basins. From Talling (1965) (North Basin) and Reynolds et al. (1982a) (South Basin).

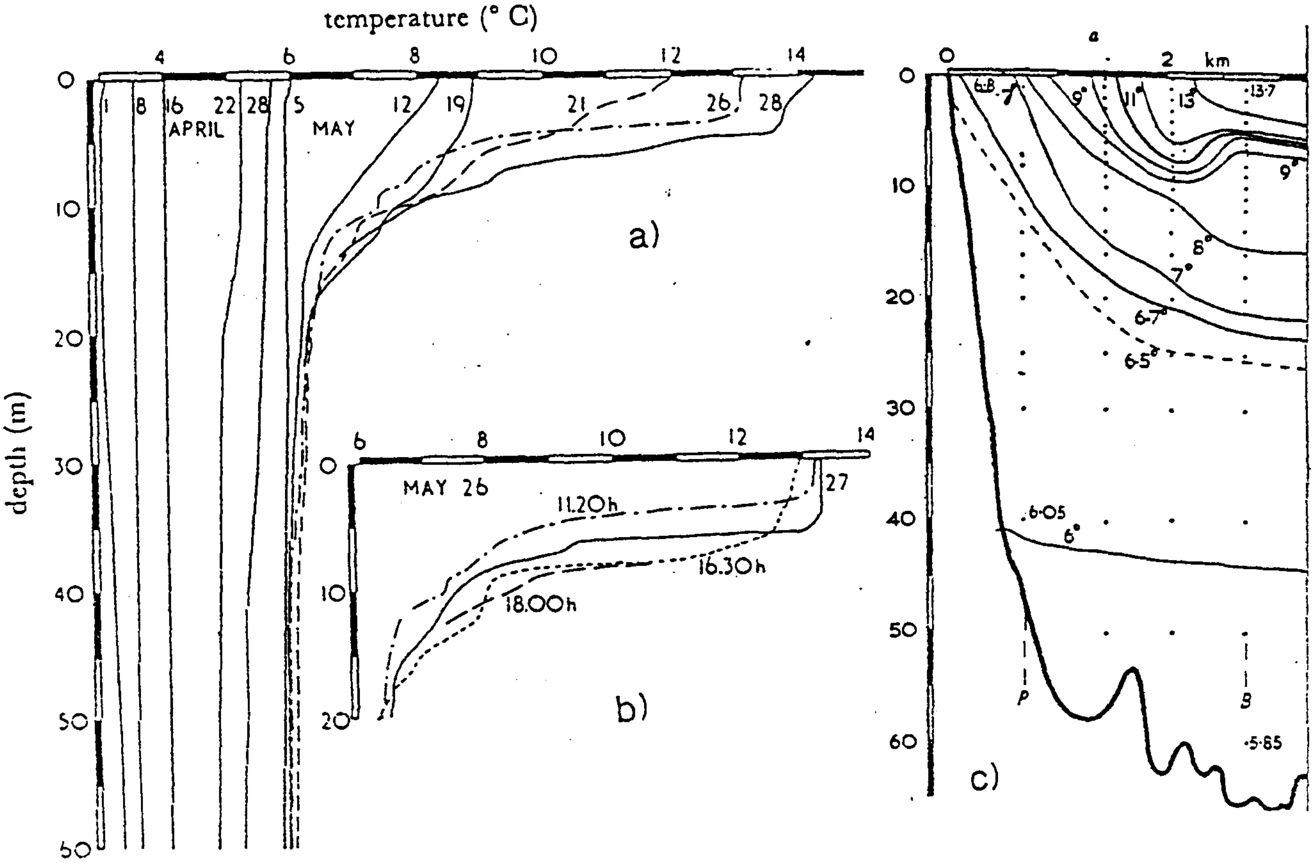


Fig. 6. Variability of temperature stratification in the North Basin, as (a) surface warming and thermocline development during April-May 1947 (b) short-term vertical shifts in thermocline depth on 26 May 1947 (c) upwelling of cold hypolimnetic water off the northern shore on 9 June 1947. From Mortimer (1952).

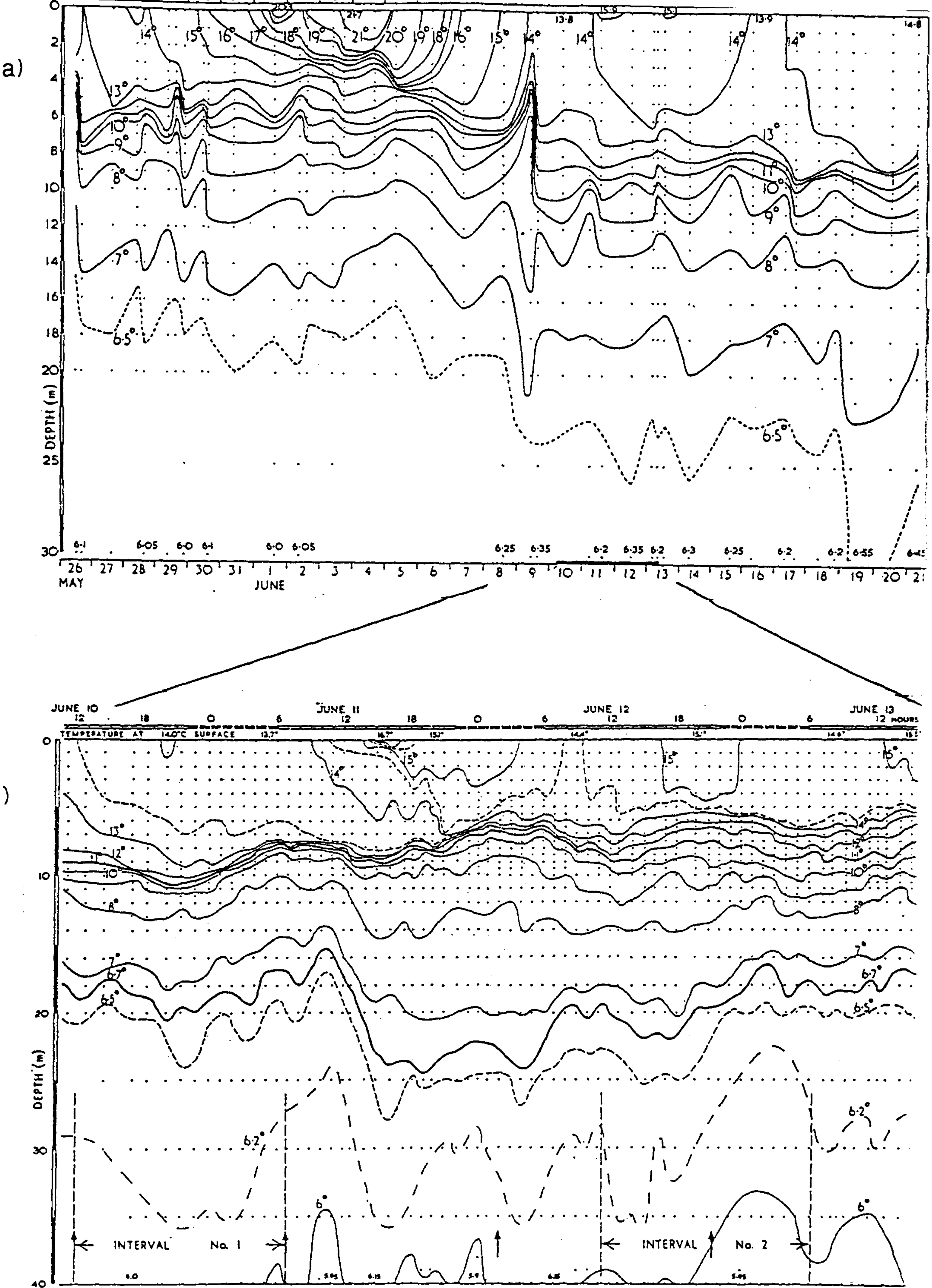


Fig. 7. Short-term variability of thermal stratification, on (a) the day-to-day scale and (b) hour-to-hour scale, in the North Basin during May-June 1947. From Mortimer (1952).

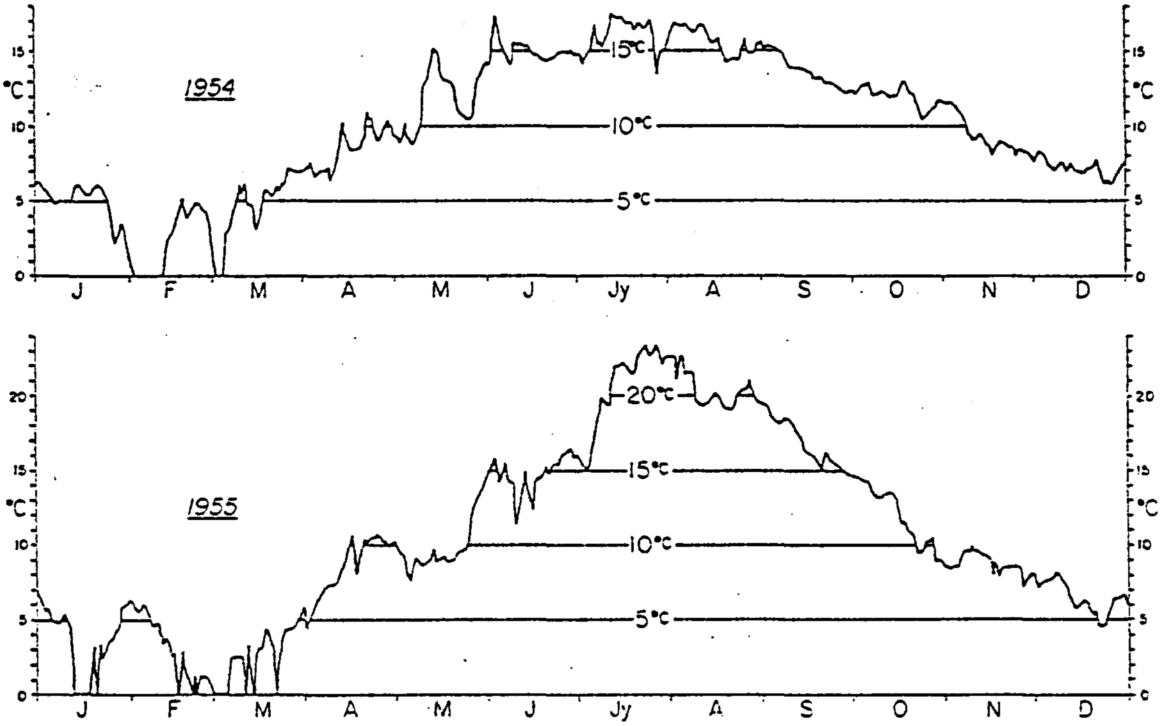
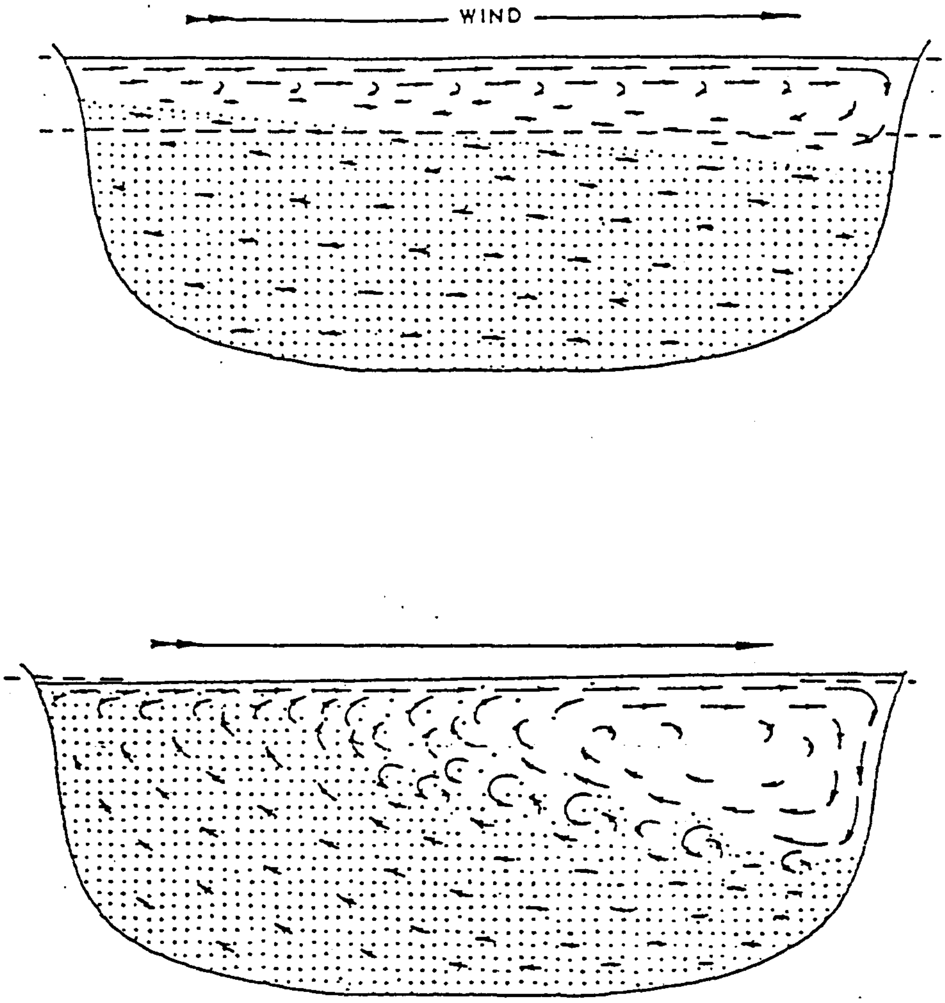


Fig. 8. Seasonal variation of surface water temperature, measured daily at a shore location, during consecutive years with unusually cool (1954) and unusually warm (1955) summers. From Kipling & Roscoe (1977).

a)



b)

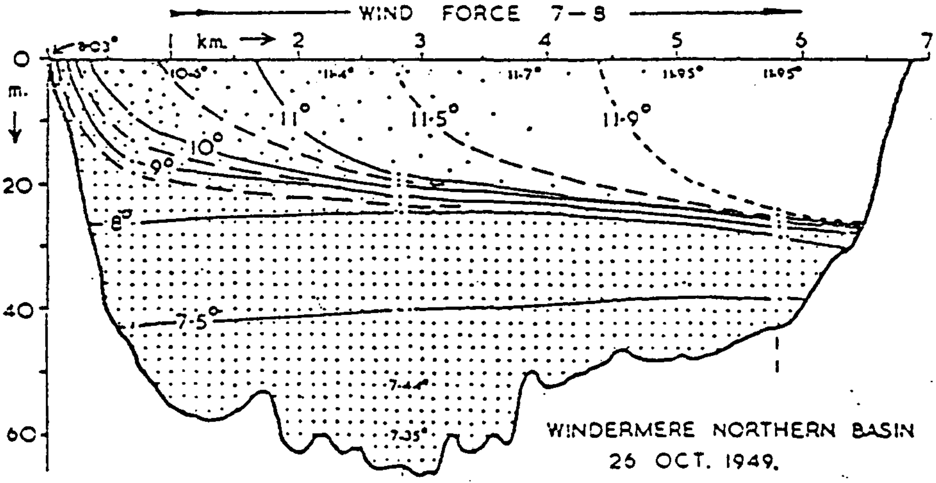


Fig. 9.(a) The effect of a strong steady wind on the disposition of isotherms in a hypothetical three-layered lake. The hypolimnion is shown stippled and the direction and velocity of flow are indicated by arrows.

(b) Field observations of temperature distribution after strong winds in the North Basin of Windermere.
(Modified from Mortimer 1954).

FIG. 10

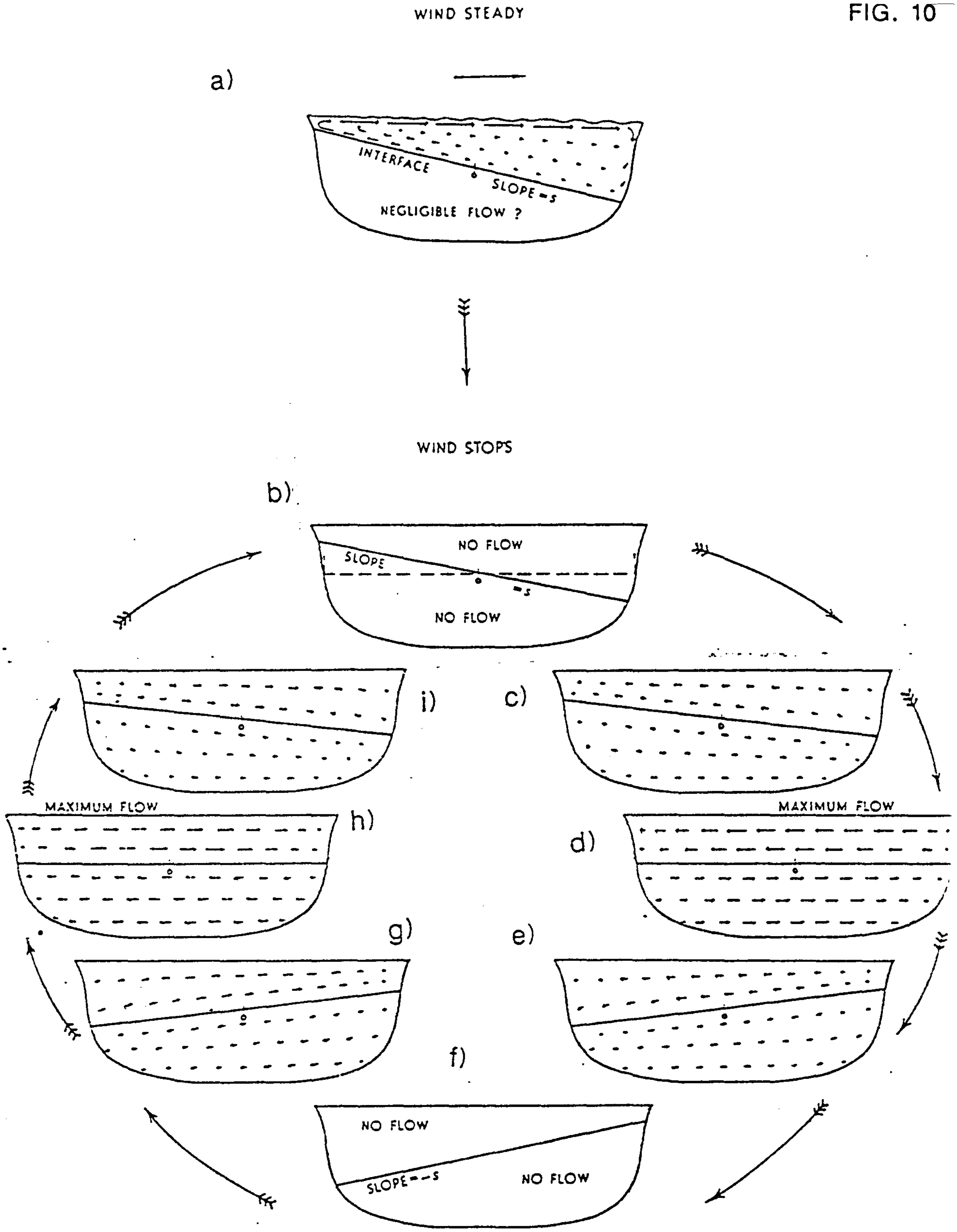


Fig. 10. The oscillations of the thermocline in a hypothetical two-layered lake:

(a) the thermocline in equilibrium with the wind stress,

(b) momentary period of no hydrostatic flow, (c-i) the oscillating thermocline.

(Modified from Mortimer 1952).

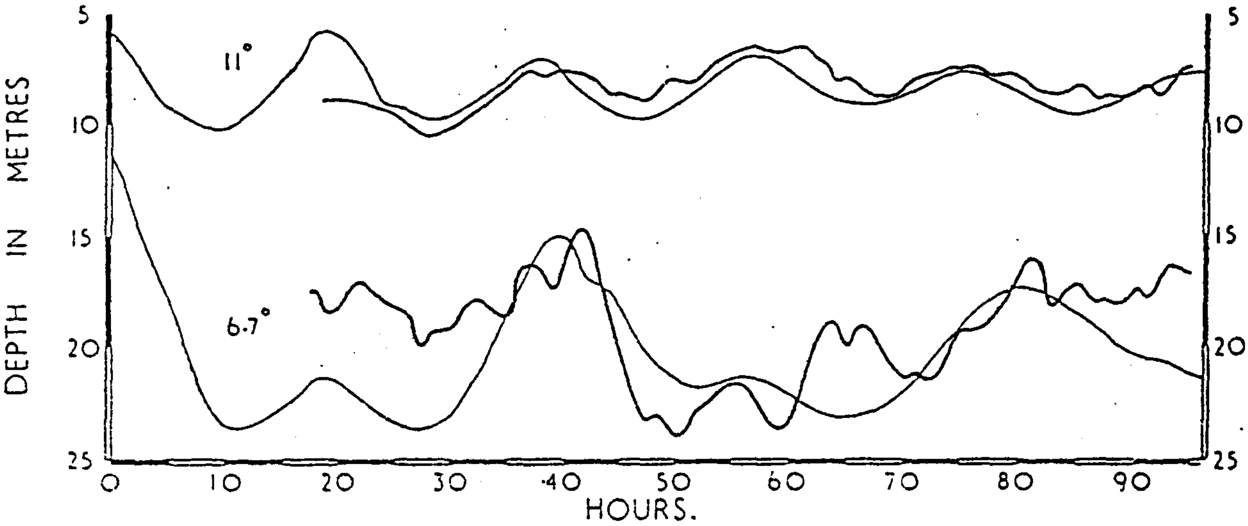


Fig. 11. Calculated (—) and observed (⟵) variations in the depth of the 11.0° and 6.7° isotherms in the North Basin of Windermere on 9 and 13 June 1947 (from Mortimer 1951).

FIG. 12

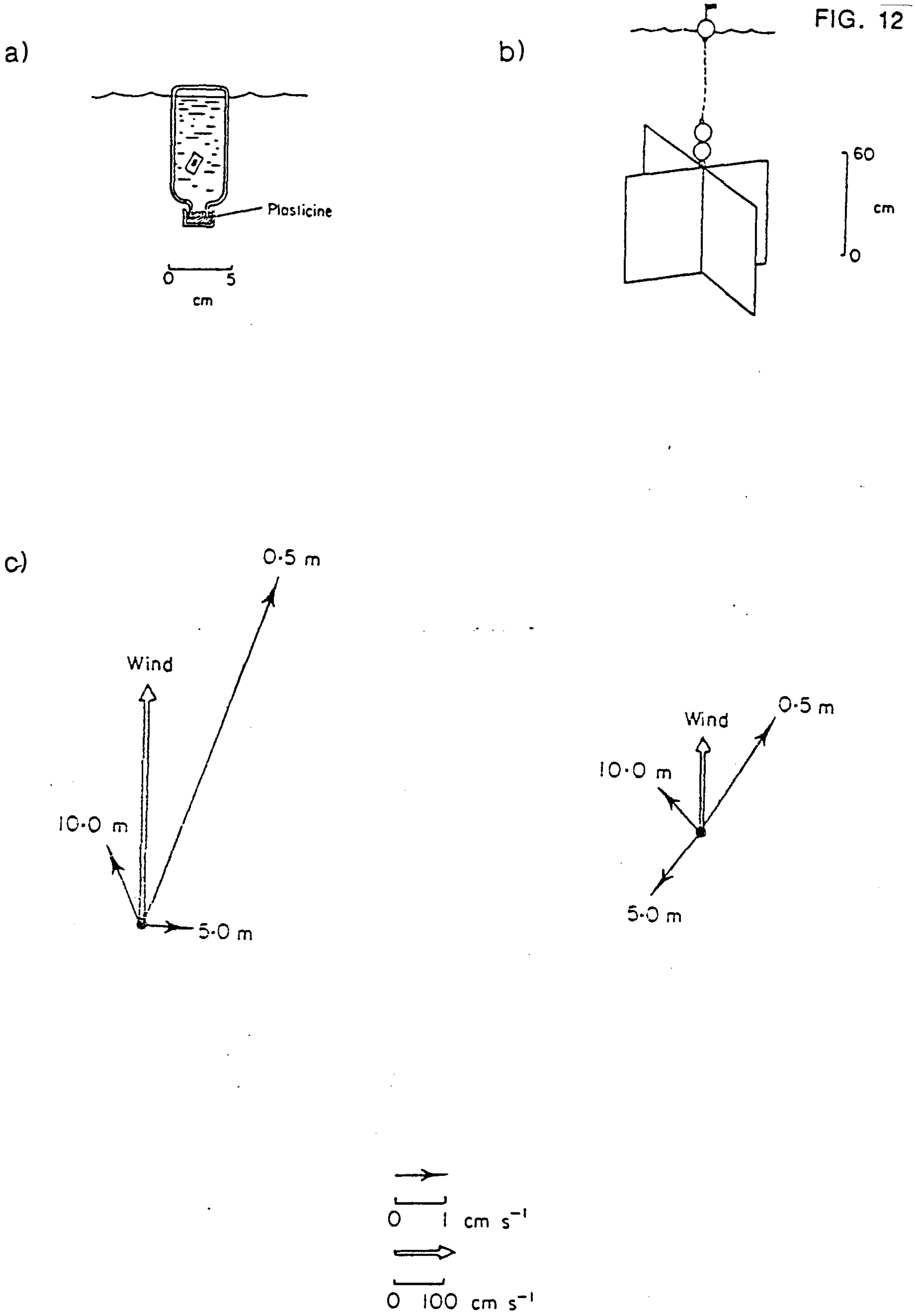


Fig. 12. (a) A drift bottle, (b) a cruciform drogue, (c) two examples of the rotation with depth of the wind-driven current (modified from George 1981a).

FIG. 13

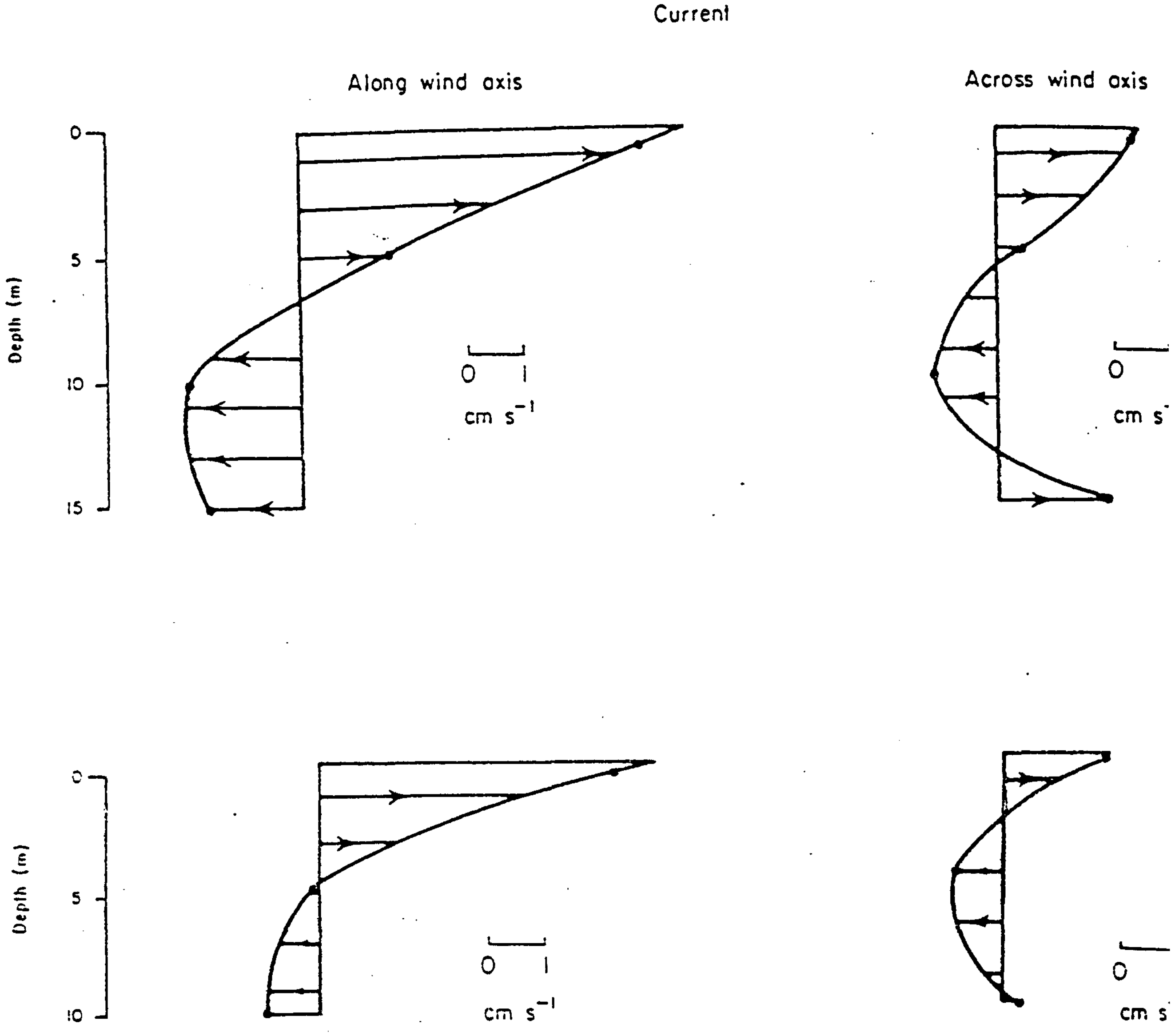


Fig.13. Resolved current profiles at an open water station in the South Basin of Windermere (modified from George 1981a).

FIG. 14

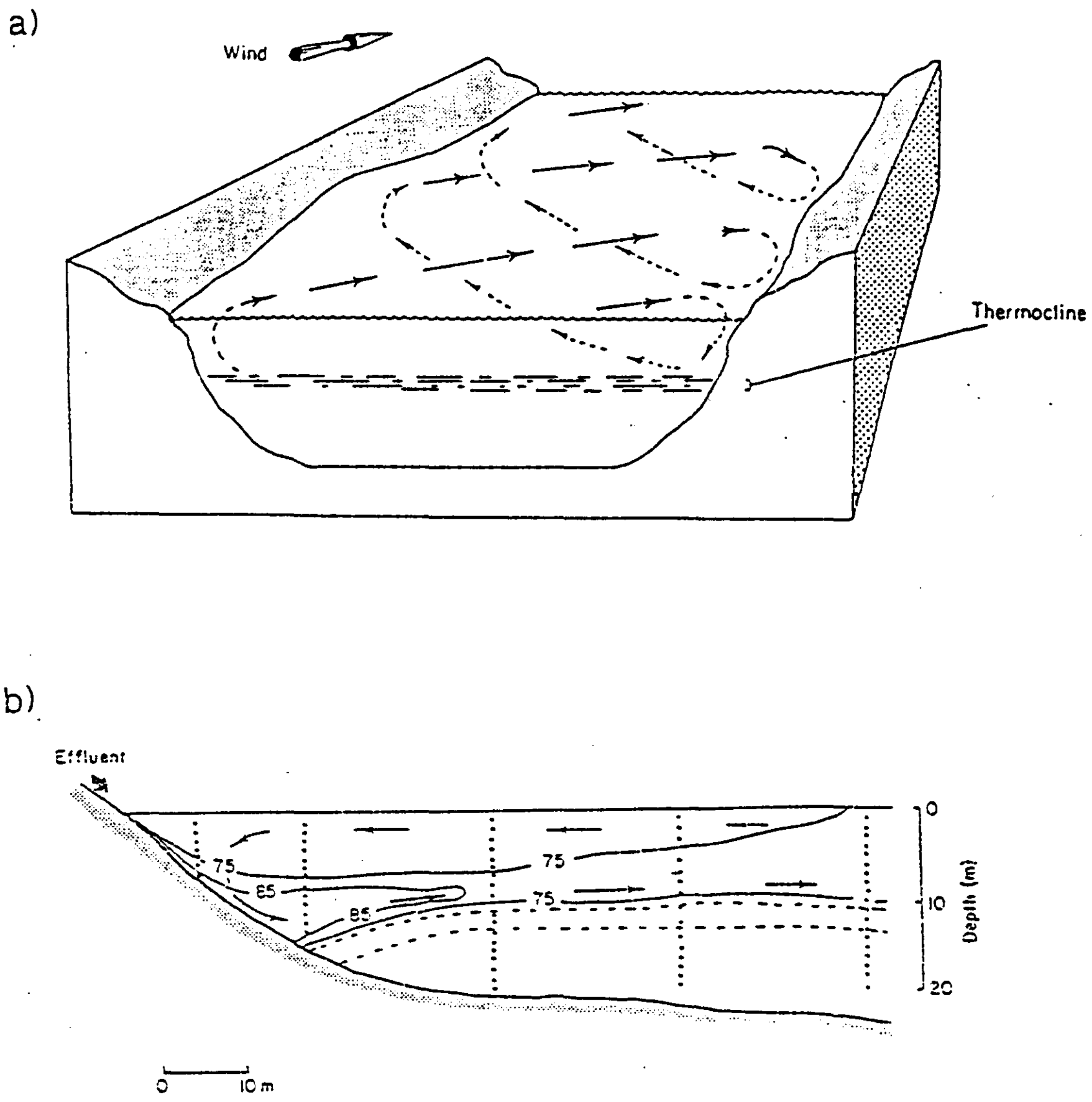


Fig. 14. (a) Schematic diagram showing the general form of circulation in the South Basin of Windermere (from George 1981a).

(b) The offshore movement of a cool effluent, of relatively high specific conductance, discharged from the Tower Wood sewage works. The contoured measurements are specific conductance ($\mu S\ cm^{-1}$);, the broken lines show the position of the thermocline and the arrows the direction of the current (from George 1981b).

FIG. 15

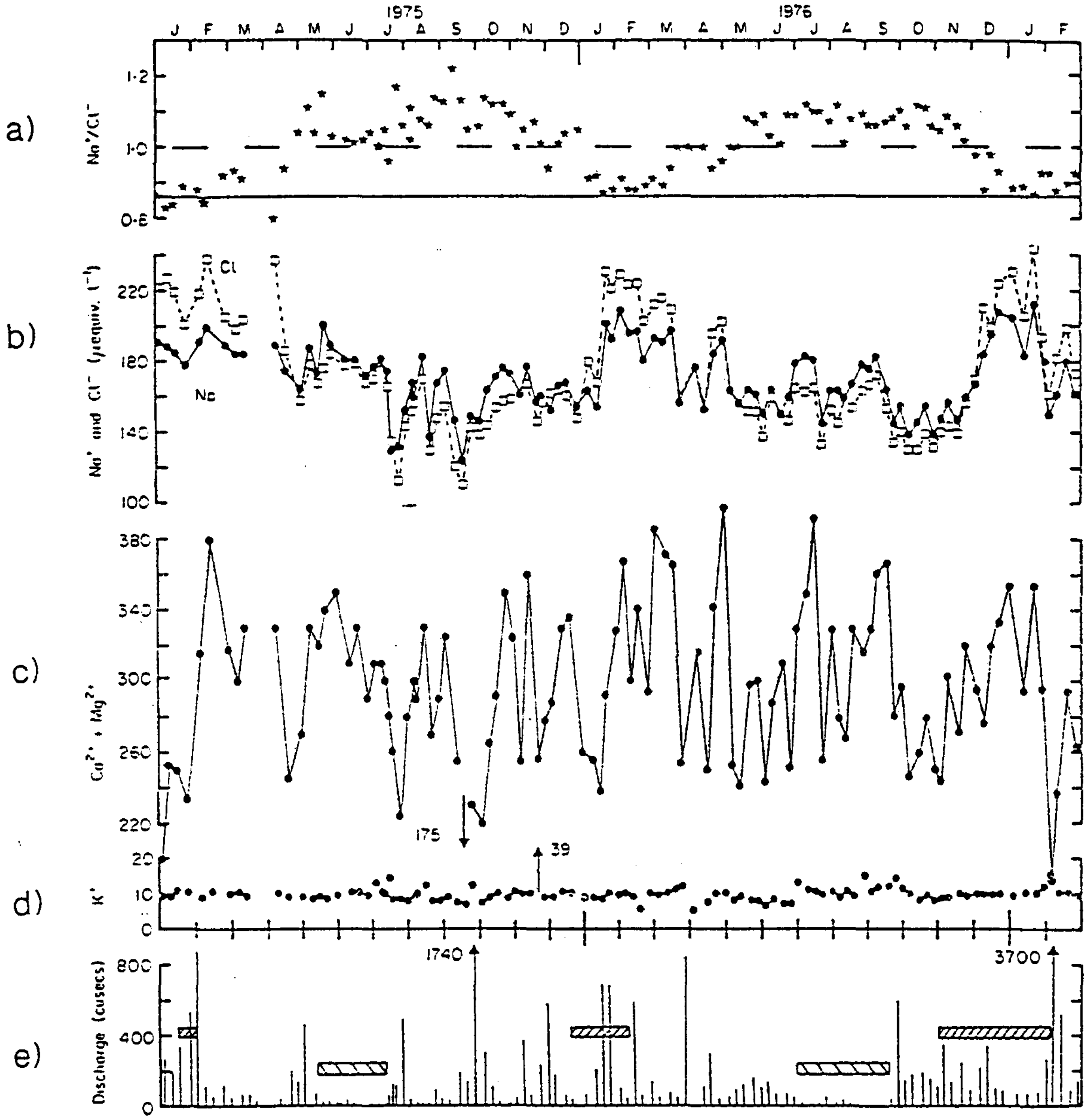


FIG.15 .(a) Ratios of sodium to chloride: concentrations (μequiv. l^{-1}) of (b) chloride and sodium, (c) calcium+magnesium, (d) potassium; (e) discharge (cusecs) at station B5, River Brathay, January 1975 to February 1977. ▨, periods when deicing salt was used extensively on main roads; ▧, periods of warm, dry weather. From Sutcliffe & Carrick (1983b).

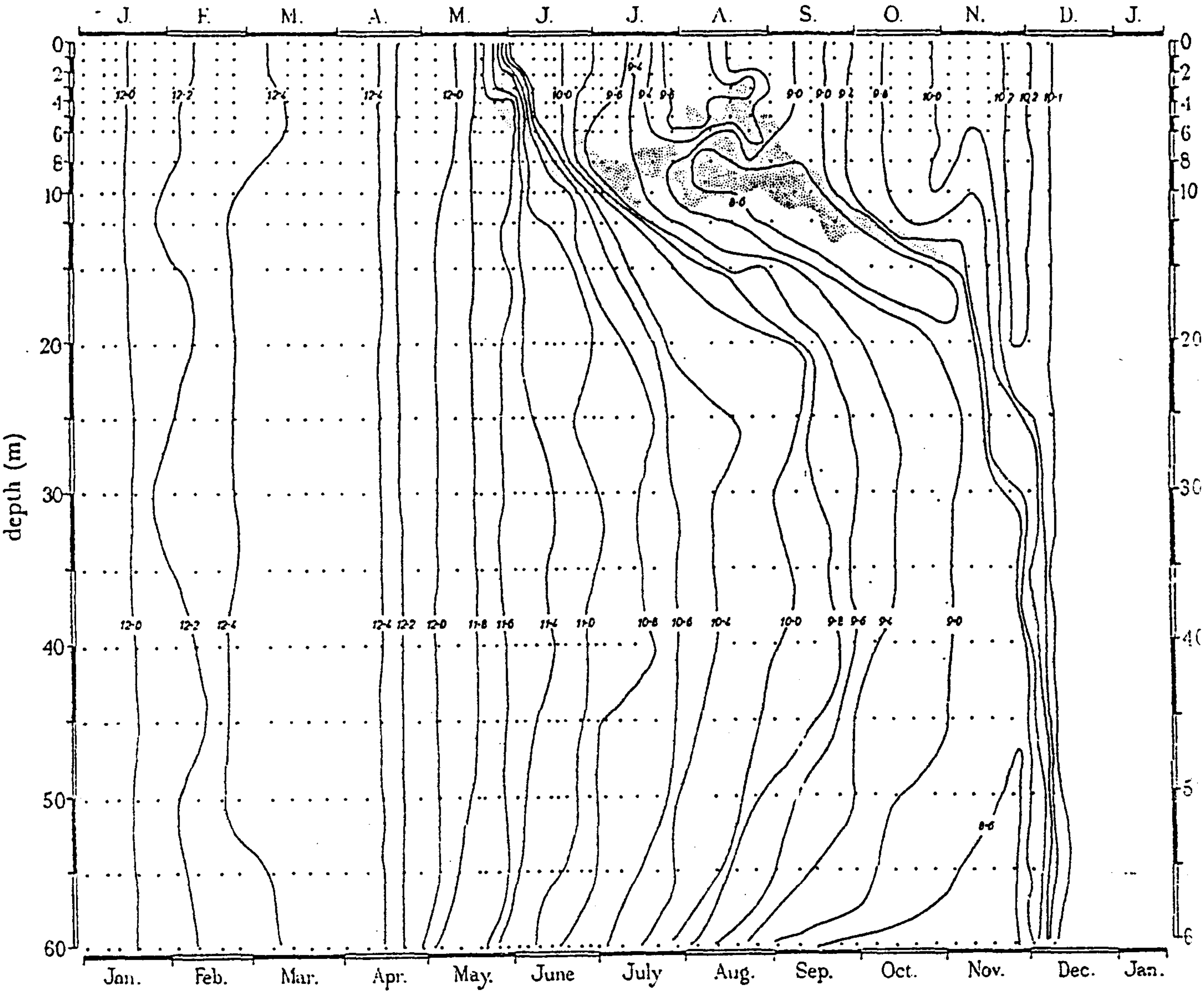
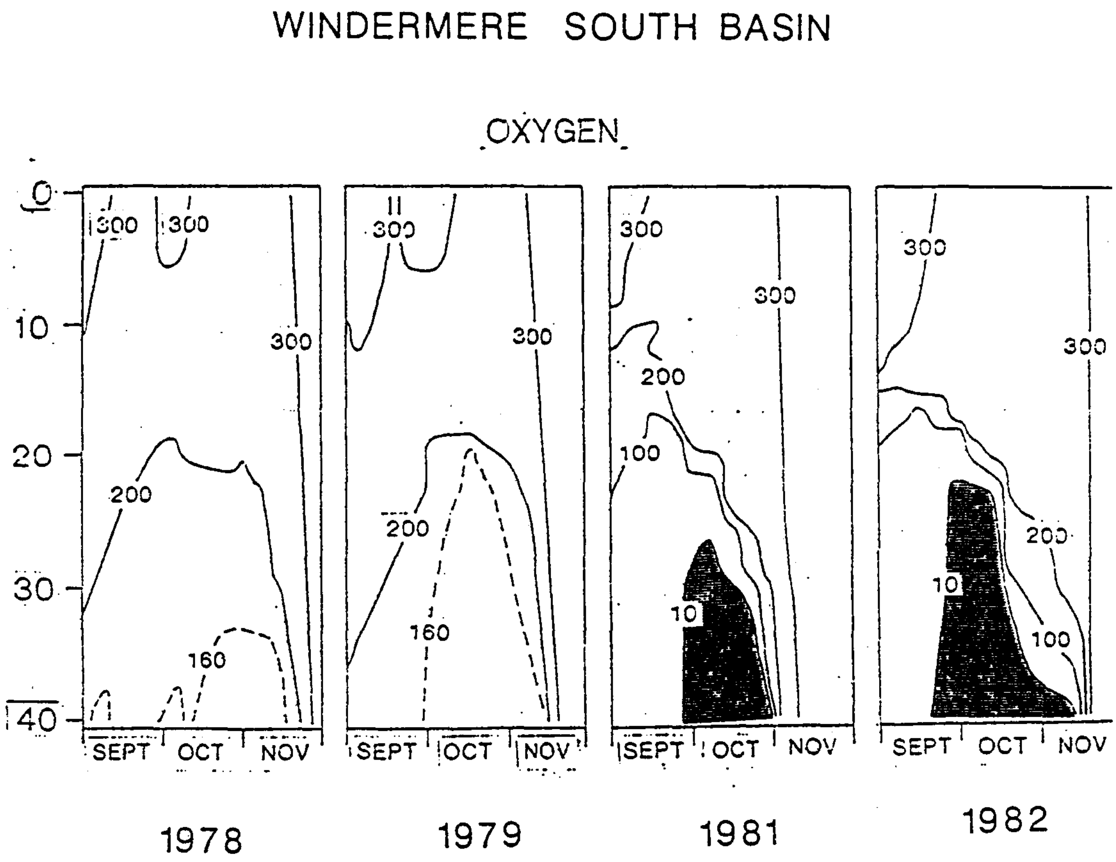


Fig. 16. North Basin: distribution of dissolved oxygen, shown by isopleth contours in mg l^{-1}, with depth and season during 1947. Regions of steep vertical temperature gradients are indicated by stippling (cf. Fig. 4). From Lund et al. (1963).


WINDERMERE SOUTH BASIN

OXYGEN

Fig. 17. South Basin: distribution with depth of dissolved oxygen, shown by isopleth contours in µmol l^{-1} (10 µmol l^{-1} = 0.32 mg l^{-1}), at the end of summer stratification during 1978, 1979 (no anoxia) and 1981, 1982 (anoxia, shaded).

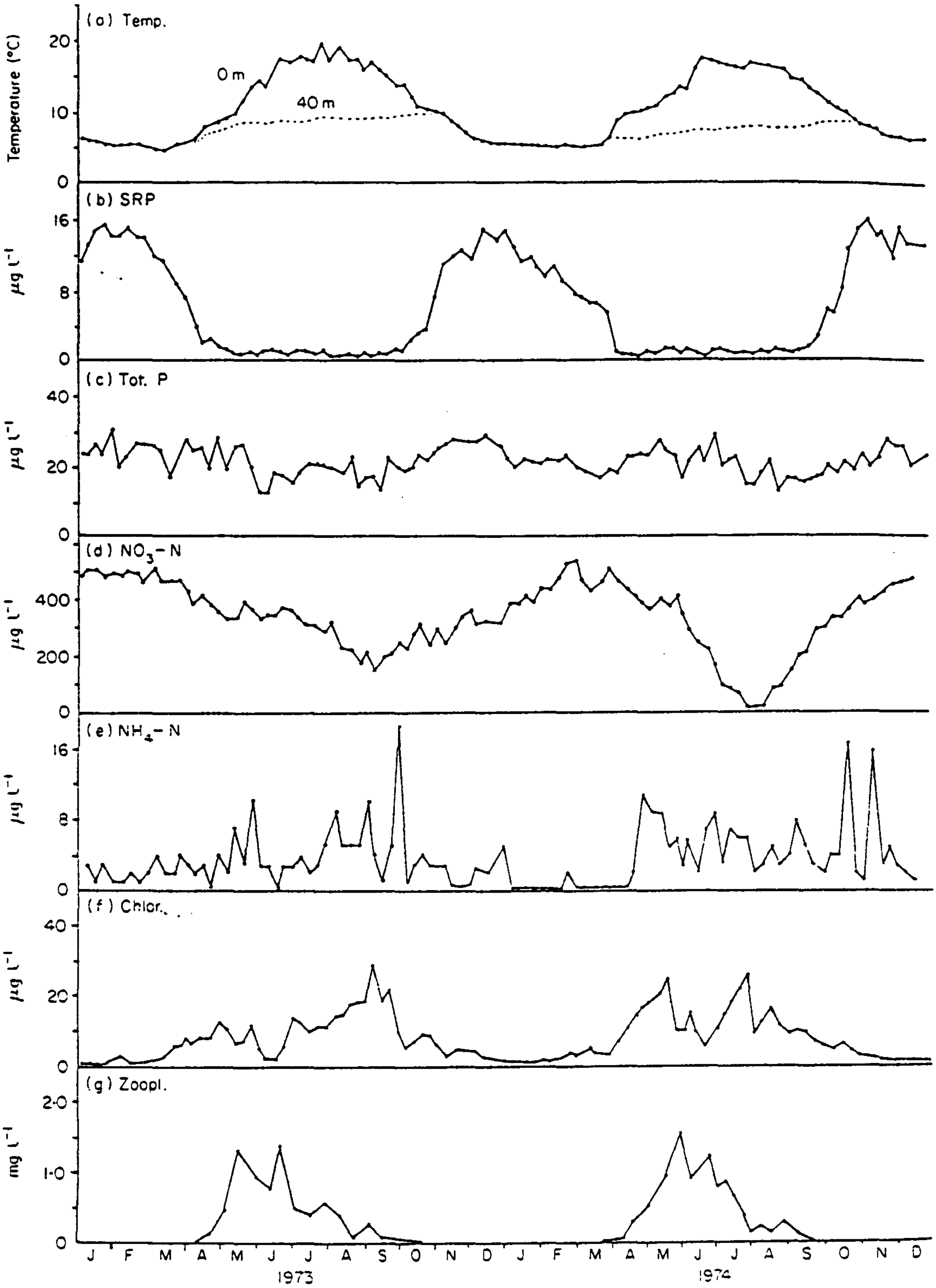


Fig. 17A. South Basin: Seasonal changes in (a) surface and bottom temperature, (b) soluble reactive phosphorus, (c) total phosphorus, (d) nitrate, (e) ammonia, (f) chlorophyll-*a*, (g) zooplankton biomass. From George (1981b).

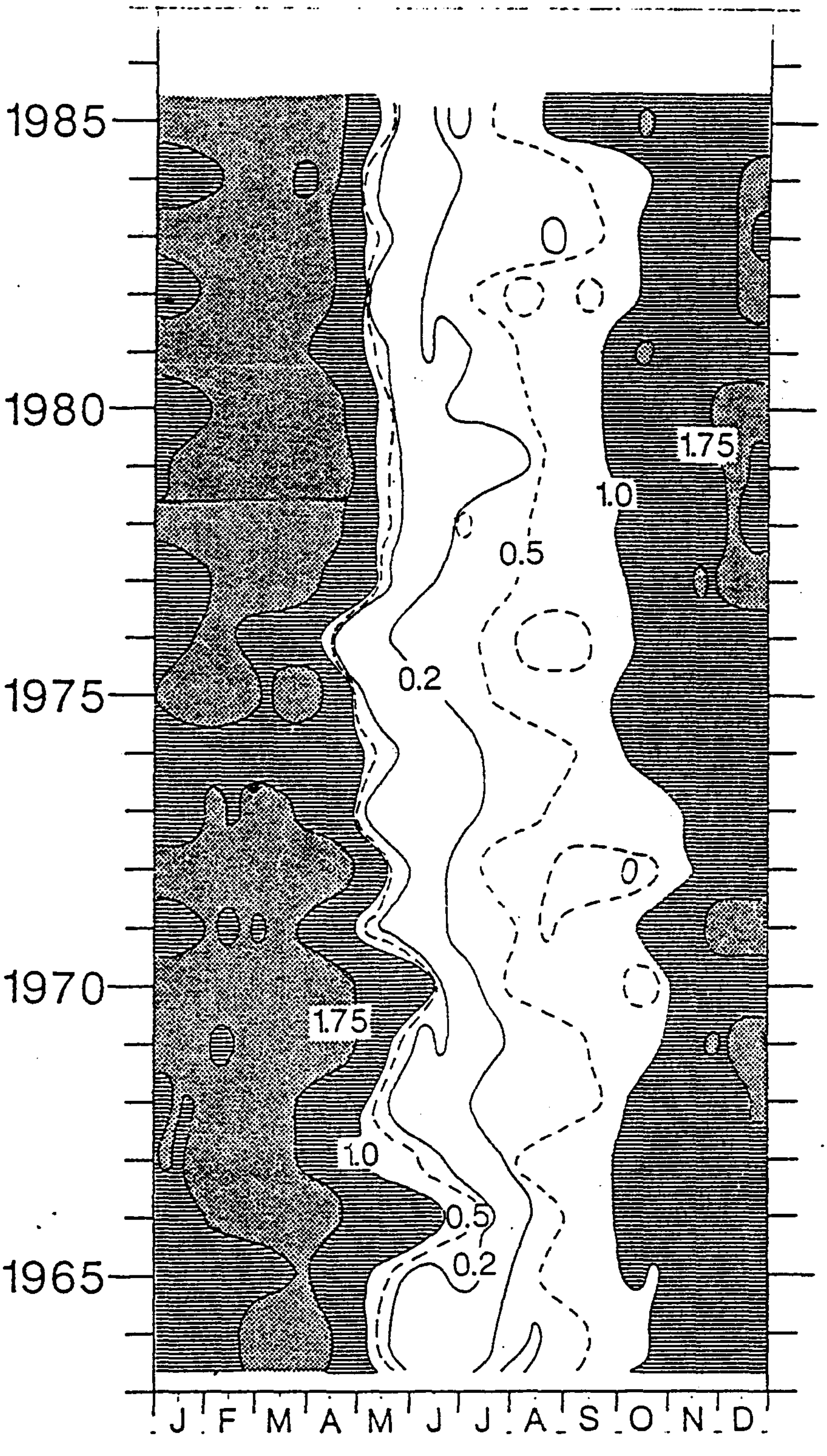


Fig. 18. North Basin: seasonal and long-term change in the concentration of soluble reactive silicon, expressed as SiO_2, from 1964 to 1985, delimited by contours in mg l^{-1}.

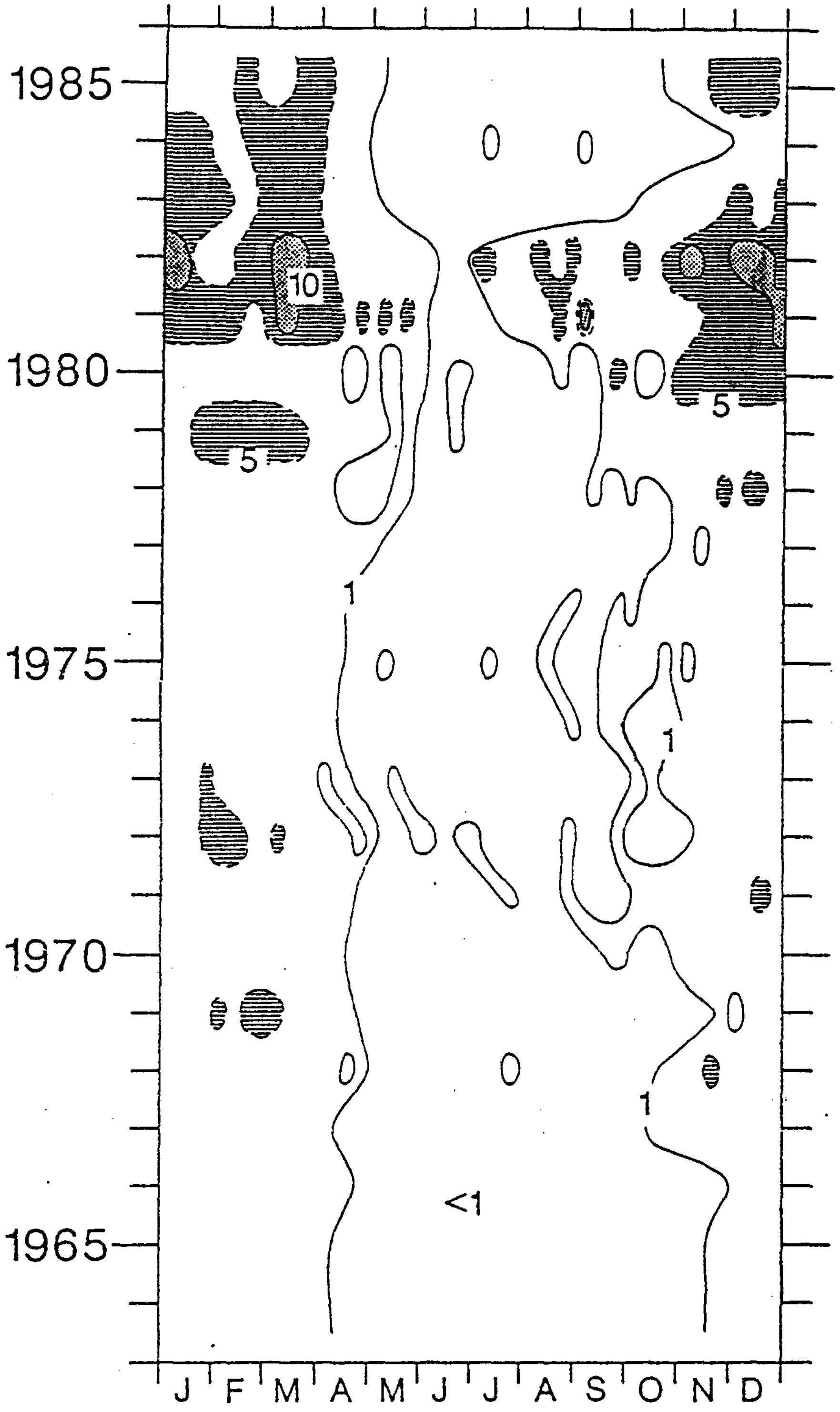


Fig. 19. North Basin: seasonal and long-term change in the concentration of soluble reactive phosphorus (PO_4-P) from 1964 to 1985, delimited by contours in µg l^{-1}.

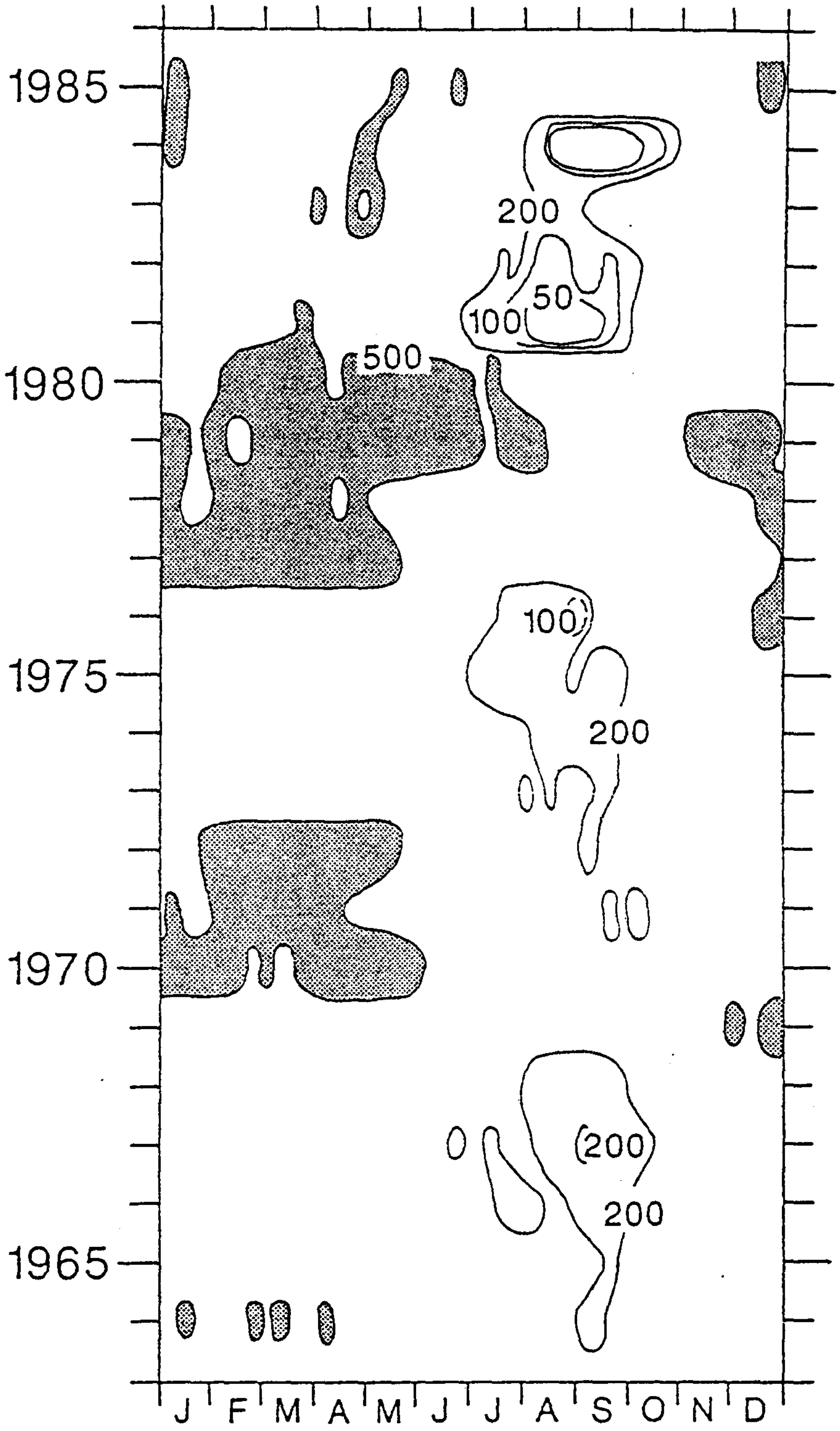


Fig. 20. North Basin: seasonal and long-term change in the concentration of nitrate nitrogen from 1964 to 1985, delimited by contours in µg l^{-1}.

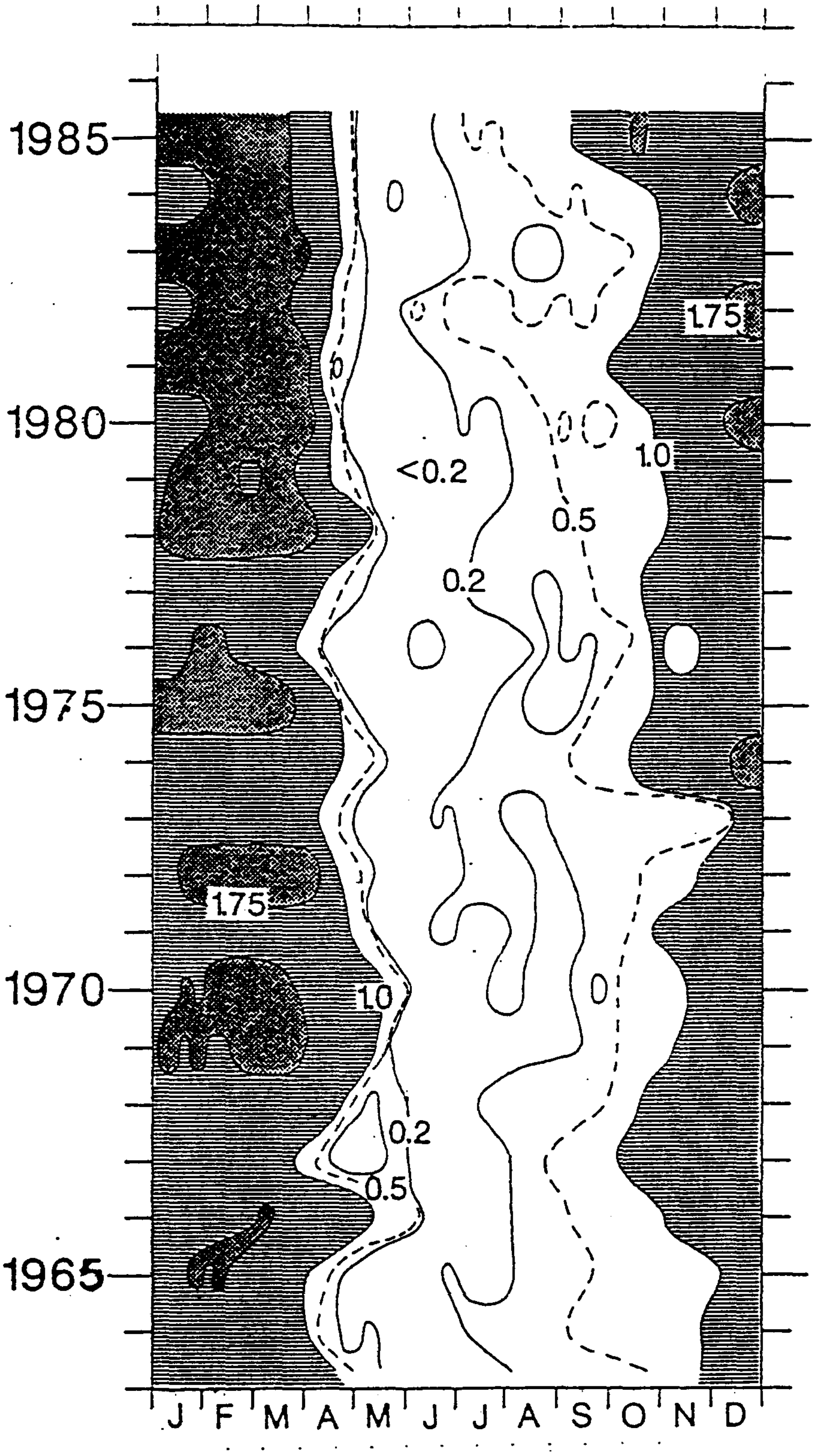


Fig. 21. South Basin: seasonal and long-term change in the concentration of soluble reactive silicon, expressed as SiO_2, from 1964 to 1985, delimited by contours in mg l^{-1}.

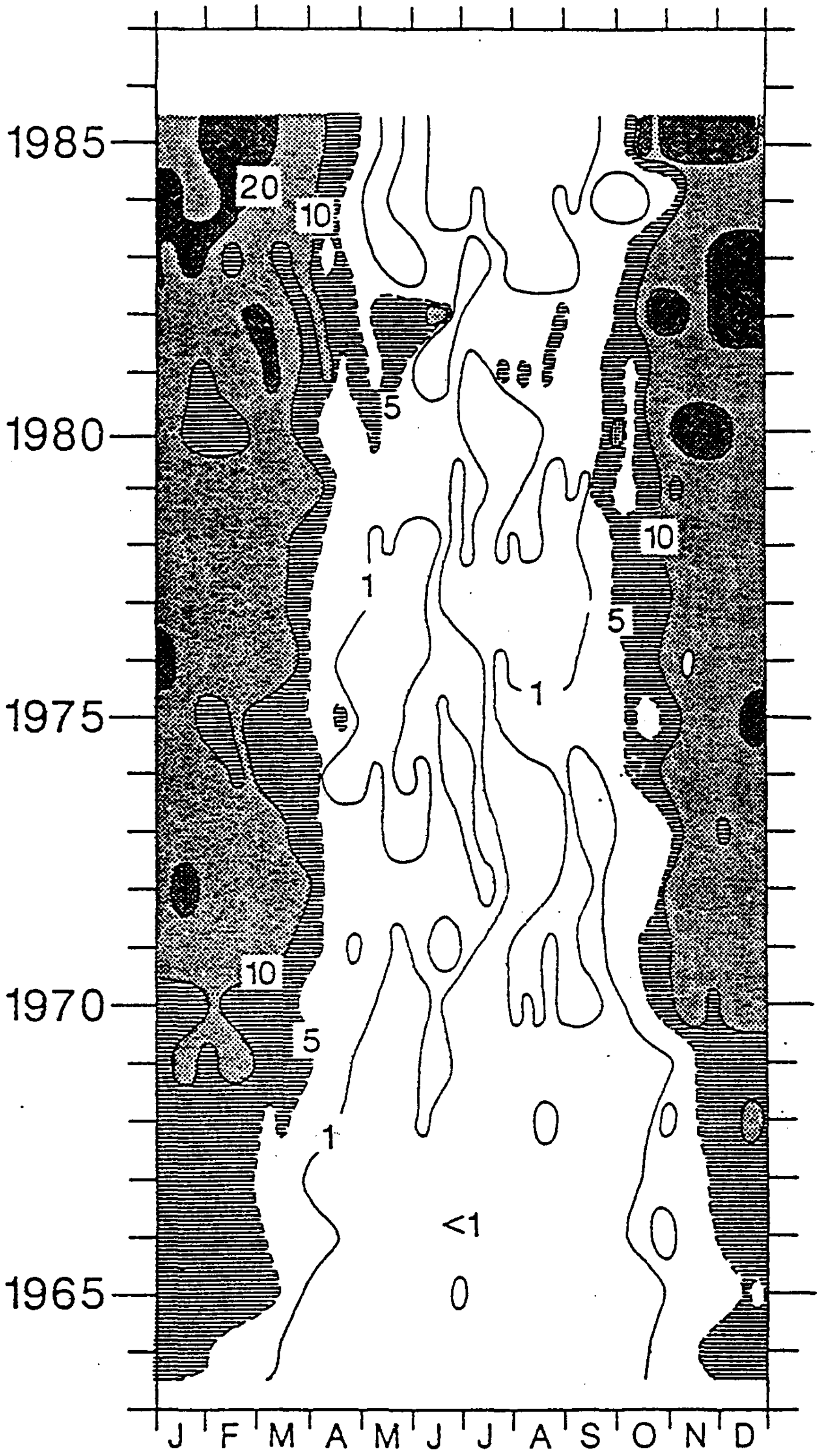


Fig. 22. South Basin: seasonal and long-term change in the concentration of soluble reactive phosphorus (PO_4-P) from 1964 to 1985, delimited by contours in µg l^{-1}.

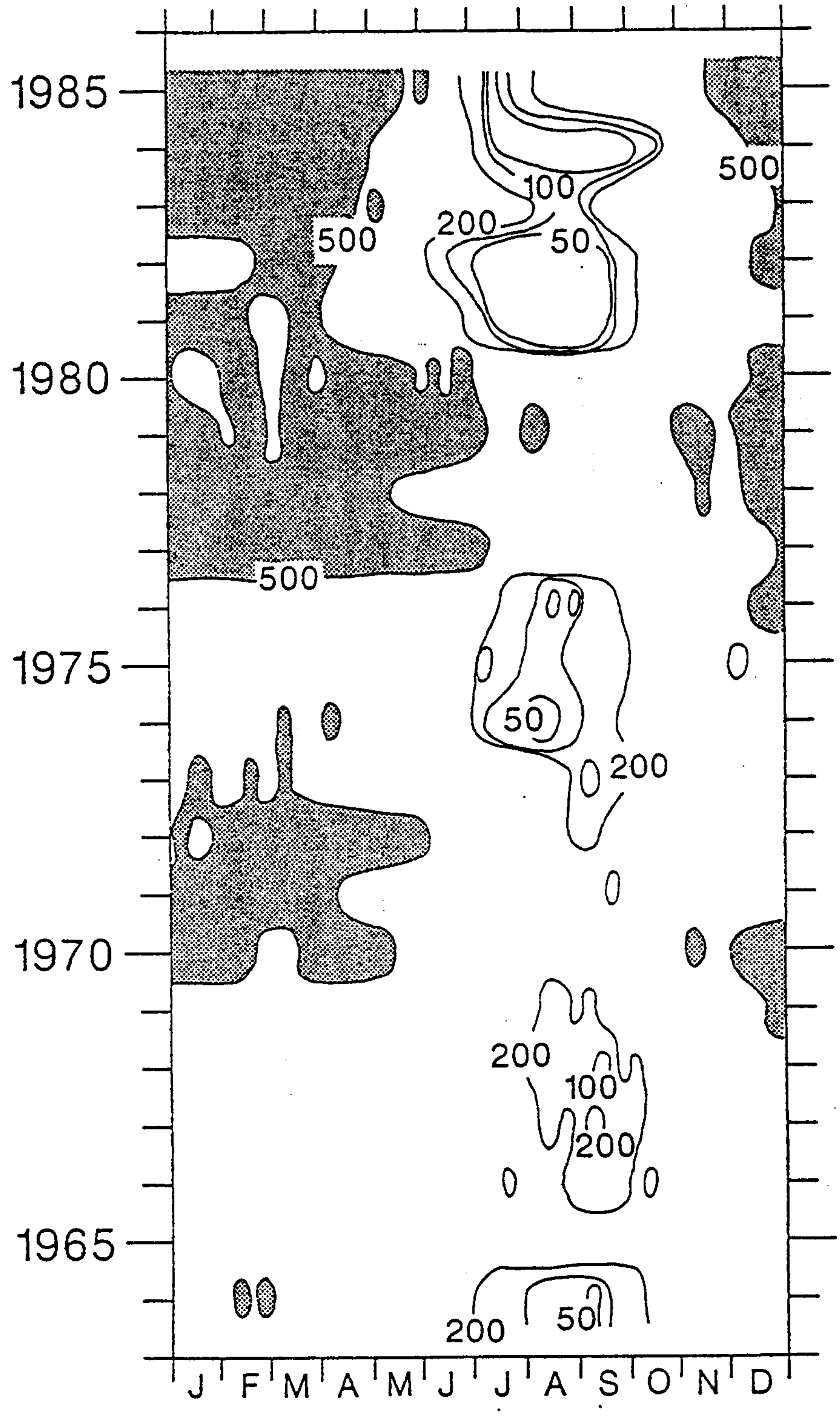


Fig. 23. South Basin: seasonal and long-term change in the concentration of nitrate nitrogen from 1964 to 1985, delimited by contours in $\mu g\ l^{-1}$.

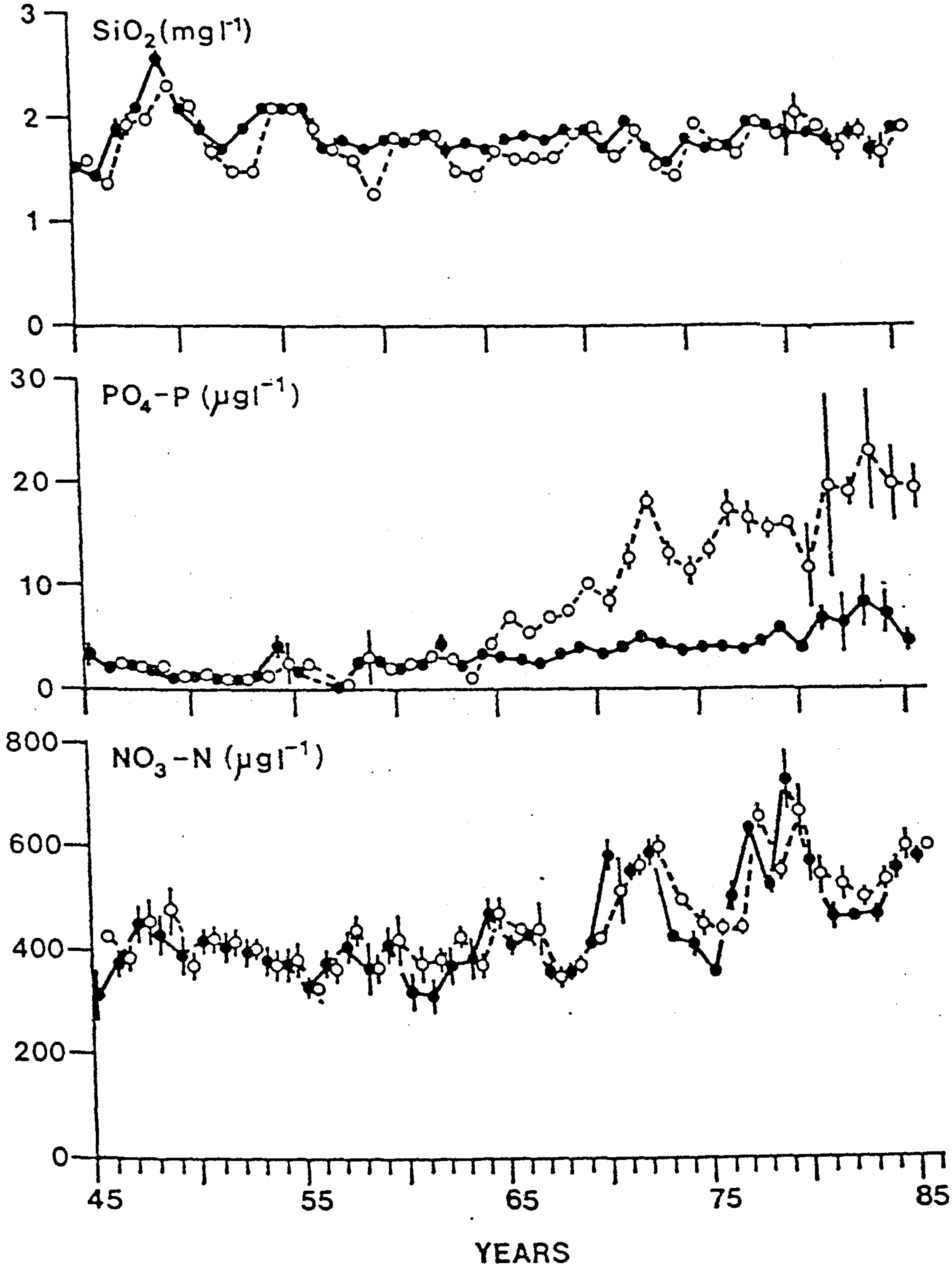


Fig. 24. Mean concentrations (± 95% confidence limits) of Si as SiO_2, PO_4-P, and NO_3-N during periods of the annual winter-spring maxima, ● North basin, o South Basin. To avoid overlap, the values for South Basin are offset to the right of those from th North Basin.

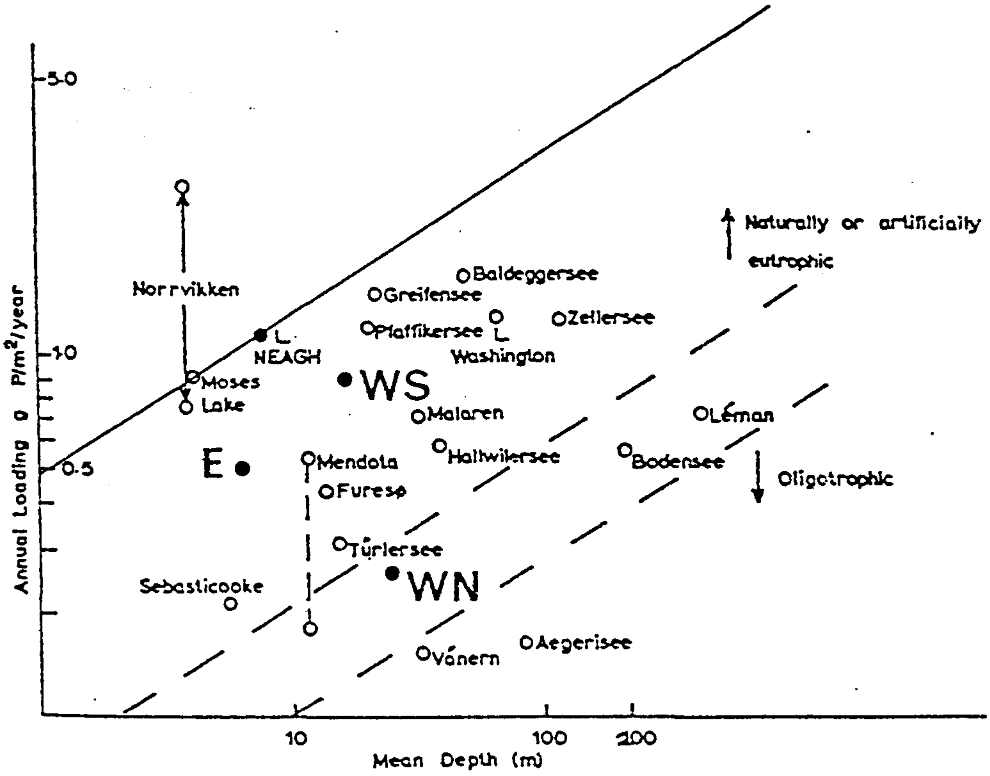


Fig. 25. Annual phosphorus loading (data for both total and soluble P included) and mean depth of some lakes, compared to those for PO_4-P of both basins of Windermere and Esthwaite Water (E).

FIG. 26

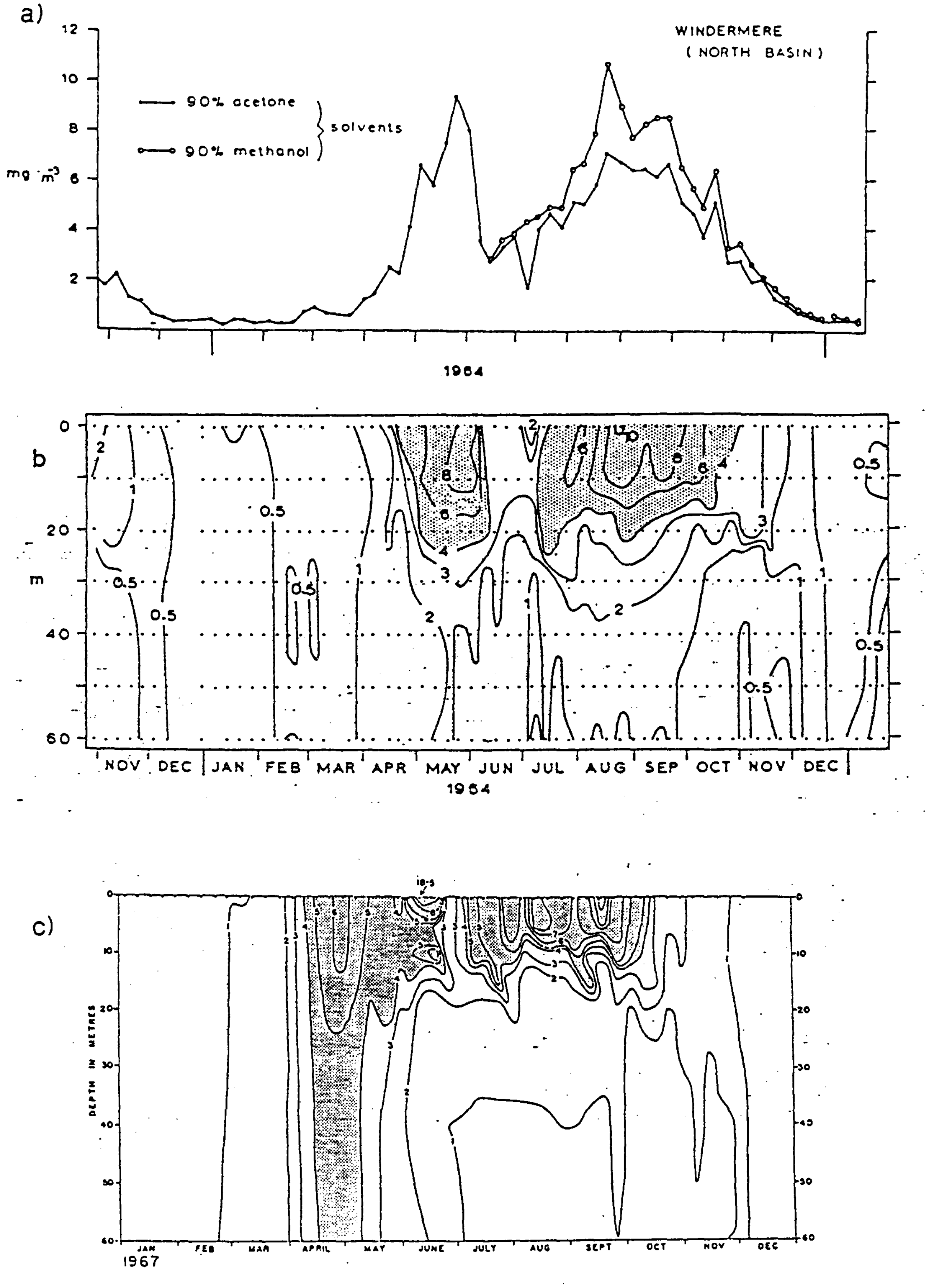


Fig. 26. North Basin: seasonal changes of chlorophyll a concentration, in µg l^{-1} = mg m^{-3}, (a) in the 0-7 m layer, 1964 (b) as depth-variation, 1964 (c) as depth-variation, 1967. (a) and (b) from Talling (1965).

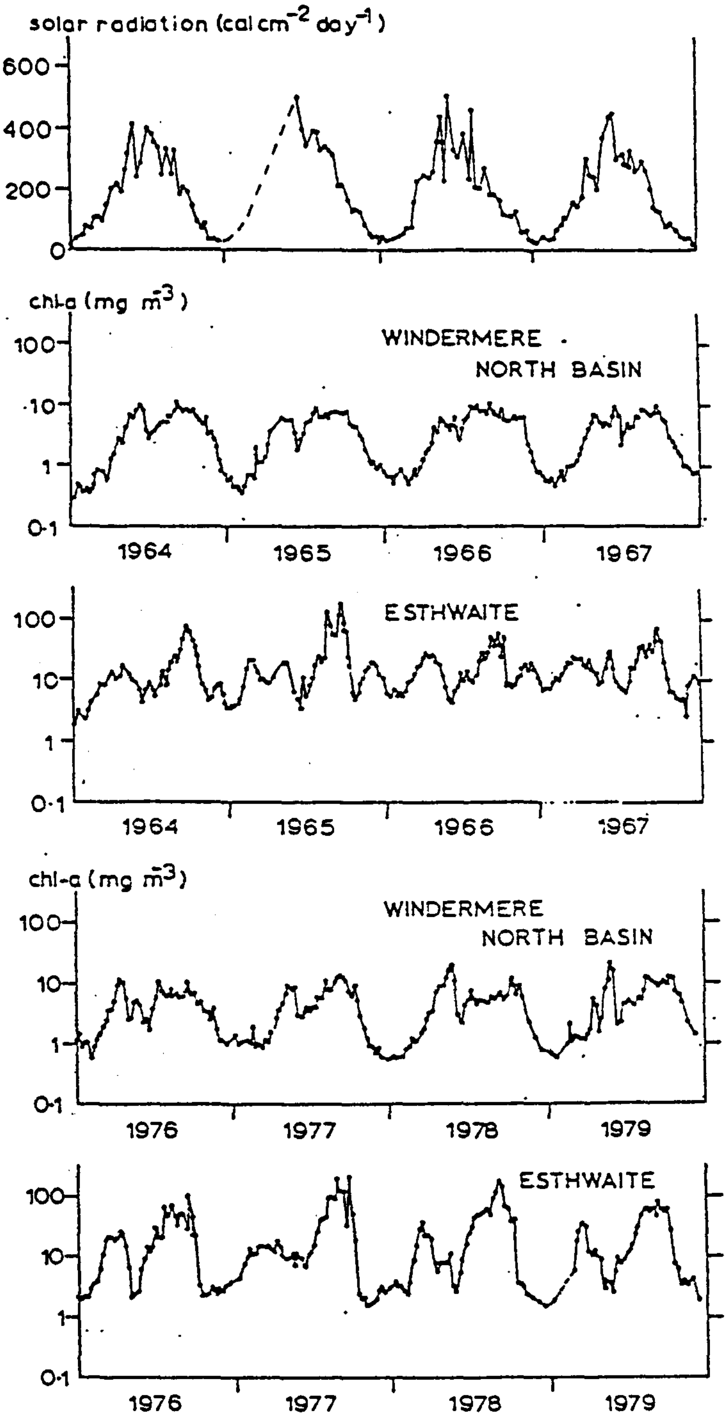


Fig. 27. Comparisons of annual cycles of chlorophyll a concentration in Windermere North Basin (0-7 m layer) with those in the more productive Esthwaite Water (0-5 m layer) for the periods 1964-7 and 1976-9. Corresponding annual cycles of incident solar radiation during the first period are also shown above.

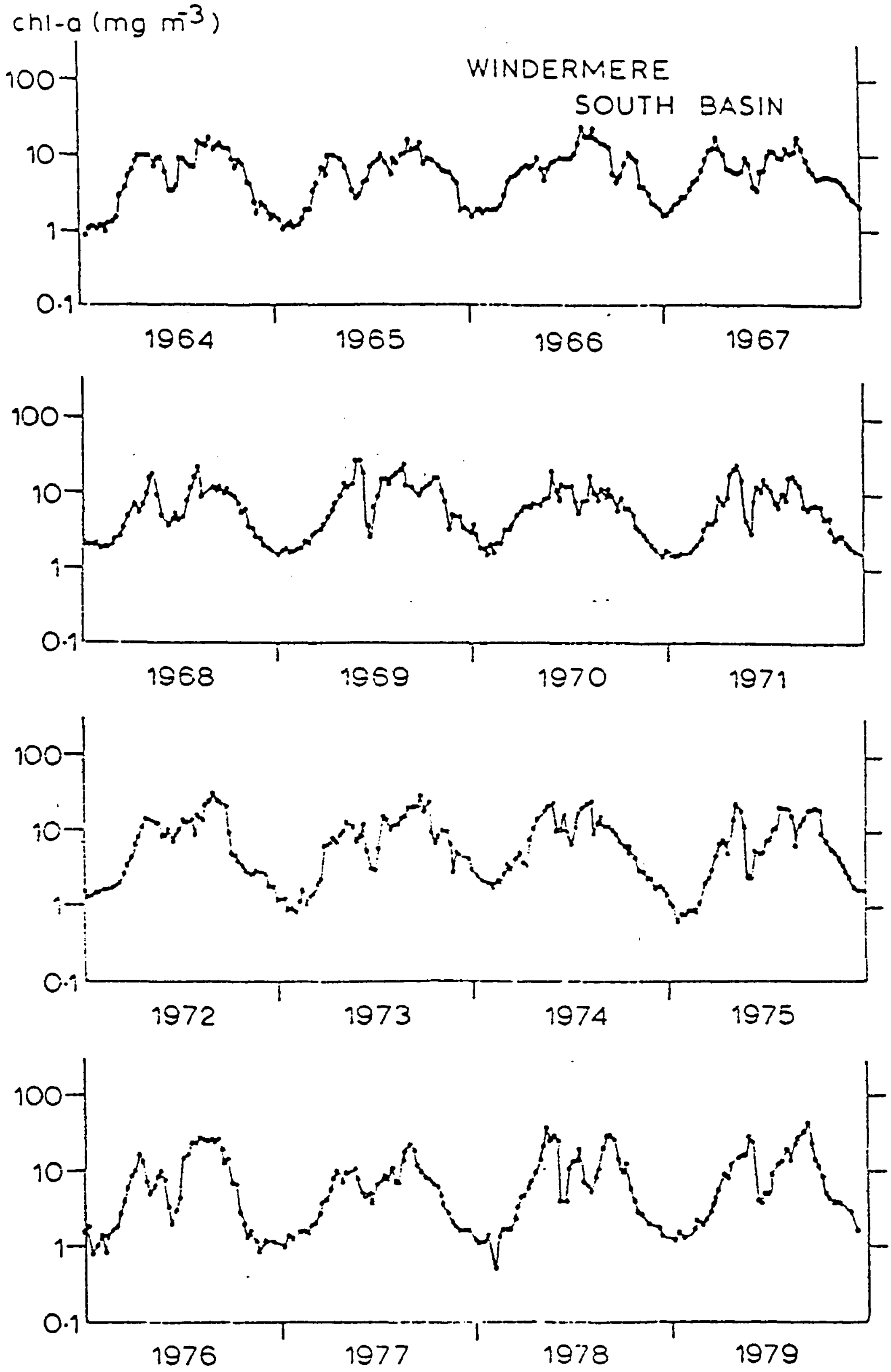


Fig. 28. South Basin: long-term variation of mean chlorophyll a concentration in the 0-7 m layer, 1964-1979.

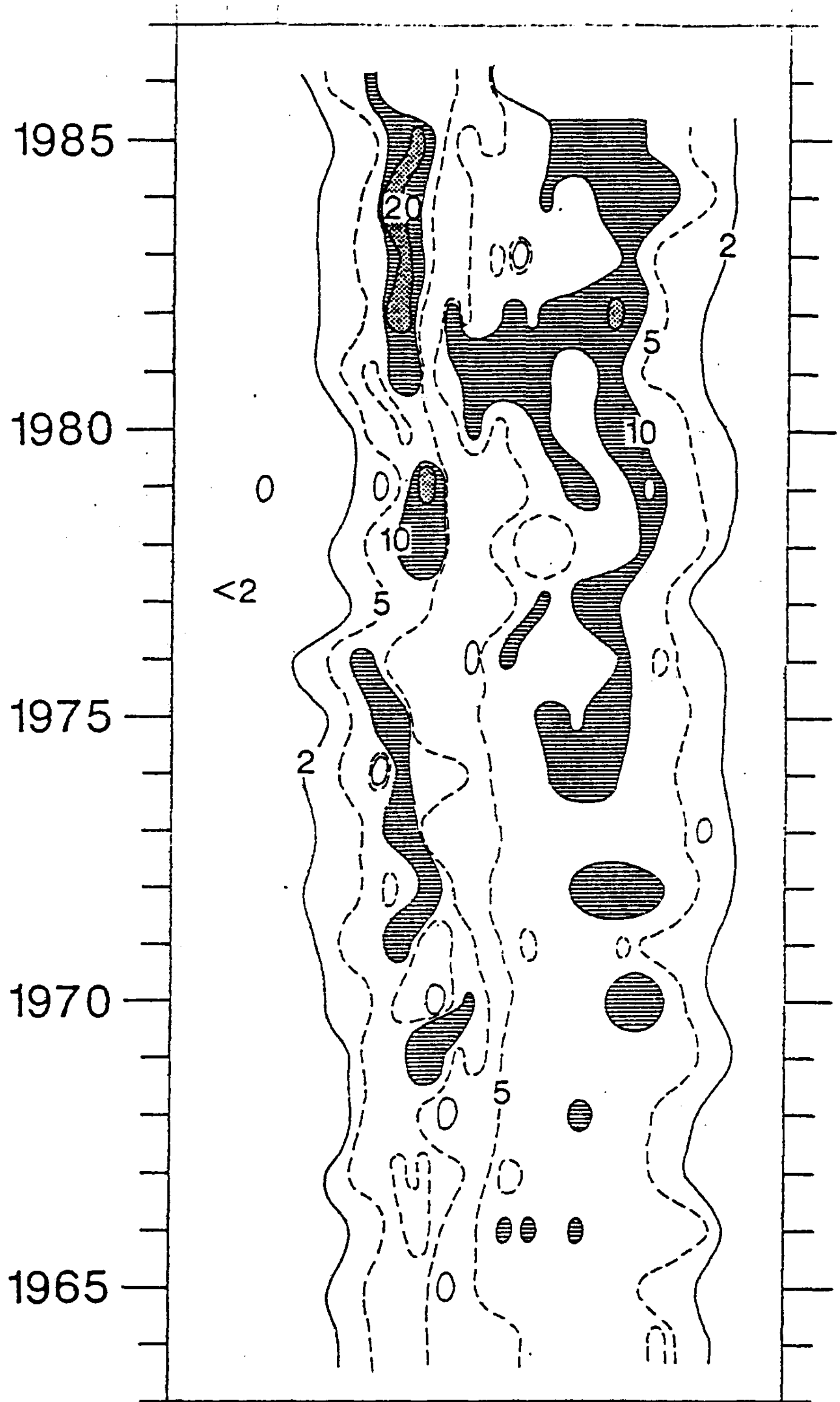


Fig. 29. North Basin: seasonal and long-term change in the concentration of chlorophyll a (0-7 m layer) from 1964 to 1985, delimited by contours in mg m^{-3} = µg l^{-1}.

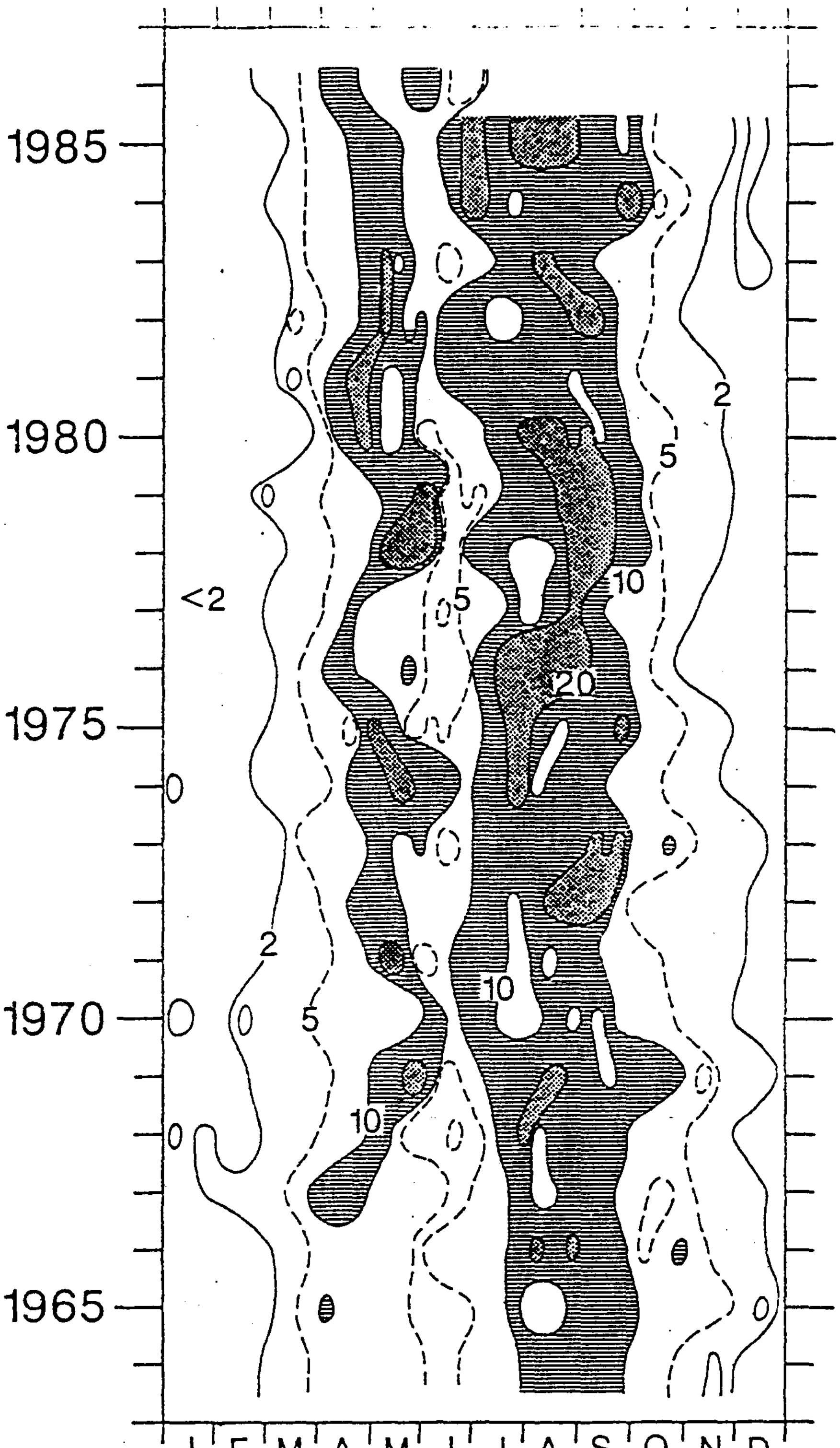


Fig. 30. South Basin: seasonal and long-term change in the concentration of chlorophyll a (0–7 m layer) from 1964 to 1985, delimited by contours in mg m^{-3} = μg l^{-1}.

FIG. 31

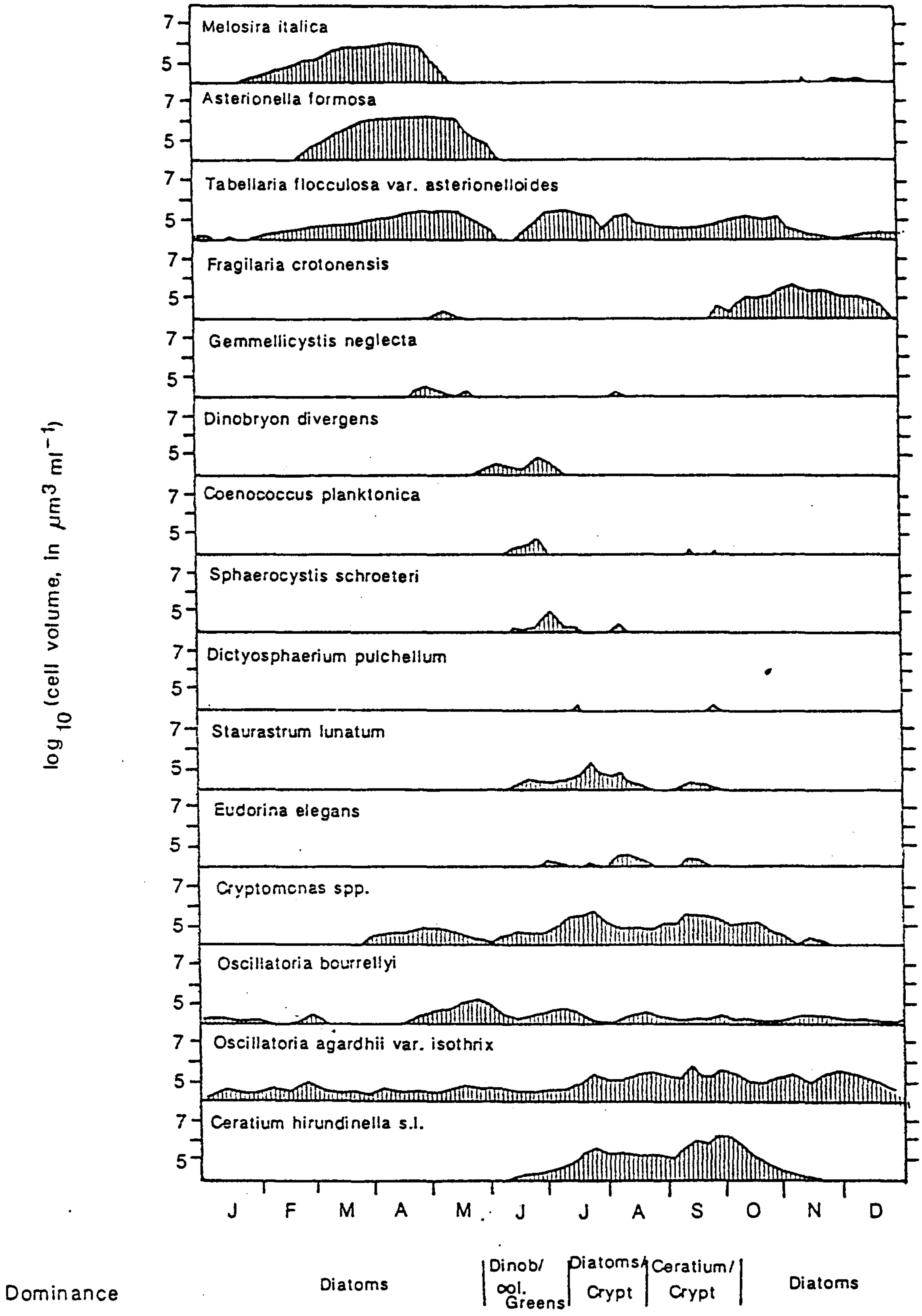


Fig. 31. The seasonal periodicity of major phytoplankton species in the South Basin of Windermere during 1965. Redrawn from Fig. 32 o Lund (in Macan 1970) with each subfigure drawn to the same logarithmic scale of approximate cell volume and with the same base line ($10^4\ \mu m^3\ ml^{-1} = 0.01\ mm^3\ l^{-1}$). Main seasonal changes in dominance are also summarized at the foot of the figure.

FIG. 32

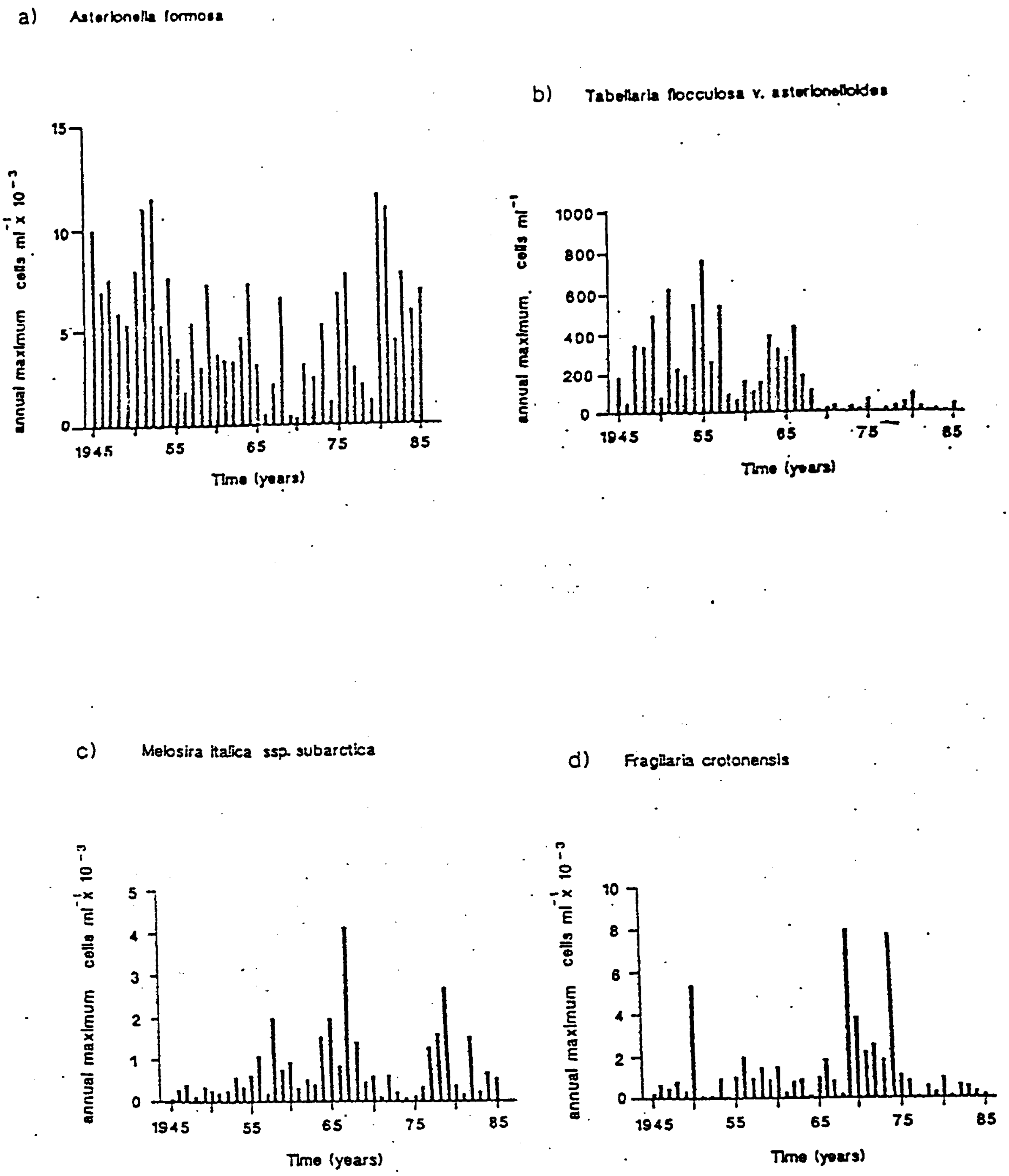
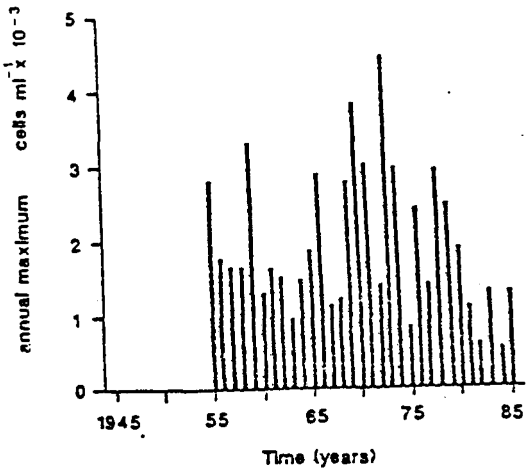


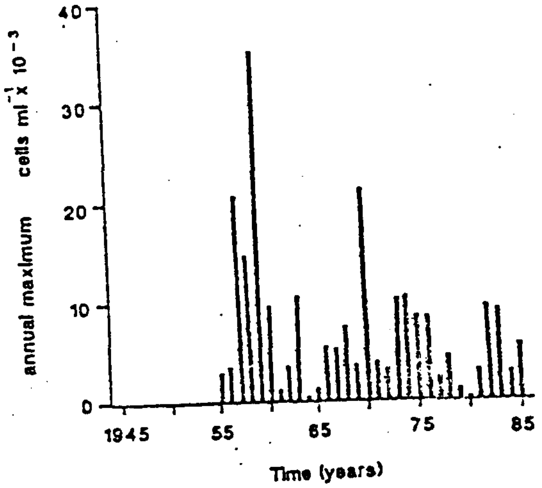
Fig. 32. Maximum abundance from 1945 to 1985 in the 0-7 m layer of Windermere South Basin of major diatoms: (a) Asterionella formosa (b) Tabellaria flocculosa var. asterionelloides, (c) Melosira italica subsp. subarctica and (d) Fragilaria crotonensis.

FIG. 33

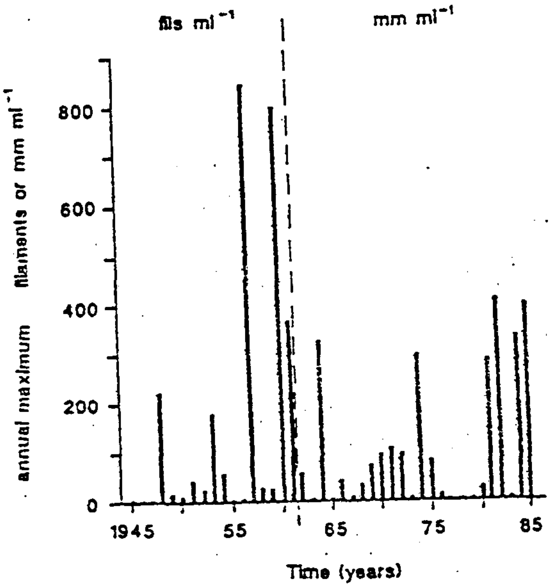
a) Rhodomonas lacustris



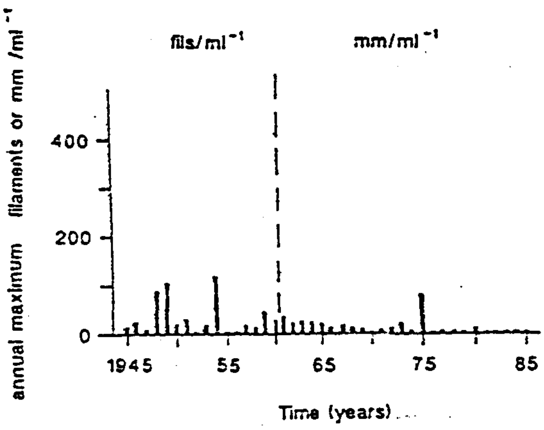
b) Chlorella sp.



c) Oscillatoria bourrellyi



d) Oscillatoria agardii v. isothrix



e) Anabaena flos-aquae + A. circinalis

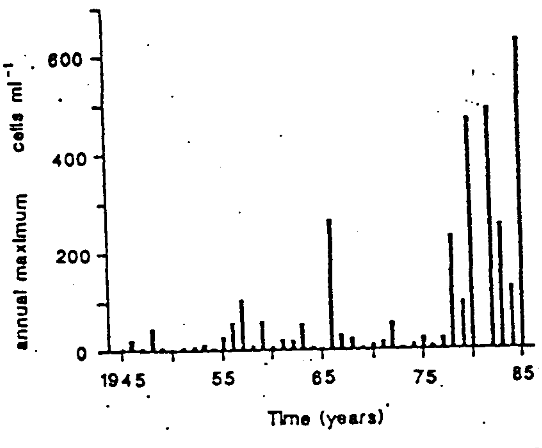


Fig. 33. Maximum abundance from 1945 to 1985 in the 0-7 m layer of Windermere South Basin of (a) Rhodomonas lacustris, (b) Chlorell spp., (c) Oscillatoria bourrellyi, (d) Oscillatoria agardhii var isothrix and (e) Anabaena flos-aquae + A. spiroides + A. circinalis (note no counts for 1981).

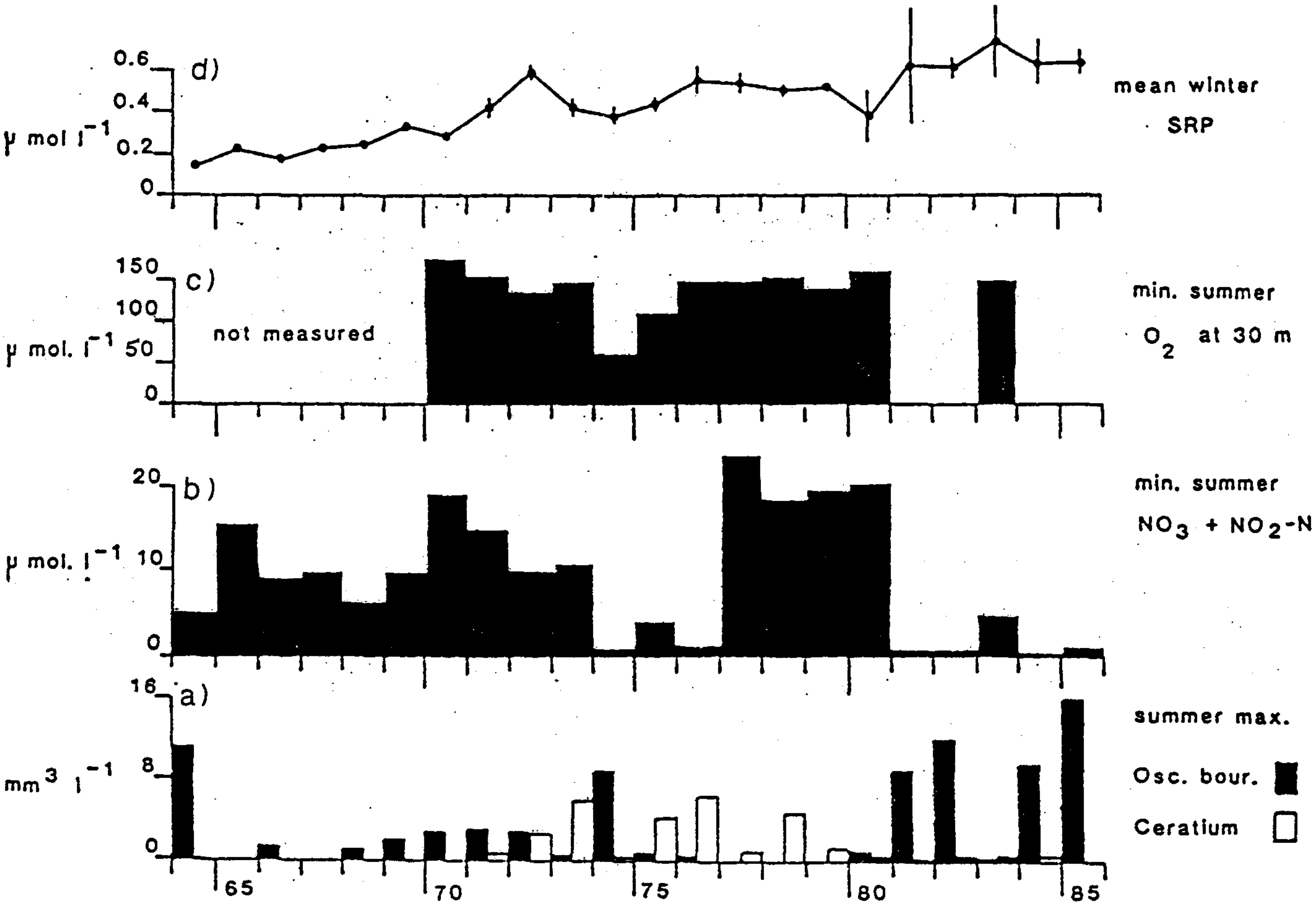


Fig. 34. (a) Seasonal maximum abundance in Windermere South Basin from 1964-85 of Oscillatoria bourrellyi and Ceratium spp. in relation to (b) minimum concentration of $NO_3 + NO_2$-N in the epilimnion, (c) minimum concentration of O_2 at 30 m depth, and (d) mean winter concentration of (PO_4-P).

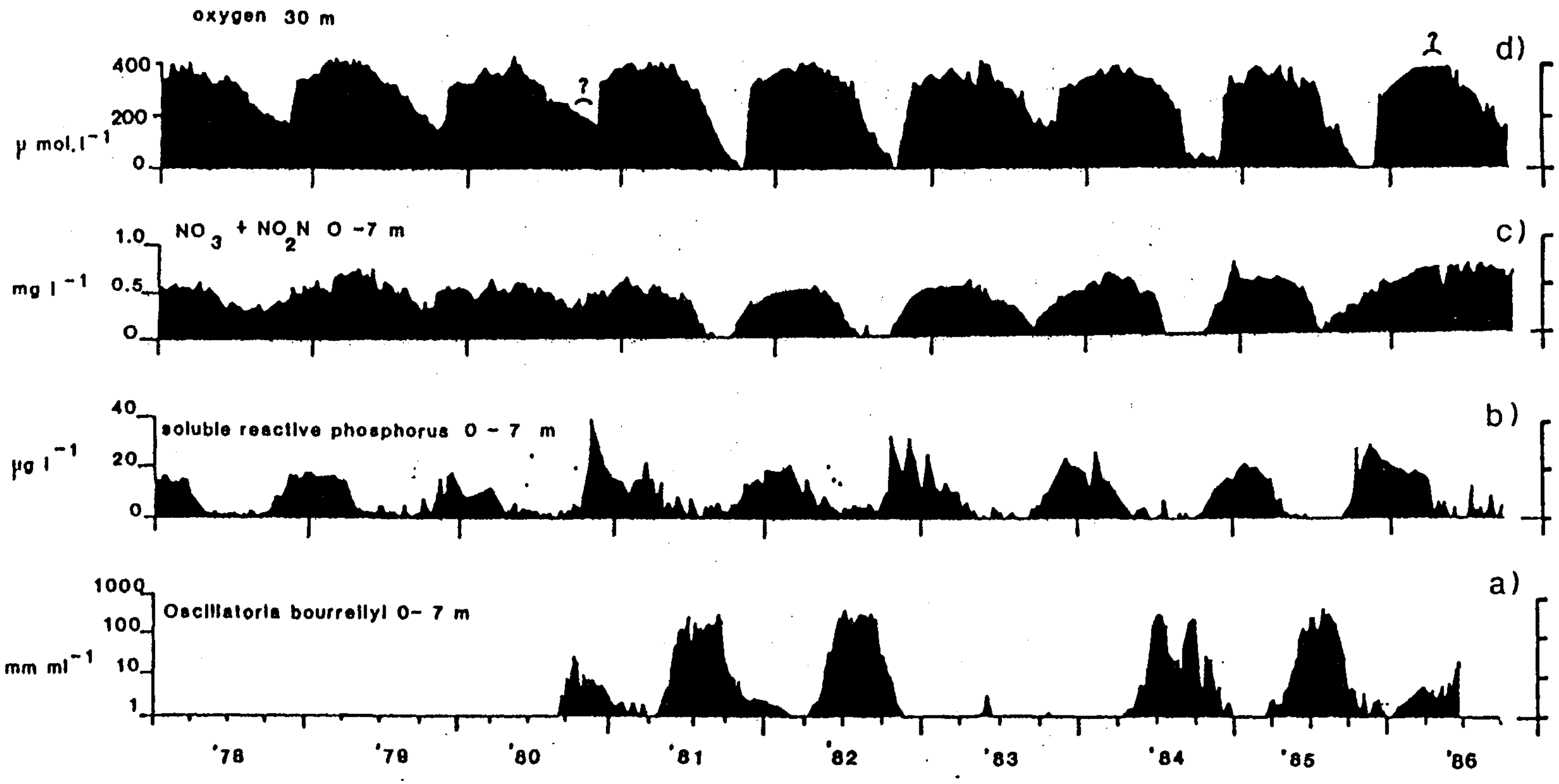


Fig. 35. Changes in the 0-7 m layer of Windermere South Basin from 1978 to late summer 1986 of (a) annual population cycle of *Oscillatoria bourrellyi*, (b) soluble reactive phosphorus, (c) nitrate + nitrite nitrogen, and (d) oxygen concentration at 30 m depth.

FIG. 35

FIG. 36

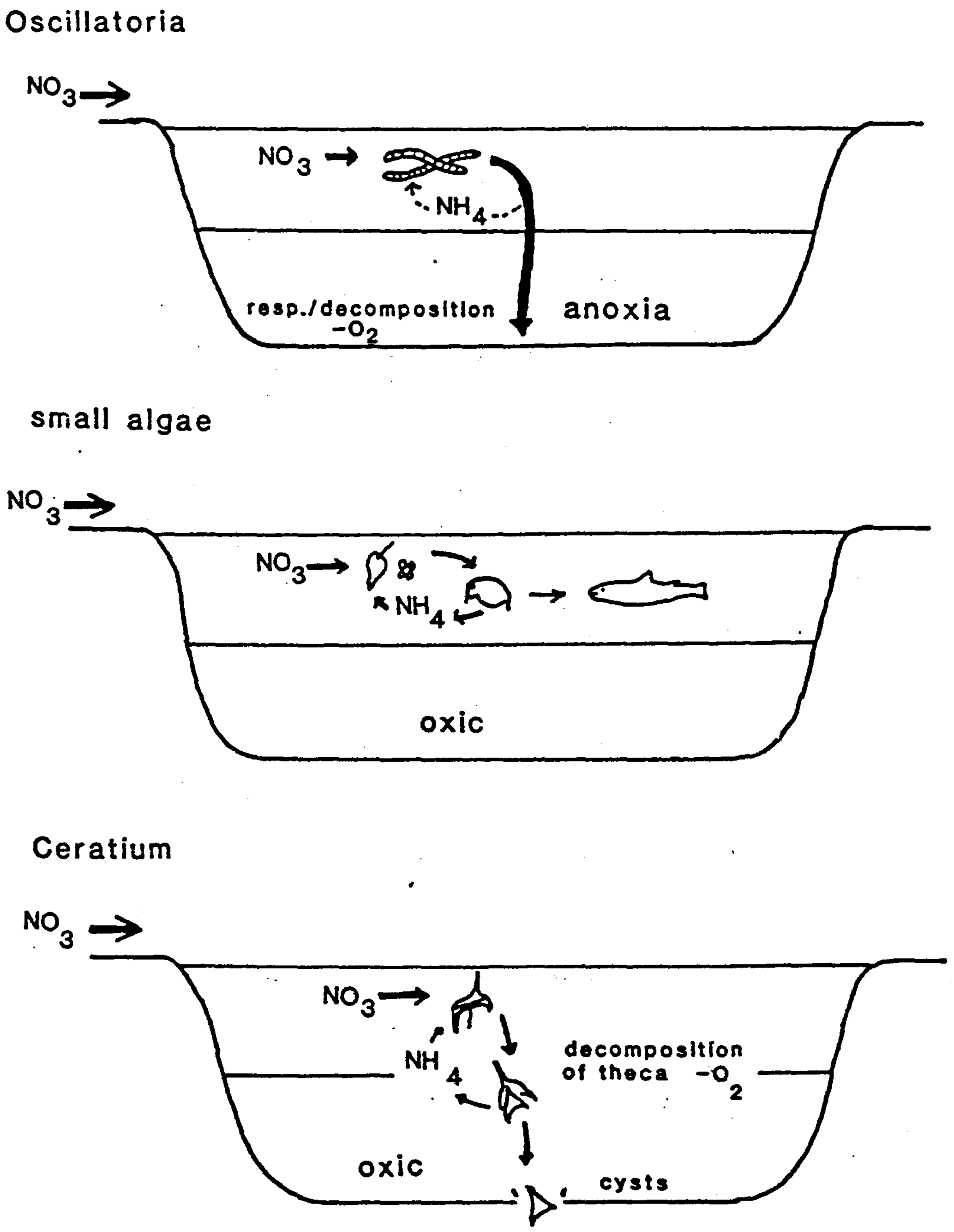
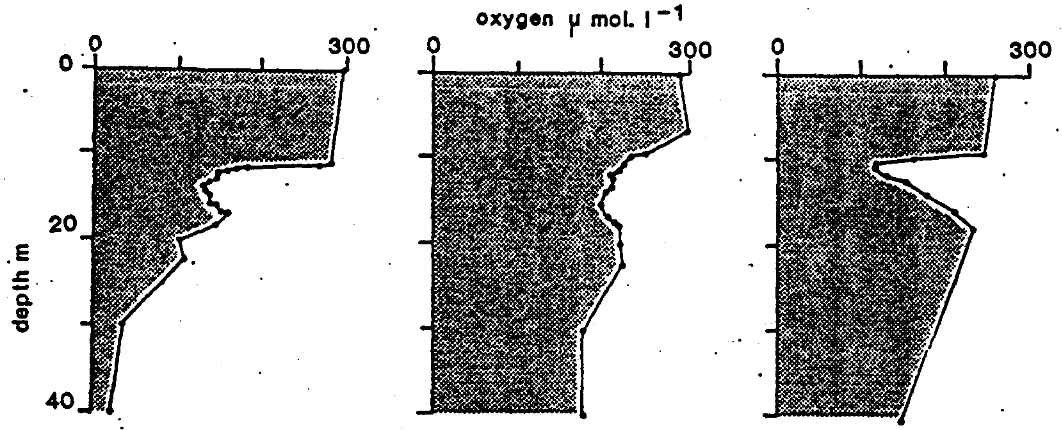


Fig. 36. Schematic representation of major pathways of algal losses in Windermere South Basin and their influence on epilimnetic nitrogen cycling and hypolimnetic deoxygenation.

FIG. 37



Oscillatoria bourrellyi

11 Sept 1984

small flagellates and greens

6 Sept 1983

Ceratium

7 Sept 1976

Fig. 37. Vertical profiles of oxygen concentration in Windermere South Basin during late summer for years with dominance of different algal groups.

FIG. 38

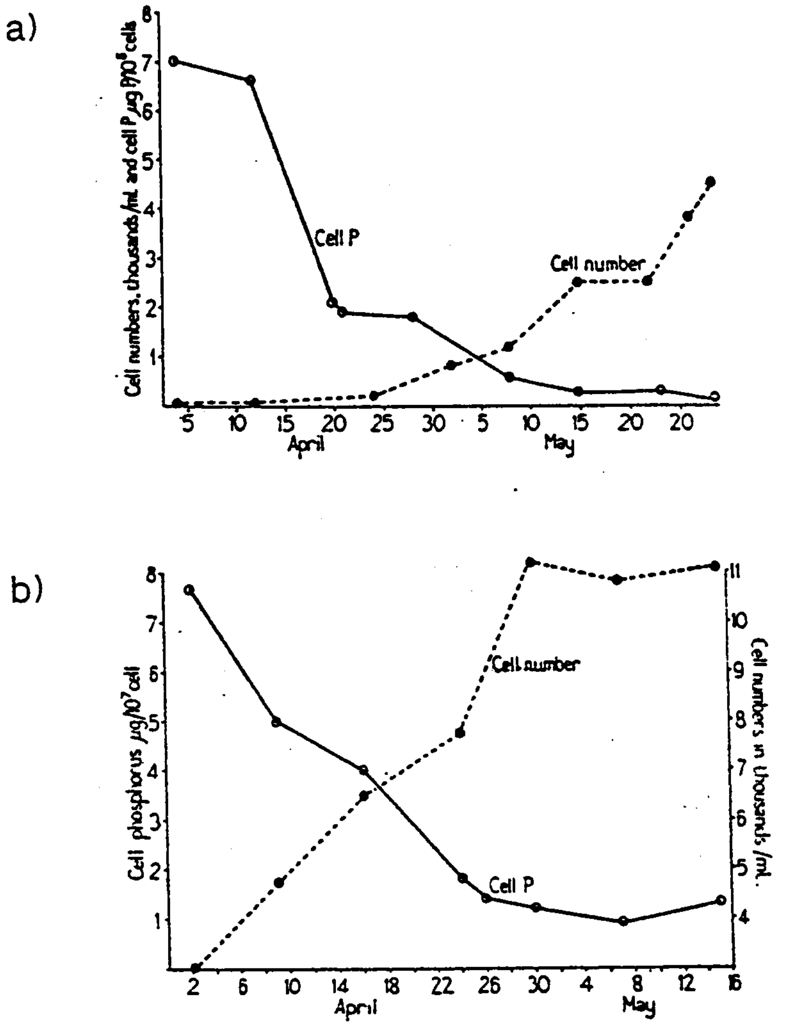


Fig. 38. The variation of cell phosphorus content (—o—) of natural <u>Asterionella formosa</u> from Windermere compared with the rise in <u>Asterionella</u> population (--●--). (a) gives 1950 data and (b) 1951 data. From Mackereth (1953).

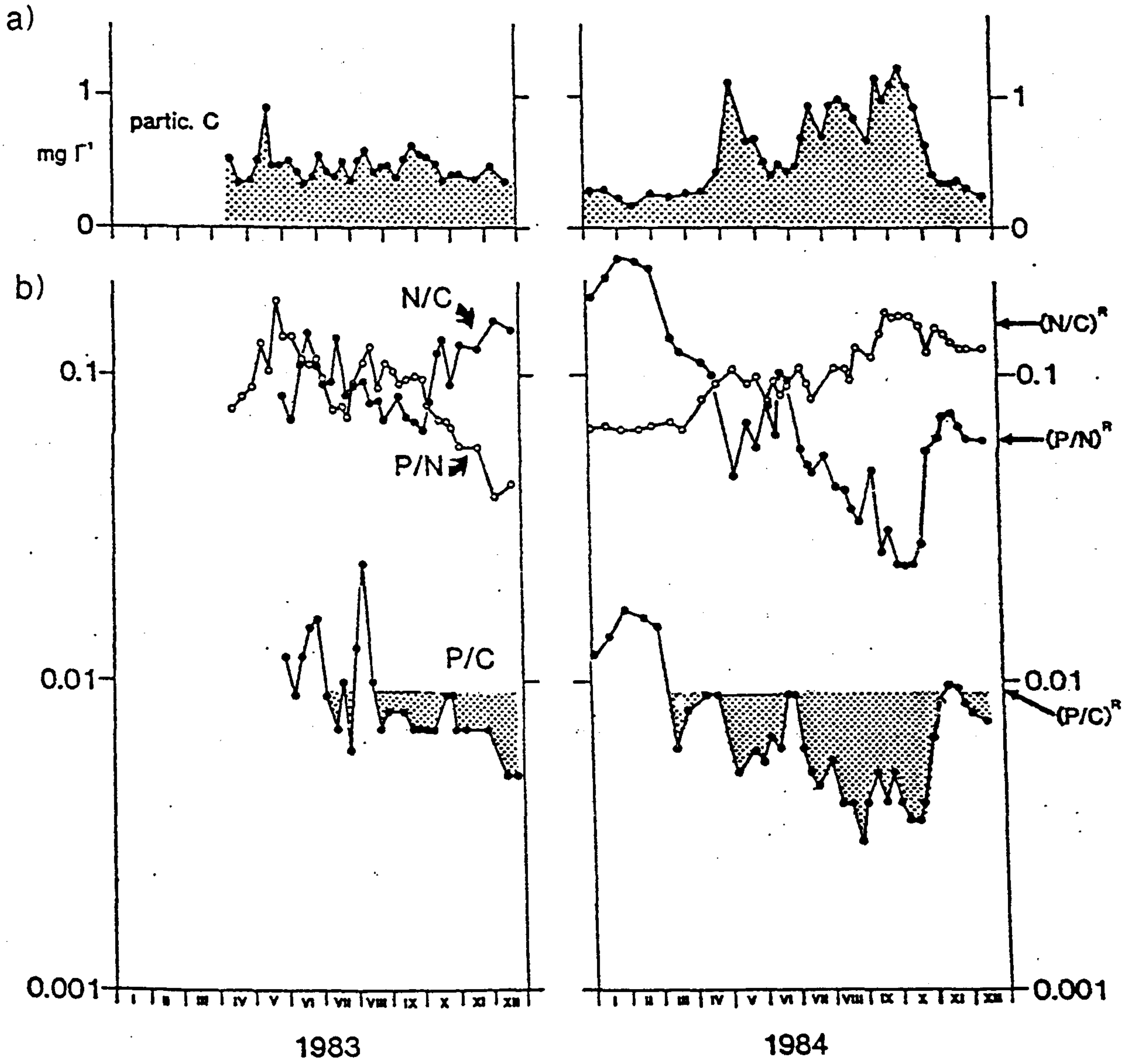


Fig. 39. North Basin: (a) the seasonal variation of particulate matter (as C content) in the 0-7 m layer during 1983 and 1984, with (b) its ratios by atoms of N/C, P/N and P/C. Arrows indicate the generalised Redfield ratios.

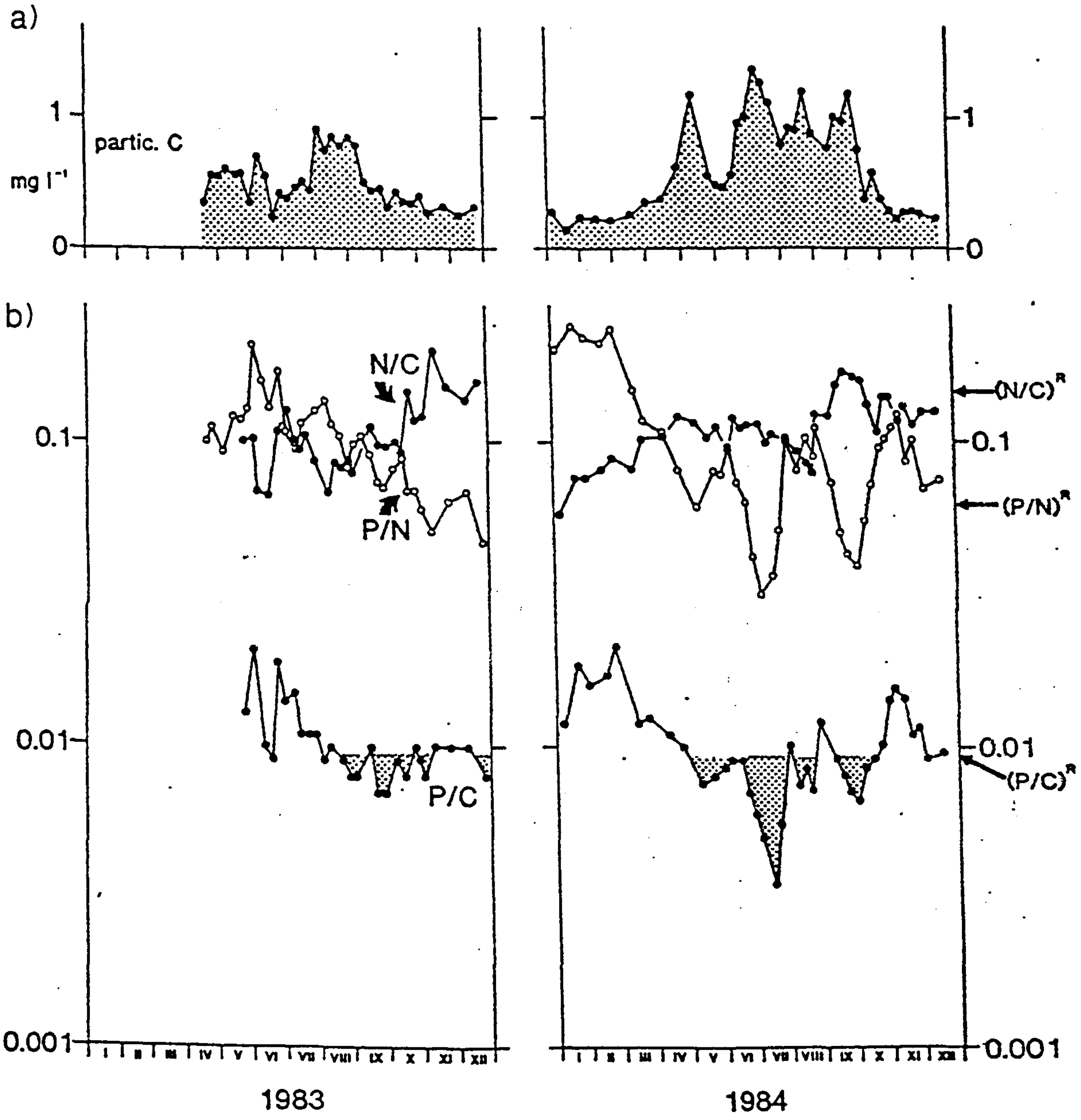


Fig. 40. South Basin: (a) the seasonal variation of particulate matter (as C content) in the 0-7 m layer during 1983 and 1984, with (b) its ratios by atoms of N/C, P/N and P/C. Arrows indicate the generalised Redfield ratios.

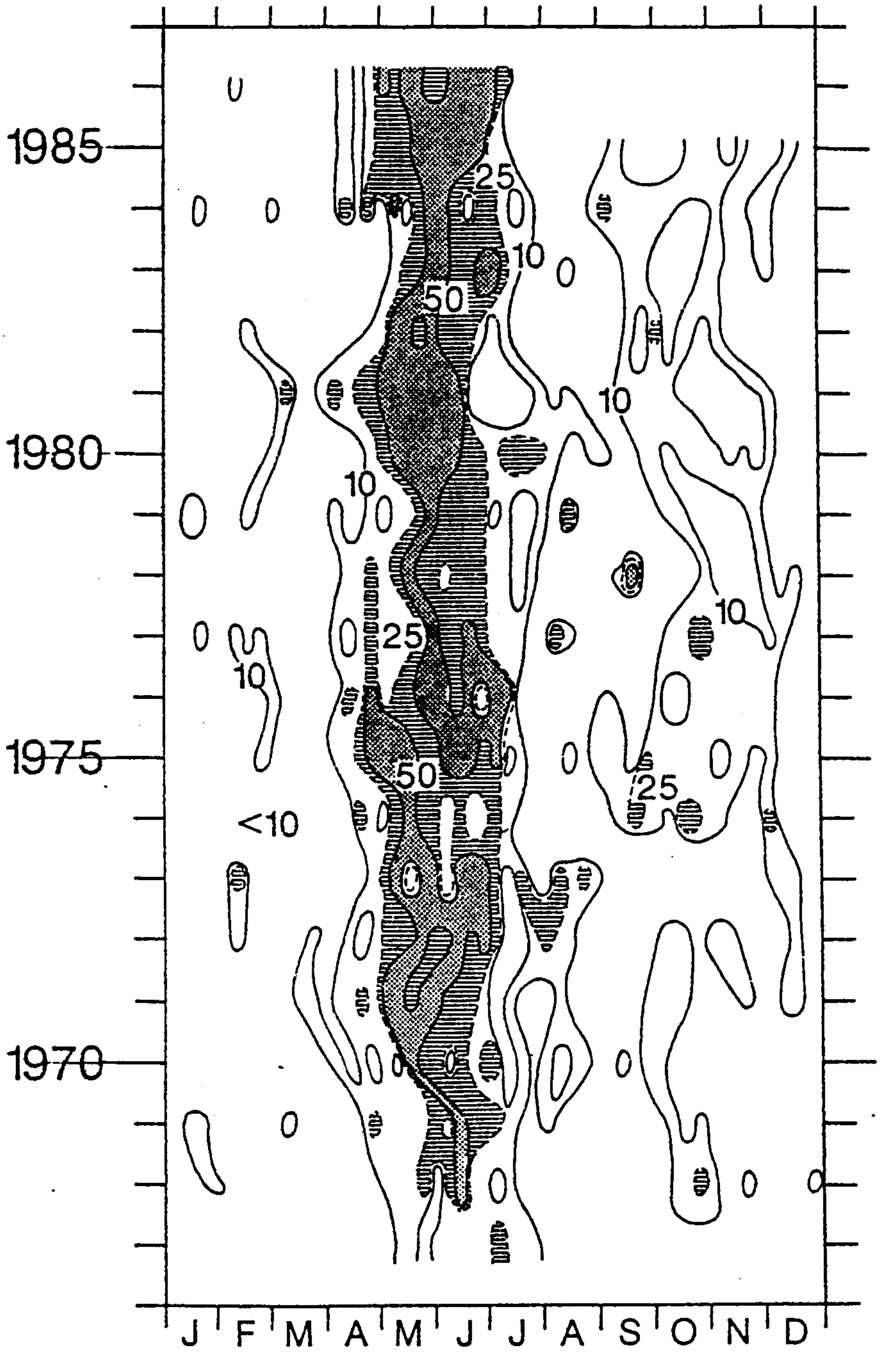


Fig. 41. North Basin: seasonal and long-term changes in the numbers of larger Crustacea (0-7 m layer) from 1967 to 1986, delimited by contours in individuals $(2\ l)^{-1}$.

FIG. 42

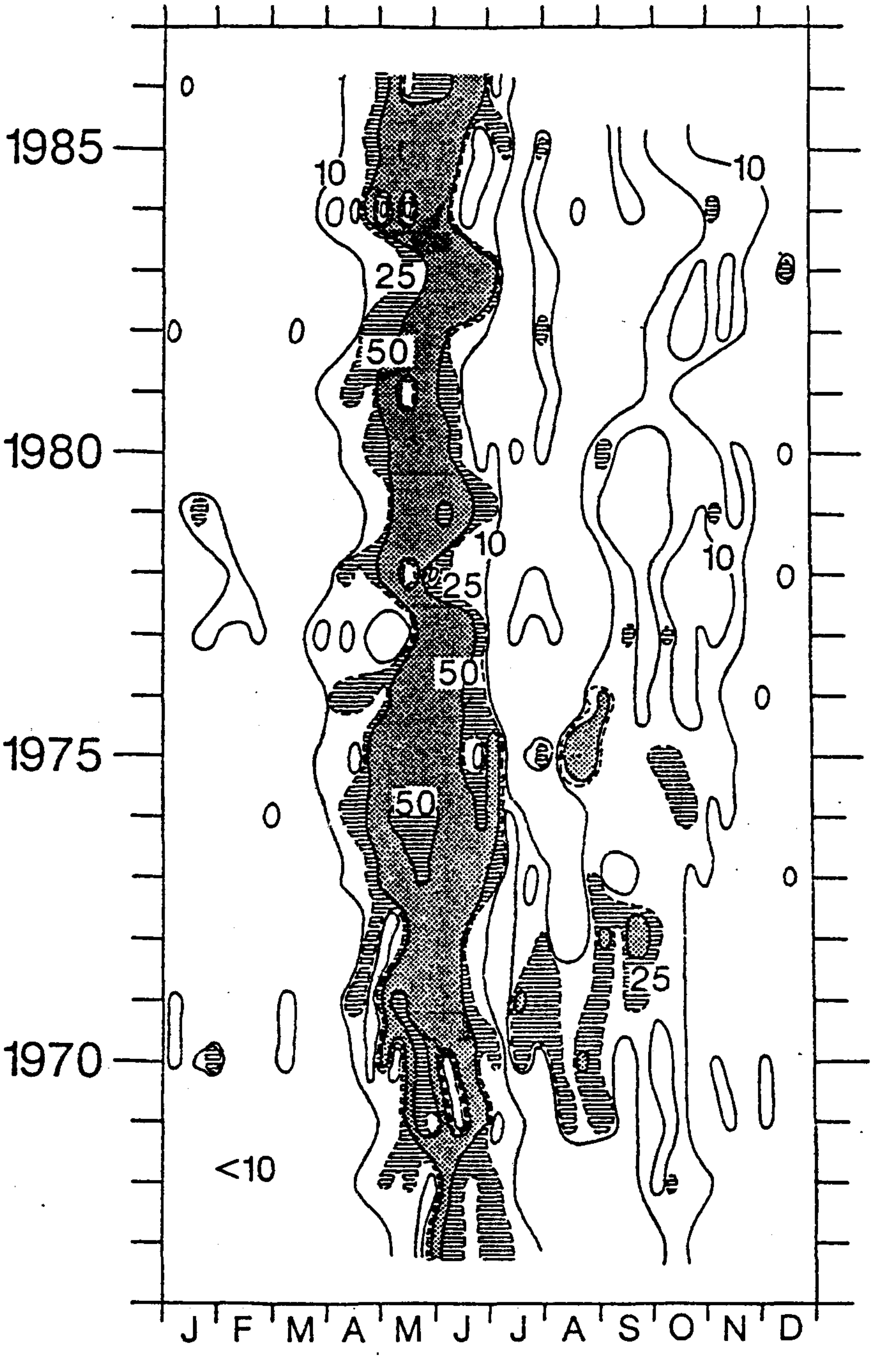


Fig. 42. South Basin: seasonal and long-term changes in the numbers of larger Crustacea (0-7 m layer) from 1967 to 1986, delimited by contours in individuals $(2\ l)^{-1}$.

FIG. 4

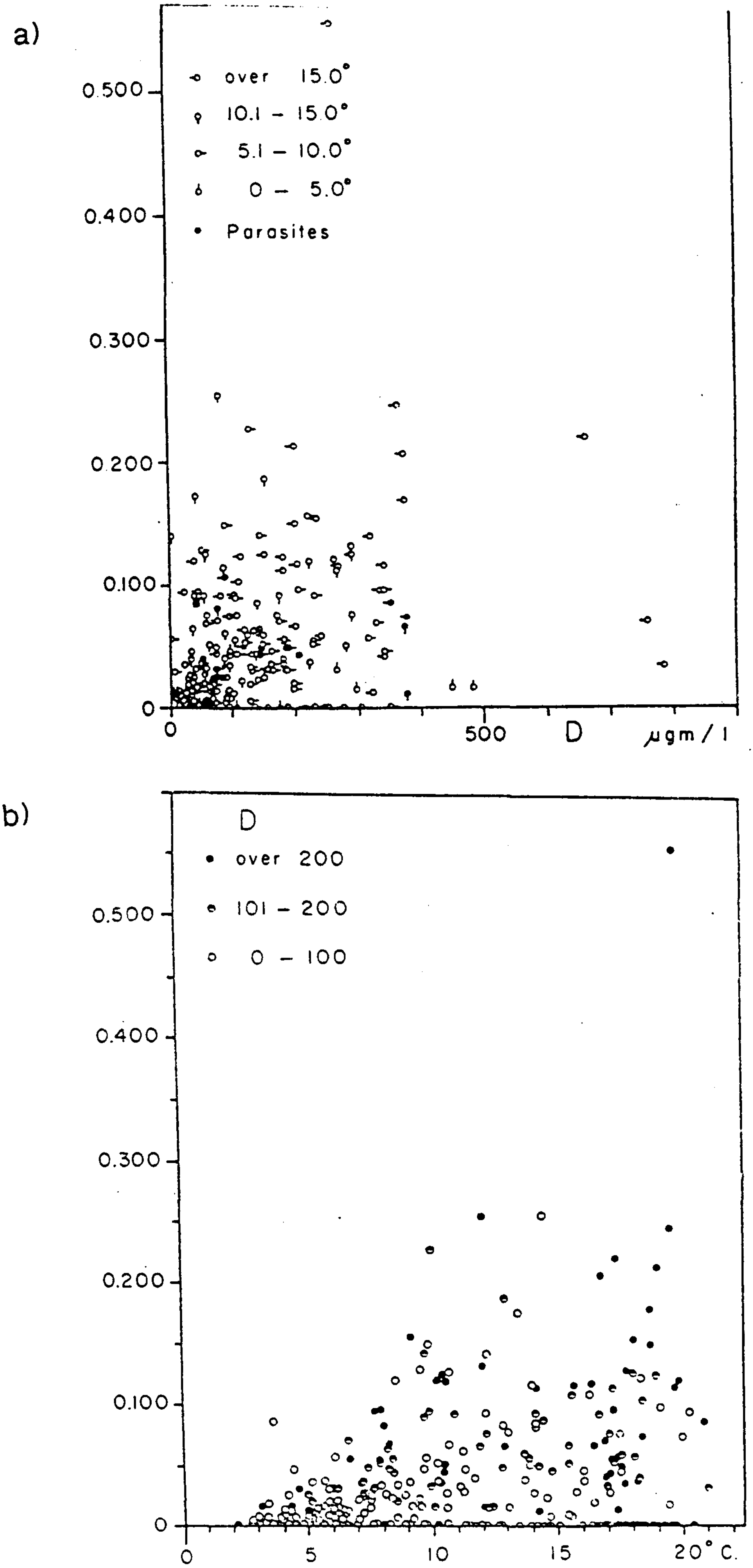


Fig. 43. The relationship between the birth rate (B) of the rotifer <u>Kellicottia longispina</u> in Windermere and (a) the abundance of food (D), (b) temperature. Symbols indicate ranges of temperature (Fig.1a), or food concentration (Fig. 1b). From Edmondson (1965).

FIG. 44

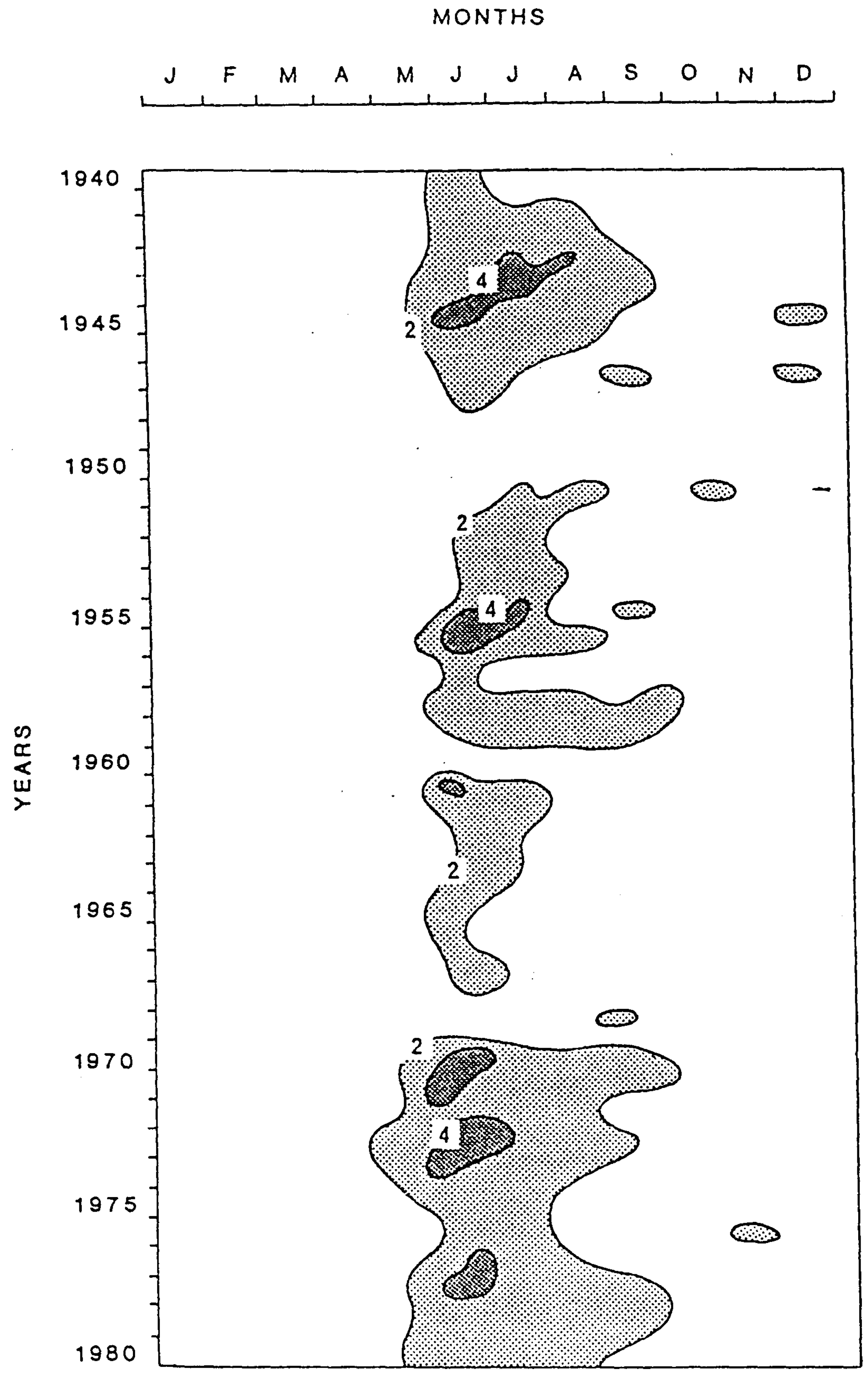


Fig. 44. The annual seasonal variations in the biomass of crustacean zooplankton in the North Basin of Windermere, 1940-1980. Values shown are dry weights m^{-2}, estimated from vertical net hauls at 2-weekly intervals.

FIG. 45

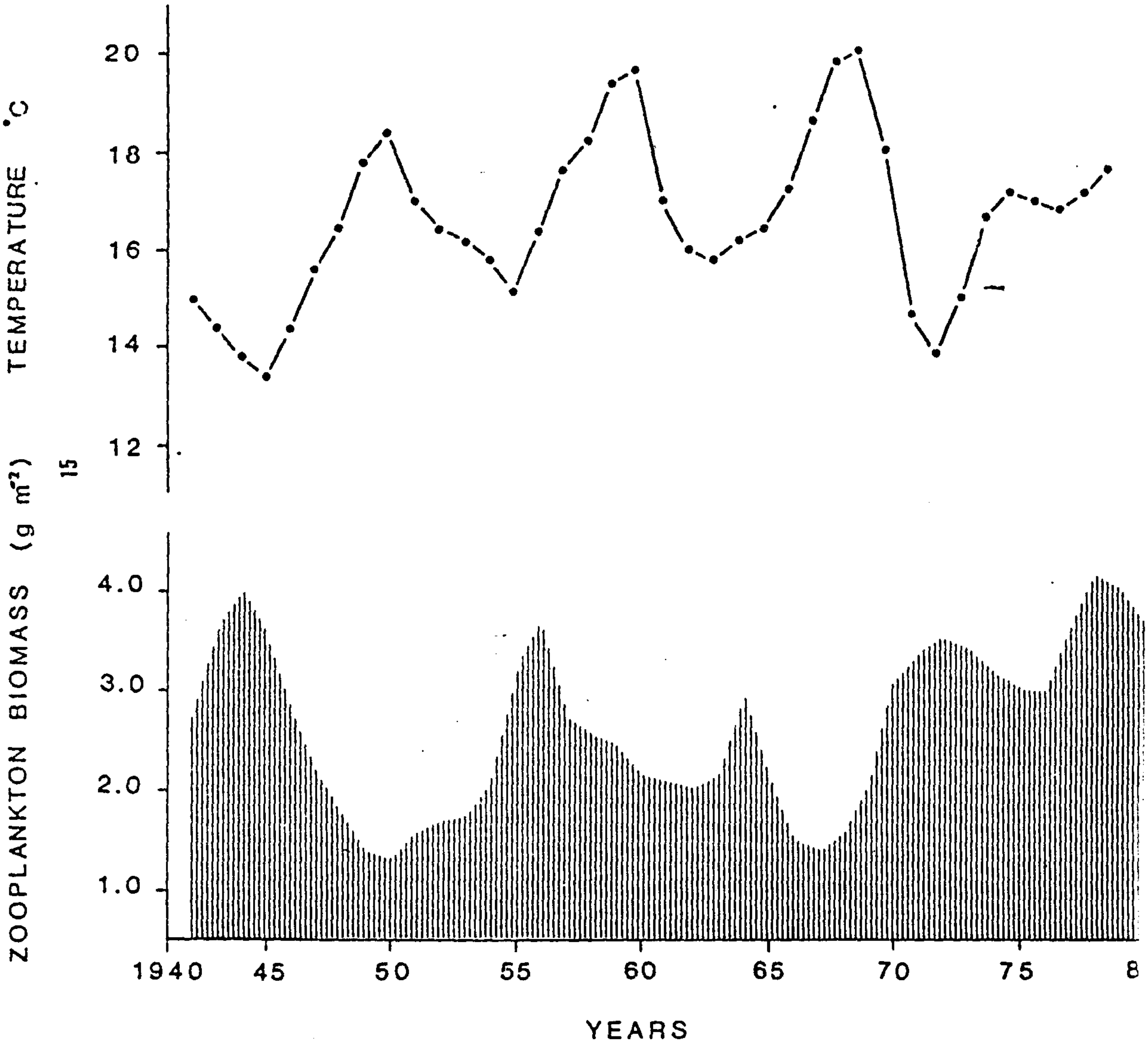


Fig. 45. Year-to-year variations in the mean summer (May to September) biomass of crustacean zooplankton compared with year-to-year variations in the mean June water temperature (0-5 m layer). The zooplankton information is taken from Fig.44, and smoothed with a three-point-centred moving average with weights 0.25, 0.5 and 0.25. Adapted from George & Harris (1985).

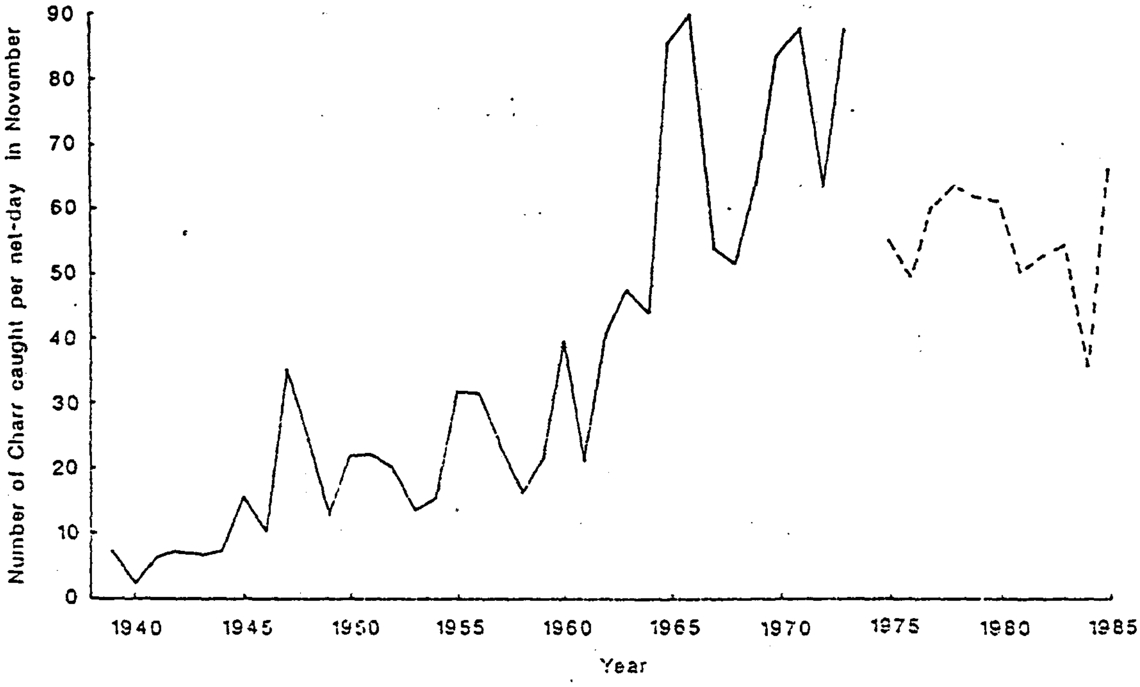


Fig. 46. The number of charr caught per net-day (CPUE) in November from 1939 to 1985. Solid line denotes Low Wray Bay; dashed line denotes Thompson Holme. The site was changed due to problems with disturbance of nets. Redrawn from Kipling (1984b) with the addition of further unpublished data.

FIG. 47

FIG. 48

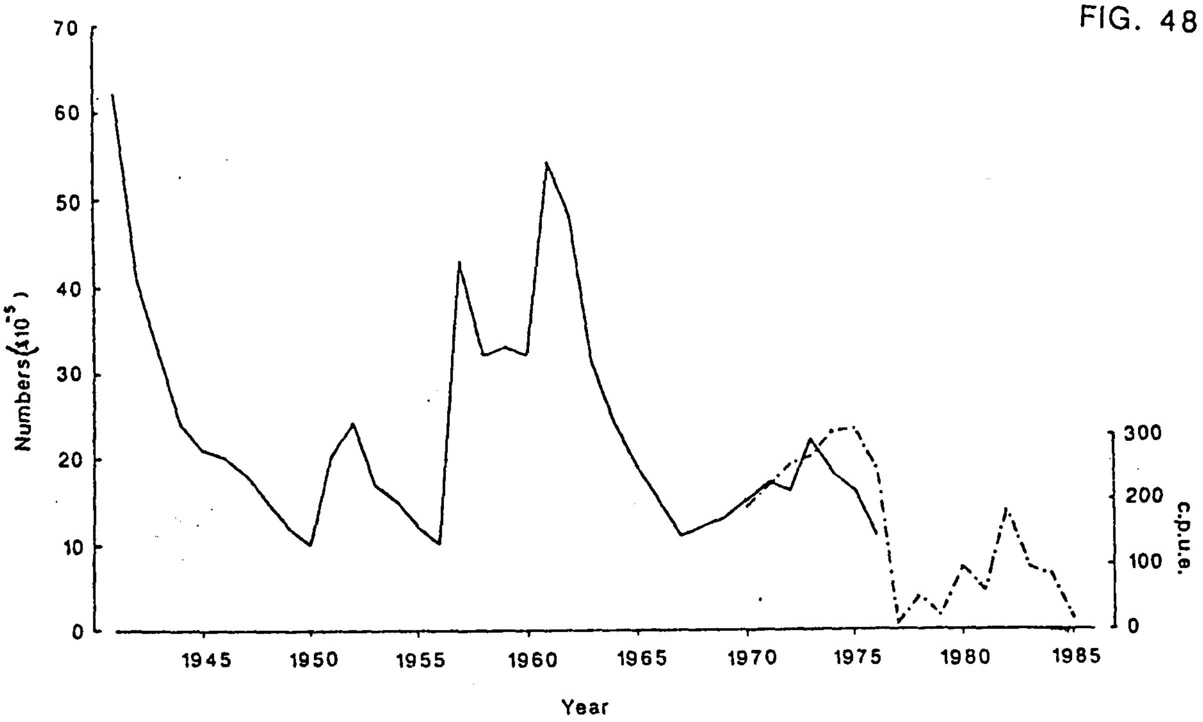


Fig. 47. The relative abundance of perch aged two years or over in the whole of Windermere from 1940 to 1985. The solid line denotes estimated population numbers. The broken line denotes data on catch per unit effort (CPUE) derived directly from the perch traps. Redrawn from Craig & Kipling (1983) with the addition of further unpublished data.

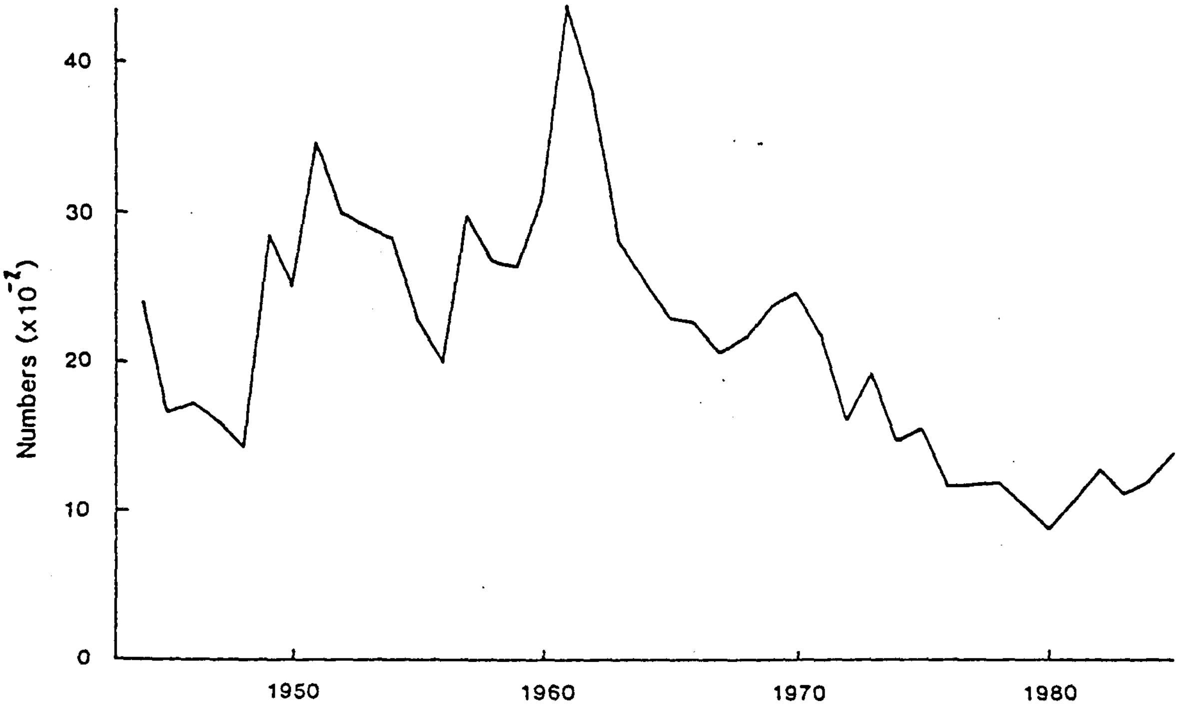


Fig. 48. The estimated numbers of pike aged two years and older in the whole of Windermere. Redrawn from Craig & Kipling (1983) with the addition of further unpublished data.

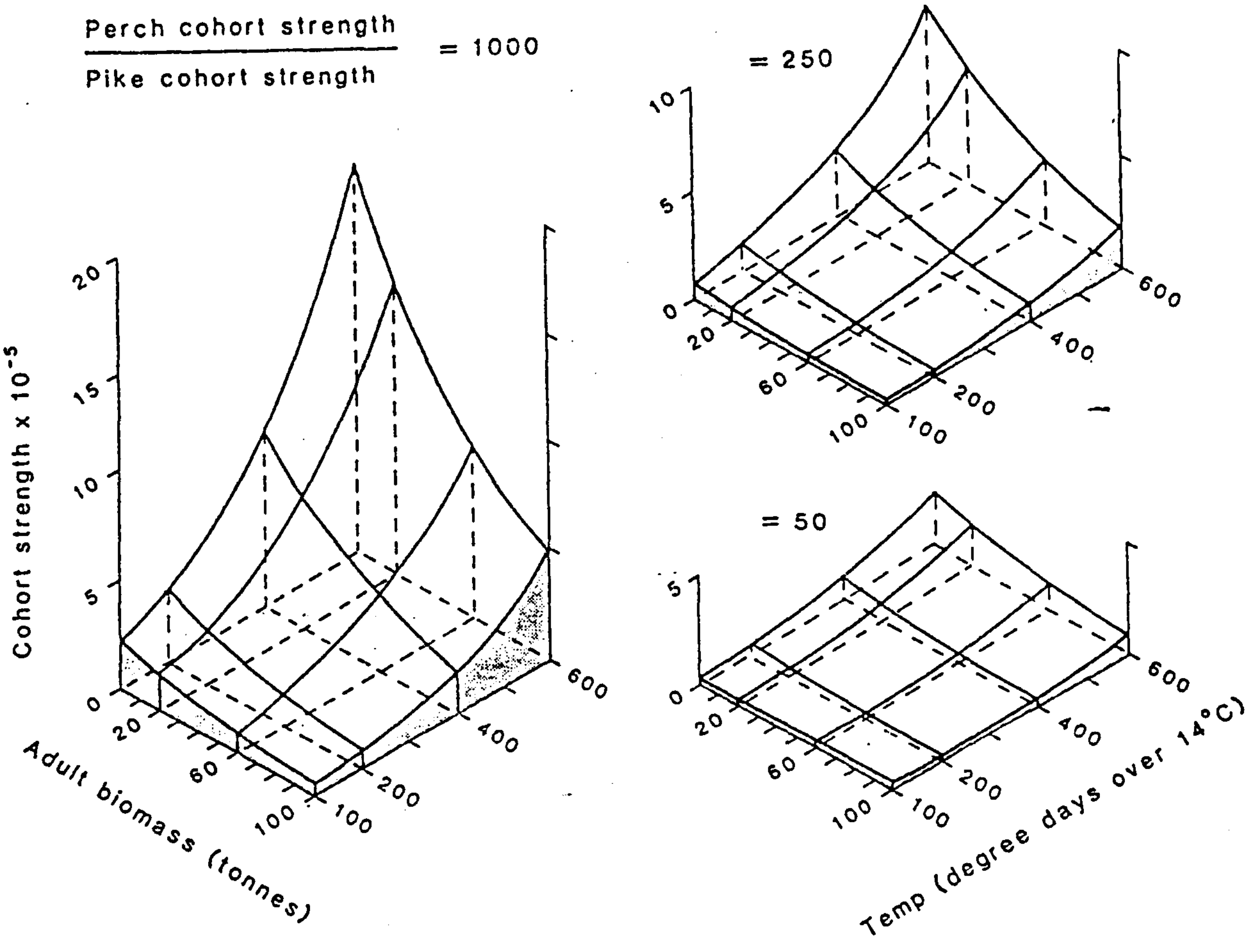


Fig. 49. Generalized relationships expressing the effect of adult biomass, temperature and pike on the cohort strength of perch at age 2 in Windermere North Basin. For a fuller description of the model see Craig (1982a), from which this figure is taken.

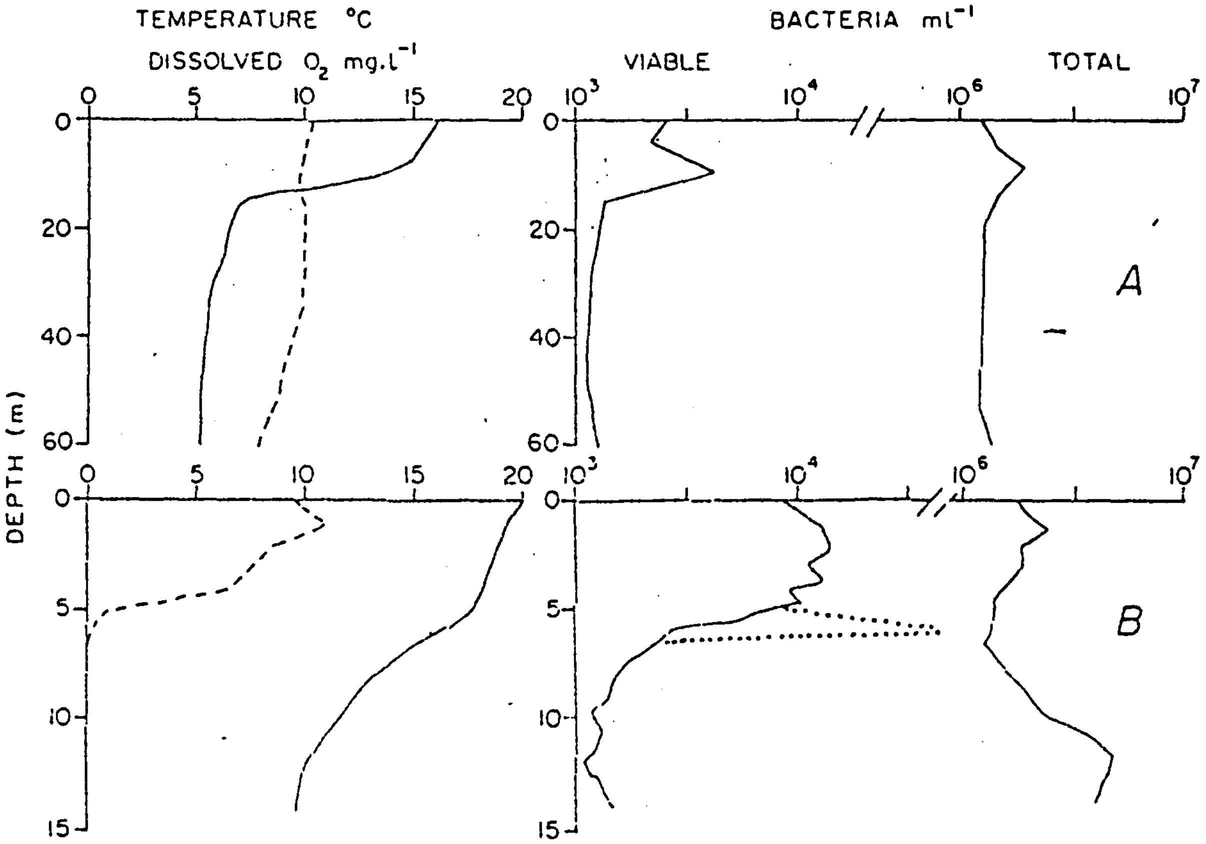


Fig. 50. The effect of stratification on the vertical distribution of bacteria in a deep and a shallow lake. A, Windermere North Basin, B, Esthwaite Water. ——— temperature, - - - dissolved O_2, ... magnitude of short term population maxima in the metalimnion. From Jones (1977).

FIG. 51

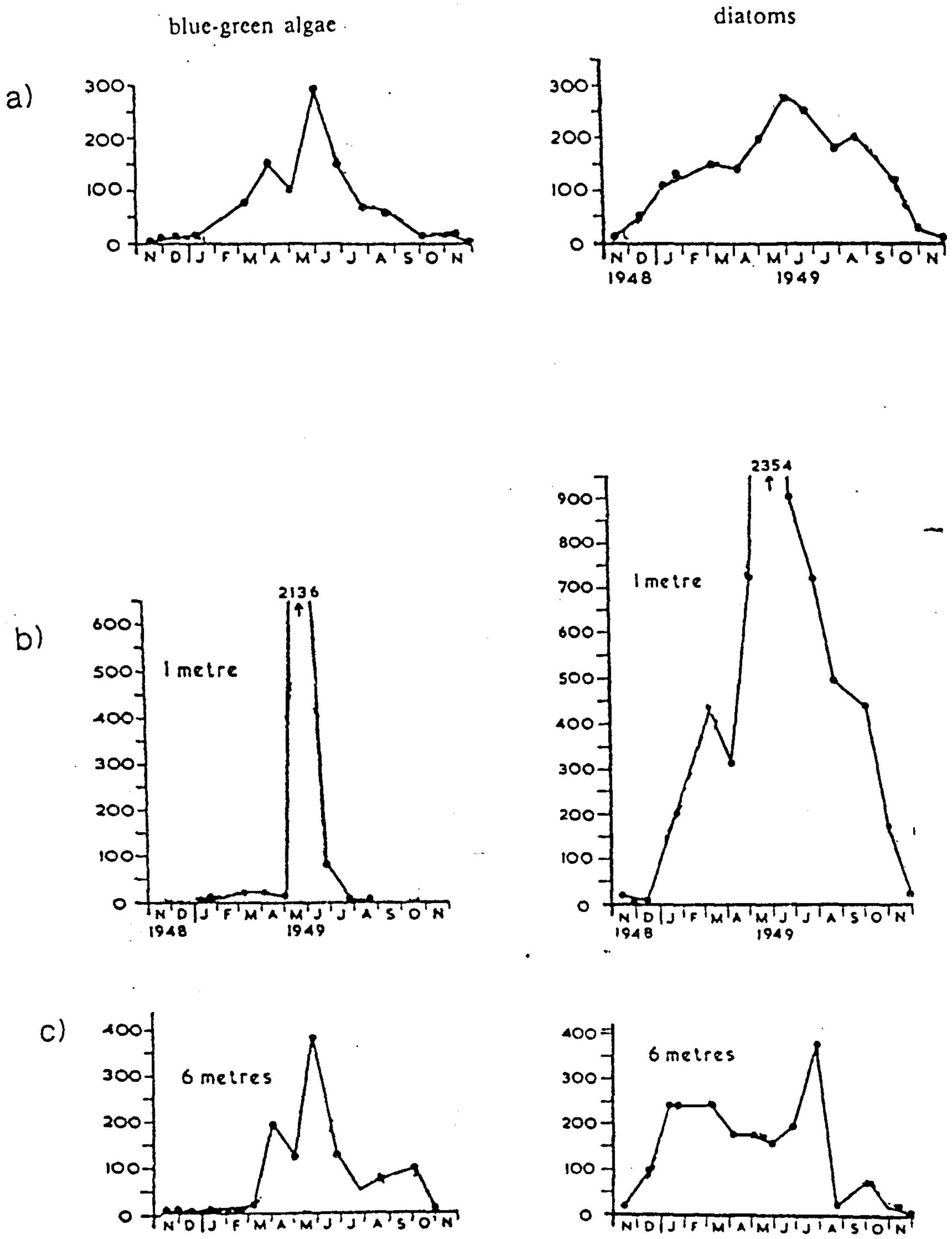


Fig. 51. An annual cycle (1948-9) in the relative numbers of (left) blue-green algae and (right) diatoms sampled from the surface of littoral sediments of the North Basin, as (a) mean numbers of stations at 1-6 m depth (b) numbers at 1 m (c) numbers at 6 m. From Round (1961b).

FIG. 52

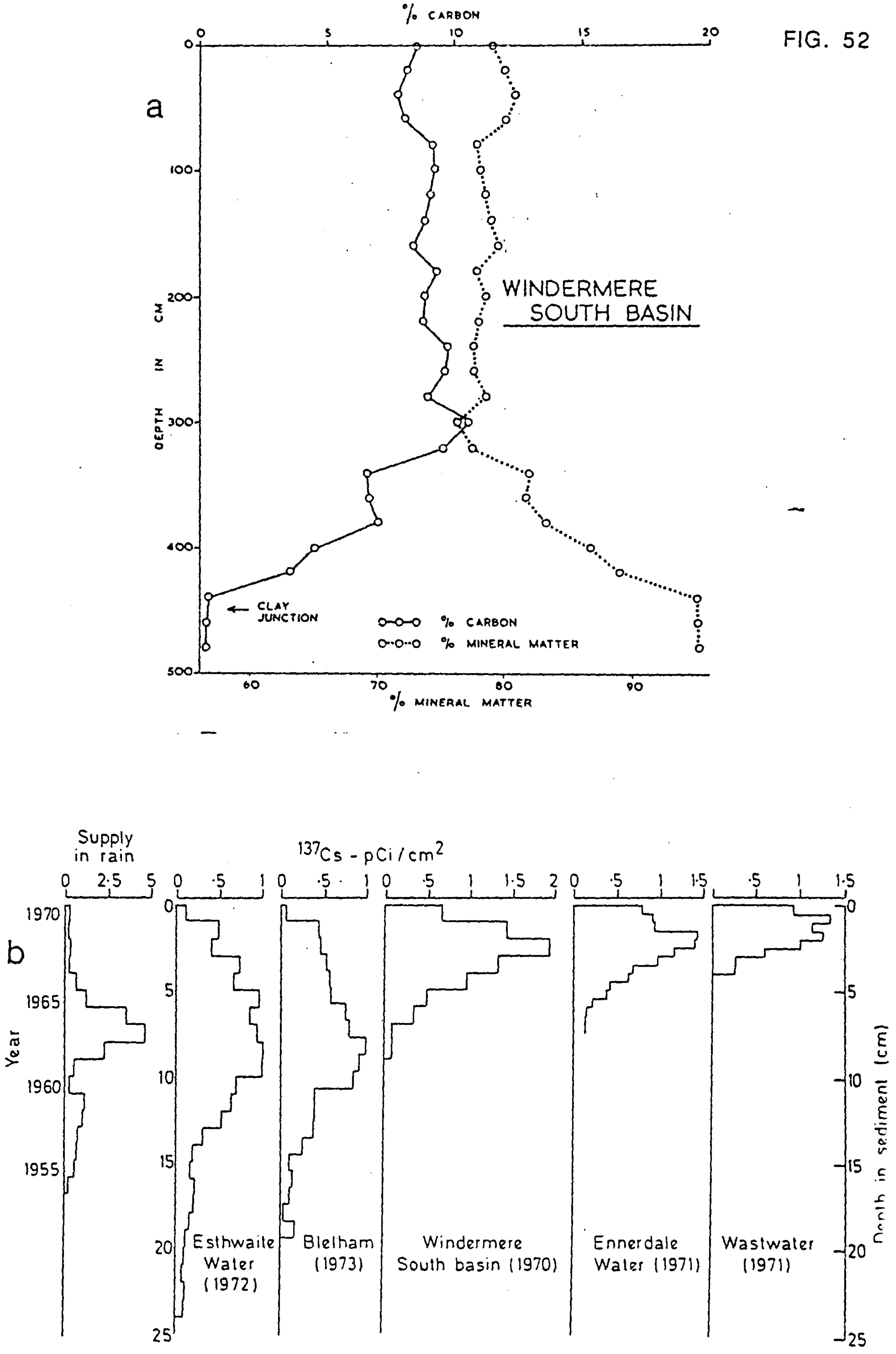


Fig. 52. Chemical profiles of lake sediments of Windermere South Basin, show (a) the changing proportions of organic carbon and mineral matter i the post-glacial period (from Mackereth 1966), (b) the sedimentary record from atmospheric input of the isotope ^{137}Cs during 1954-197 (Pennington 1973).

FIG. 53

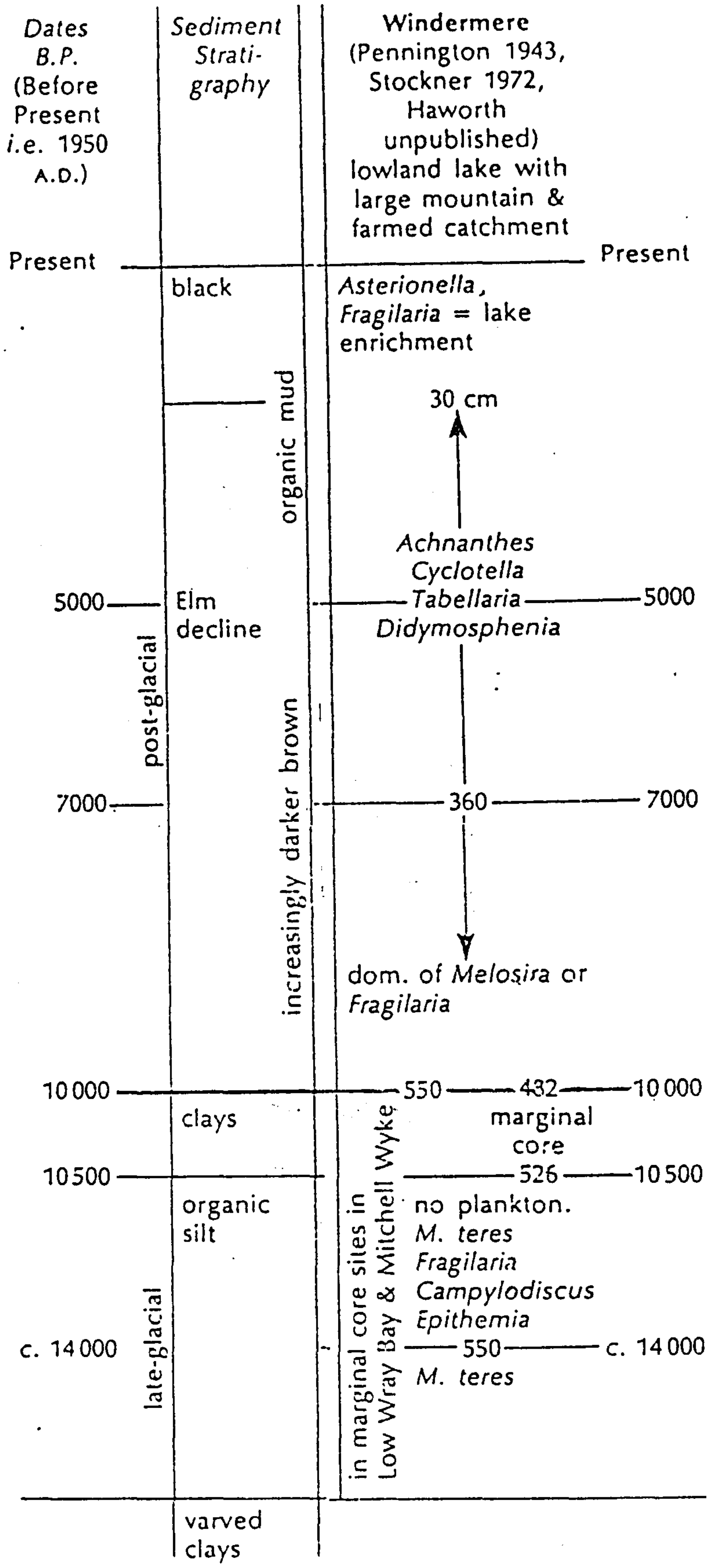


Fig. 53. A vertical, dated sequence of changing sediment types and diato representation in Windermere since the last ice-age (adapted fr Haworth 1985).