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An assessment of changing nutrient inputs
to Windermere and their influence on water
quality and charr population dynamics

by

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1. INTRODUCTION

Windermere (area 14.76 km²) is the largest natural English lake situated in an area of outstanding natural beauty in Cumbria. It is a Site of Special Scientific Interest and provides part of the water supply to the North West. The lake and its catchment provide a centre for intensive tourism and recreation.

In the early eighties the lake showed evidence of increasing nutrient enrichment. This was evident from regular summer blooms of the blue-green alga (cyanobacteria) Oscillatoria bourrellyi in the South Basin, followed by the development of anoxia in the deeper waters. In the light of this knowledge, North West Water (NWW) commissioned the Freshwater Biological Association (FBA now Institute of Freshwater Ecology IFE) to provide a general assessment of environmental and biological features of Windermere and their susceptibility to change (Atkinson et al., 1986). This Report showed that algal production is generally phosphorus limited. However, since 1945 there has been a c. 20-fold increase in the winter maximum of soluble reactive phosphorus (SRP) in the South Basin and a large estimated loading of SRP ($0.9 \text{ g P m}^{-2} \text{ yr}^{-1}$) to this basin. The North Basin showed less phosphorus enrichment and an estimated annual loading one third that of the South Basin. There has also been a small change in maximal algal biomass as indicated by chlorophyll a concentration, but significant shifts of algal quality during summer to regular growths of blue-green algae. The Report also indicated that the charr population, one of the 8 in England, might be particularly sensitive to the development of deep water anoxia.

Following this Report, NWW commissioned a two year study of Windermere to provide further information on its water quality, a more refined phosphorus budget, and an investigation of the biology and population structure of charr. The present report integrates these studies to provide an assessment of the nutrient status of the lake and its implications for the charr.

2. METHODS

2(a) Water quality

Regular sampling was undertaken at buoys near the deepest positions of both basins (N and S in Fig. 3). Vertical profiles of water temperature ($\pm 0.1^\circ\text{C}$) and oxygen (resolution $6 \mu\text{mol l}^{-1}$) were measured in situ using a combined thermistor and oxygen electrode. For a period, October to 8 November 1988, there were difficulties with stability of the oxygen electrode. Nevertheless, the very low oxygen values recorded from the hypolimnion of the North Basin at this time are unlikely to have an error greater than 14%.

Secchi disc transparency was obtained with a white disc of 30 cm diameter.

Water samples for chemical analyses and algal counts were collected using either a weighted plastic tube (Lund, 1949) from the 0-7 m layer, or using a Friedinger sampler for samples from discrete depths. A sub-sample was immediately fixed in the field with Lugol's iodine for subsequent algal counts using the Utermöhl inverted microscope technique (Lund et al., 1958). Measurements of filament lengths of blue-green algae were made using a modification of the squared-eyepiece-graticule technique of Olson (1950).

Total phosphorus, $\text{PO}_4\text{-P}$ (SRP), $\text{NH}_4\text{-N}$ and dissolved silicon were analysed as described by Mackereth et al., (1989) with the $\text{NH}_4\text{-N}$ method adapted for use with a discrete analyser, and ascorbic acid as the reductant for dissolved silicon. Nitrate nitrogen was analysed as described by Hilton & Rigg (1983).

Samples for total iron and total manganese were evaporated to dryness, digested with a mixture of perchloric and nitric acids, and determined as described in Mackereth et al., (1989).

Chlorophyll a was determined after separation of algae on glass-fibre filters (Whatman GF/C), extraction with boiling methanol, and estimation as the chlorophyll a equivalent (Talling, 1974).

2(b) Charr

Mature charr were gill-netted on their spawning sites using mesh sizes ranging from 19 to 46 mm (bar). Adult and juvenile charr were also netted outside of the spawning season from depths between 15 and 55 m using mesh sizes ranging from 10 to 46 mm (bar). Charr were also obtained from anglers catches. More details are given in Mills (1990). The long term FBA/IFE data from North Basin autumn spawning sites was collected by regular gill netting with 32 mm (bar) mesh during each November from 1939 to the present. Anglers catch per unit effort (CPUE) data is expressed here in terms of charr caught per boat per hour fished. The earliest set of angling diaries (angler 1) do not give precise information on the length of each fishing session. The six hours used here is a best estimate. Anglers 2 and 3 were able to provide very detailed information on hours fished as well as on the number of charr caught on each day and the basin in which they were caught.

3. PHYSICAL BACKGROUND

3(a) Hydrological Water Balance

This is given in detail in Atkinson *et al.*, (1986) and summarized below. Discharges from Windermere gauged by NWW at Newby Bridge Weir from 1939-1984 inclusive indicate that annual discharges from the lake have fluctuated in the range 110×10^6 to $689 \times 10^6 \text{ m}^3$. These values imply retention times for the whole lake of between 2.8 years and 5.5 months and for the South Basin of between 1 year and 1.9 months. The annual discharges and implied mean annual retention times for 1987 and 1988 were $431 \times 10^6 \text{ m}^3$, 8.8 months, and $537 \times 10^6 \text{ m}^3$, 7.0 months respectively. 1984, the most recent drought summer, had an annual discharge of $381 \times 10^6 \text{ m}^3$ with an implied mean annual retention time of 9.9 months.

The total monthly rainfall measured at Ambleside for 1987 and 1988 is given in Fig. 1 and shows that January, July and August were considerably wetter in

1988 than in 1987. Corresponding values of mean monthly lake level and discharge are given in Fig. 2.

3(b) Temperature stratification

The general pattern of stratification was similar for both 1987 and 1988 (Fig. 3). The temperature of the epilimnion and hypolimnion of the South Basin with its smaller volume and shallower depth tended to be marginally warmer (1°C) during stratification than in the larger and deeper North Basin. Similarly, as a result of its smaller heat capacity, the minimum winter temperatures of the South Basin were lower than in the North Basin.

Both years were relatively warm during winter, spring and early summer. Except for a brief period in January 1987, temperatures did not fall below 4°C and stratification was well established by April of both years. 1987 was characterized by a period of early warming and stratification was well developed during late April and July. An exceptionally warm early summer in 1988 resulted in temperatures of the upper 0-5 m layer exceeding 18°C by the end of June with steeply developed stratification in the 0-15 m layer. This was followed by a period of cooling and mixing during July, a further period of warming in early August and then a gradual deepening of the thermocline until overturn. In both years overturn occurred in early December in the North Basin and somewhat earlier in the South Basin.

3(c) Light attenuation

The depth at which a white disc of 30 cm diameter (Secchi disc) disappears from view when lowered into the water gives a useful measure of transparency. Secchi disc values are given for both basins for 1987 and 1988 superimposed against measurements of chlorophyll a, an index of algal biomass (Fig. 4).

There was a general pattern of annual underwater light penetration which was inversely correlated with algal abundance. Associated with the spring

diatom growth there was a marked decline in water transparency with Secchi disc values as low as 2 m depending upon the size of the diatom population. Diatom sedimentation following silicon depletion resulted in a "clear water phase" where Secchi disc values exceeded 8 m (e.g. North Basin, June 1988). The steepness, extent and duration of the rise in water clarity, was determined by the strength of stratification which enabled rapid sedimentation of silicon-limited diatom populations, and upon the timing of appreciable new algal growth. This new summer growth occurred early in the South Basin during 1988 and resulted in a poorly developed "clear water phase". The mean annual Secchi disc values and standard deviations for the North Basin for 1987 and 1988 were 4.76 ± 1.51 and 4.68 ± 1.27 m respectively; the corresponding values for the South Basin were 4.14 ± 1.37 and 4.13 ± 1.15 .

4. CHEMICAL LEVELS AND DYNAMICS

4(a) Dissolved oxygen

Oxygen is produced as a result of photosynthesis by phytoplankton in the euphotic zone of the upper layers of the lake. It is consumed in the lower aphotic zone by respiration and decomposition. Isopleths of oxygen concentration for both basins of Windermere for 1987 and 1988 are given in (Fig. 5). There was considerable variation in patterns of oxygen depletion both between basins and between years.

In Windermere depletions of oxygen can be seen within the thermocline. Such depletions were apparent in the North Basin particularly during July and August 1987, and to a certain extent, but much less developed, in 1988. No appreciable oxygen minima however were apparent in the South Basin in either year.

In the South Basin depletions of oxygen were much more obvious in the hypolimnion. During 1987 oxygen concentration only fell to $> 10 \mu \text{mol l}^{-1}$ or 1% saturation by November. This was in contrast to 1988 when anoxic conditions

within the hypolimnion occurred between the end of September and mid-November extending upwards to a depth of about 25 m. In the North Basin the minimum percentage saturation of oxygen at 60 m depth during 1987 and 1988 were 45% (September) and 17.5% (November) respectively. The 1988 minimum is the lowest oxygen value ever recorded from the North Basin. At this time water below 30 m depth (19% of the North Basin volume) was less than 25% saturated ($< 100 \mu \text{mol l}^{-1}$) indicating an unprecedented deterioration of water quality.

Oxygen depletions within the thermocline or hypolimnion represent different depth locations of algal recycling within the lakes. There is a correlation between algal quality and quantity and location and extent of oxygen depletion. This is particularly apparent with the blue-green alga (cyanobacterium) Oscillatoria bourrellyi which was associated with hypolimnetic depletions of oxygen following its decline in the surface waters and sedimentation. Its earlier population growth and sedimentation in the South Basin during 1988 compared to 1987 (Fig. 17) was associated with an earlier development of hypolimnetic anoxia in 1988. Compared to the South Basin, maximum population densities of O. bourrellyi in the North Basin were appreciably lower, resulting in a smaller carbon flux into a larger hypolimnetic volume. In 1987 most of the O. bourrellyi biomass in the North Basin was retained in the upper layer until after overturn resulting in negligible hypolimnetic deoxygenation. In 1988 there was a marked decline in population density in the surface waters during September with a subsequent pronounced deoxygenation well before overturn. The phasing of the sedimentation of O. bourrellyi from the surface layers of both basins is closely correlated with the degree and timing of hypolimnetic deoxygenation (Atkinson et al., 1986).

Increases in alkalinity and pH are largely a consequence of increased biological production. pH levels may rapidly rise and fall with removal of dissolved CO_2 from surface waters through photosynthesis and its replacement by gas exchange with the atmosphere as a result of mixing episodes. Alkalinity can, to some degree, be regarded as an integrator of seasonal production although altered by form of nitrogen uptake by phytoplankton (nitrate uptake, increased alkalinity; ammonia uptake, decreased alkalinity), and dilution from inflows.

Seasonal changes of alkalinity (Fig. 6) and pH (Fig. 7) are given for 1987 and 1988 for both basins of Windermere. Alkalinity showed a marked annual increase reaching its maximum during September and October. The annual increment in both basins was greater during the drier summer of 1987.

pH showed much greater increases ($> \text{pH } 9$) in the South Basin than in the North Basin during major phases of algal growth under stable weather conditions. For both years the maximum values of pH for the North and South Basins were 8.3 and 9.4 respectively.

4(c) Major plant nutrients

The major factors affecting long-term and seasonal changes of plant nutrients in Windermere have been described and discussed by Atkinson *et al.* (1986), Heaney *et al.* (1988) and Talling & Heaney (1988). The elements carbon, phosphorus, nitrogen, and for diatoms silicon, are the major nutrients required for growth of phytoplankton. Except for carbon which can be replenished rapidly by atmospheric exchange, the other nutrients are mainly supplied from the catchment, including inputs from treated sewage. Plant nutrients increase during winter months when algal production is low and consumed during the growing seasons. Figures 8-10 show the concentrations of SiO_2 , $\text{PO}_4\text{-P}$, $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ in the 0-7 m layer for the North and South Basins of Windermere during 1987 and 1988.

Concentrations of dissolved silicon (present as silicic acid) declined from maximum winter concentrations of c. $2 \text{ mg SiO}_2 \text{ l}^{-1}$ during the spring diatom growth phase in both basins (Fig. 8). This took place earlier (March/April) in the South Basin than in the North Basin (April/May). The spring diatom growth reduced dissolved silicon to very low concentrations after which it was gradually resupplied from the catchment, particularly during autumn and winter.

The concentrations of soluble reactive phosphorus for both basins of Windermere for 1987 and 1988 are given together with those of dissolved silicon in Fig. 8. This shows the approximately 2-fold greater concentrations of winter $\text{PO}_4\text{-P}$ in the South Basin compared to the North Basin. The increased phosphorus enrichment of the South Basin is further indicated by the simultaneous decline of both dissolved silicon and $\text{PO}_4\text{-P}$. This is in marked contrast to the North Basin where $\text{PO}_4\text{-P}$ decreases much earlier than dissolved silicon indicating a much higher degree of phosphorus depletion of the spring diatom population than for that of the South Basin. The concentrations of $\text{PO}_4\text{-P}$ remained near the limit of detection ($< 0.6 \text{ } \mu\text{g P l}^{-1}$) for most of the summer in both basins. However, unlike the sixties and seventies (Heron 1961; FBA unpublished results) there is now evidence of internal phosphorus recycling during summer months, especially in the South Basin. The very rapid recovery of $\text{PO}_4\text{-P}$ during October of both years in the South Basin was largely the result of entrainment of deep hypolimnetic concentrations with the autumnal deepening of the thermocline prior to overturn (Fig. 12). Appreciable concentrations of $\text{PO}_4\text{-P}$ were absent from the hypolimnion of the North Basin (Section 4d). The mean annual concentrations and standard deviations of $\text{PO}_4\text{-P}$ in the upper 0-7 m layer of the North Basin for 1987 and 1988 were 0.0022 ± 0.0025 and $0.0025 \pm 0.0031 \text{ } \mu\text{g l}^{-1}$ respectively, and for the same years in the South Basin 0.0085 ± 0.0091 and $0.0092 \pm 0.0100 \text{ } \mu\text{g l}^{-1}$ respectively.

Winter concentrations of nitrate-nitrogen of both basins declined from c. $600 \mu\text{g l}^{-1}$ to variable summer minima as a result of both uptake by algae and bacterial denitrification. Summer concentrations fell to below the limit of detection ($< 14 \mu\text{g l}^{-1}$) in the South Basin at the end of August 1987 and during July 1988. The timing of the summer minima corresponded to the maximum biomass of Oscillatoria bourrellyi (Fig. 17). The concentration of $\text{NO}_3\text{-N}$ did not fall to the limit of detection in either year in the North Basin possibly reflecting the lower biomass (approximately one third) of O. bourrellyi compared to the South Basin.

Phytoplankton normally use ammonia-nitrogen in preference to nitrate-nitrogen. Consequently high levels of ammonia-nitrogen are usually associated with either mineralization of phytoplankton in the upper layers or entrainment of hypolimnetic water rich in ammonia near the time of the autumnal overturn. Examples of epilimnetic recycling of ammonia-nitrogen can be seen for the two basins for both years during early spring and autumn (Fig. 10). Entrainment of hypolimnetic ammonia-nitrogen was only appreciable for the South Basin (Section 4(d) Fig. 12).

As in nearby Estwaite Water (Heaney & Butterwick, 1989) concentrations of total phosphorus (Fig. 11) showed little correspondence to algal biomass in either basin. For the South Basin the increase of total phosphorus between October and December is enhanced by inputs of $\text{PO}_4\text{-P}$ from hypolimnetic entrainment during overturn. The mean annual total phosphorus concentrations and standard deviations in the upper 0-7 m layer in the North Basin for 1987 and 1988 were 0.0139 ± 0.0034 and $0.0142 \pm 0.0048 \mu\text{g P l}^{-1}$ respectively, and for the same years in the South Basin 0.0251 ± 0.0047 and $0.0249 \pm 0.0059 \mu\text{g P l}^{-1}$ respectively.

4(d) Summer stratification

The vertical distribution at selected depths of concentrations of chlorophyll a, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, total Fe and total Mn between June and October 1987 and June and November 1988 are shown in Fig. 12. This shows algal biomass mainly restricted to the upper layers of the lake and the increase with depth of plant nutrients in the South Basin. Particularly noteworthy are the marked increases in $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ in the shallower South Basin.

The development of reducing conditions in soft-water Cumbrian lakes is accompanied by first an increase in total manganese followed by total iron during complete anoxia (e.g. Mortimer, 1941-42, Heaney et al., 1986). During 1987 and 1988 both basins showed an increase in concentration of total manganese. This increase was much more pronounced in the South Basin. Appreciable increases in total iron with depth were not detected in either basin.

5. AN ASSESSMENT OF NUTRIENT INPUTS

5(a) Phosphorus budget for Windermere

Mackereth (1953) showed that phosphorus was present in cells of the diatom Asterionella formosa in very low amounts and that this element could limit its growth in Windermere. Further measurements of particulate phosphorus and carbon of the phytoplankton of Windermere during 1983 and 1984 indicated that in spite of considerable phosphorus enrichment since the fifties, phosphorus was still the element most likely to control the growth of phytoplankton in the lake (Atkinson et al. 1986). An approximate assessment of phosphorus inputs to Windermere in Atkinson et al., (1986) also indicated that the South Basin is now receiving a high annual loading of soluble reactive phosphorus ($0.91 \text{ g PO}_4\text{-P m}^{-2} \text{ yr}^{-1}$) sufficient to support large algal biomass. The North

Basin was estimated to have an annual loading about one third that of the South Basin ($0.28 \text{ g PO}_4\text{-P m}^{-2} \text{ yr}^{-1}$) but still sufficient for moderate algal production.

In 1988 NWW requested the FBA to prepare a phosphorus budget for Windermere and sought a preliminary opinion as to the likely effect of removing or not removing approximately 80% of the phosphorus from the Tower Wood outfall (Heaney & Talling (1988)). The phosphorus budget determined is reproduced in this present report as Table 1 and Fig 13. There is no new data and the calculations and assessment contained in Heaney & Talling (1988) are unaltered. In summary:

1. The total phosphorus loading to the whole lake is $1.04 \text{ g P m}^{-2} \text{ yr}^{-1}$ and to the North and South Basins 1.10 and $1.67 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively.
2. The soluble reactive phosphorus loading to the whole lake is $0.60 \text{ g P m}^{-2} \text{ yr}^{-1}$ and to the North and South Basins 0.32 and $1.18 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively.
3. The most probable annual flux of total phosphorus to the lake sediments is $6.8 \text{ tonnes yr}^{-1}$ out of a total input of 15.48 tonnes .
4. The contributions of soluble reactive phosphorus from the Ambleside and Tower Wood sewage treatment works are likely to be 1.97 and $6.01 \text{ tonnes yr}^{-1}$ respectively. The former works contributes 23% of the total phosphorus to the North Basin and the latter 53% of the total phosphorus to the South Basin.
5. Removal of 80% of the phosphorus from the Tower Wood outfall, whilst beneficial in reducing the phosphorus loading to the South Basin, may not assure the well-being of the lake. However, an 80% removal of the phosphorus inputs from both the Ambleside and the Tower Wood sewage works would result in a loading of soluble reactive phosphorus to the whole lake of only $0.17 \text{ g P m}^{-2} \text{ yr}^{-1}$. This would place the whole lake within the

mesotrophic zone of the figure of annual loading versus mean depth of Vollenweider (1968) (see Atkinson et al., 1986, Fig. 25).

5(b) Phosphorus loading to Windermere taking account of mean depth and residence time of the water

Vollenweider (1976) refined his earlier phosphorus loading/mean depth relationship to take account of the residence time of the water. The shorter the residence or replacement time for the lake volume, the less susceptible the lake will be to increased phosphorus loading. Vollenweider (1976) examined this relationship for phosphorus-controlled lakes, and deduced that the critical loading value which determines the transition between oligotrophy and eutrophy can be described by equation (1).

$$L_c = (10 \text{ to } 20) \cdot q_s (1 + \sqrt{\bar{z}/q_s}) \quad (1)$$

where L_c = critical specific loading ($\text{mg m}^{-2} \text{yr}^{-1}$)

\bar{z} = mean depth (m)

q_s hydraulic load ($\text{m yr}^{-1} = Q_y/A_o$)

where Q_y = total yearly discharge ($\text{m}^3 \text{yr}^{-1}$)

A_o = lake surface area (m^2).

The range of critical loadings of total phosphorus thus defined and applied to the whole of Windermere and its two basins is given in Table 2 using discharge data for 1984, 1987 and 1988. This shows that using the criteria of general limnological experience in Vollenweider's model, the upper range of critical total phosphorus loadings for Windermere and its South Basin are very similar to the estimates of total phosphorus loadings in Table 1. The North Basin is within the range of critical loading but towards its lower end. The same data for mean depth and hydraulic load are placed on the graphical relationship of Vollenweider (1976) (Fig. 14). This indicates the lower limit of the critical loading for total phosphorus according to equation (1) taking a mean value of hydraulic load for the years 1984, 1987 and 1988. The mean lower limits of the

critical loading for these years for the whole lake, its North and South Basins are 558, 890 and 980 $\text{mg total P m}^{-2} \text{ yr}^{-1}$ respectively.

These values can be compared with the effect of removing 80% of the phosphorus from the effluents of the Tower Wood and Ambleside sewage works entering Windermere. Removal of 80% of the phosphorus from the effluent of the Tower Wood works only would reduce the total phosphorus to the South Basin to 959 $\mu\text{g total P m}^{-2} \text{ yr}^{-1}$ which is very close to the lower limit of the critical range of phosphorus loading. Removal of 80% of the phosphorus from the effluents of Tower Wood and Ambleside sewage works (it is estimated that 50% of the phosphorus from Ambleside sewage works transfers to the South Basin) would reduce the total phosphorus loading to the whole lake and its North and South Basins to 609, 760 and 840 $\mu\text{g P m}^{-2} \text{ yr}^{-1}$. These values for the two basins are about 15% below the lower limit of critical phosphorus loading as defined by Vollenweider's equation (1). That the loading value as estimated for the whole lake is above the lower limit of the critical phosphorus loading is not particularly relevant as the North Basin to some degree acts as a settling basin for particulate phosphorus thus unavailable to the South Basin. Removal of 80% of the phosphorus from both sewage treatment works would keep below the range of critical phosphorus loading values.

It is noteworthy that the North Basin is more sensitive to catchment derived phosphorus than to the relatively smaller contribution from phosphorus in sewage effluent from Ambleside. As a consequence this basin would be sensitive to increasing phosphorus from the catchment through changes in agricultural practice and land use including tourism via sewage effluent from Grasmere and Elterwater. The situation is reversed in the South Basin where sewage derived phosphorus contributes over 50% of the phosphorus loading.

Although it is generally the case that phosphorus is the element most likely to limit algal growth in Windermere, acute depletions of silicon, carbon and nitrogen can also occur as in nearby Esthwaite Water (Heaney et al., 1986).

Of these nitrogen may have the greatest general influence, particularly in warm dry summers, when it falls to negligible quantities in the upper layers of the lake. Should conditions arise as in 1983 and 1989 where warm stable summers enabled Oscillatoria bourellyi to settle from the upper layers, then there is a possibility of it being replaced by nitrogen-fixing gas vacuolate blue-green algae with the potential for forming surface blooms.

6. PHYTOPLANKTON LEVELS AND DYNAMICS

6(a) Total biomass

The seasonal variation of total algal biomass is indicated by that of chlorophyll a in Fig. 4. Both basins show two well developed maxima of chlorophyll a corresponding to the spring diatom growth followed by a summer/autumn growth dominated mainly by filamentous blue-green algae.

The size of the spring diatom population as chlorophyll a in the North and South Basins during 1987 (29 and 30 $\mu\text{g l}^{-1}$ respectively) was appreciably greater than during 1988 (16 and 18 $\mu\text{g l}^{-1}$ respectively). However, maximum summer biomass levels in the South Basin were markedly greater in both years than those in the North Basin. Maximum values of chlorophyll a in the South Basin for 1987 and 1988 were 30 and 40 $\mu\text{g l}^{-1}$ respectively and for the same years in the North Basin 16 and 18 $\mu\text{g l}^{-1}$ respectively.

The mean annual concentration, and standard deviations of chlorophyll a in the upper 0-7 m layer of the North Basin for 1987 and 1988 were 8.75 ± 6.45 and 7.76 ± 5.23 respectively, and for the same years in the South Basin were 13.05 ± 11.40 and 11.50 ± 8.95 respectively.

5(b) Major species

Only the dominant species of the larger diatoms and blue-green algae are included in this report as they have the greatest impact on water quality. Nevertheless, as in other Cumbrian lakes many other species occur including

various flagellates (green algae, cryptomonads, chrysophytes and a few dinoflagellates) and green algae. Some of these are ubiquitous occurring throughout the year as with the small flagellate Rhodomonas lacustris, or are most abundant during the "clear water phase" mentioned earlier. These flagellates and some green algae are often the edible forms which sustain the food chains within the lake and hence are of considerable importance. Any tendency to restrict the growth and abundance of these edible forms by others less susceptible to grazing such as larger diatoms and blue-green algae may limit zooplankton and fish production.

The annual occurrence of dominant species of diatoms and blue-green algae in the upper (0-7 m) layer of both basins is shown in Figs 15-19 as plots of \log_{10} cells ml^{-1} or filament length ml^{-1} for 1987 and 1988; zero values represent counts of one unit or less for particular species. Asterionella formosa and Melosira italica subsp. subarctica (now Aulacoseira subarctica) are the main species comprising the spring growth. Although previously absent or uncommon, M. islandica subsp. helvetica reached moderate numbers in both basins in 1988. The onset of growth takes place earlier in the shallower South Basin with its better light conditions for the average circulating cell (Talling, 1971). The maximum population size of the spring diatom maximum in both basins is determined by the supply of dissolved silicon and has not changed markedly since the forties (Atkinson et al., 1986). Smaller, secondary growths of both species occurred during summer and autumn dependent upon the resupply of dissolved silicon and mixing episodes.

Fragilaria crotonensis, Tabellaria flocculosa var. asterionelloides and T. fenestrata can generally be regarded as summer species of diatoms. As dissolved silicon is at low concentrations in the upper layers during this period the abundance of these species is restricted both by silicon availability and strength of stratification. In both basins F. crotonensis was more successful than the combined numbers of both species of Tabellaria during 1987 and 1988 (Fig. 16).

During the summers of 1987 and 1988 the blue-green alga Oscillatoria bourellyi dominated the phytoplankton of both basins but differed in the timing and size of population maxima. Greatest population densities were attained in the more productive South Basin reaching a record 614 mm ml^{-1} during early September 1987 and 560 mm ml^{-1} during mid-July 1988. The delayed growth during 1987 was almost certainly the result of growth from a low inoculum after the unexplained very rapid collapse of O. bourellyi from both basins of the lake during June 1986. In the North Basin maximum biomass of the alga was reached during late October 1987 (135 mm ml^{-1}) and during early August (168 mm ml^{-1}) 1988. Except for 1987 in the North Basin where there was no marked decline in algal density until after the basin was fully mixed, severe oxygen depletion or anoxic conditions in the hypolimnia followed the decline of O. bourellyi populations. This provides additional evidence to that in Atkinson et al., (1986) that respiration and decomposition of sedimenting filaments of this alga are likely to be the causes of large deep-water depletions of oxygen. The size of the populations of O. bourellyi appear to be determined by nutrient supply and sufficient mixing in the upper layers. Periodicity of the alga is governed, at least in part, by the size of the overwintering population from the previous year.

Although not covered by the period of this Report, it is noteworthy that populations of O. bourellyi grew strongly in both basins during 1989 until June. By mid-July they had been lost from the upper mixed layer as a result of sedimentation during the extremely warm, stable weather conditions prevailing at this time. During sedimentation the alga forms a temporary maximum at the thermocline. A similar settling of the alga occurred during the fine warm June of 1988 as shown in Fig. 18. However, in 1988 this warm weather was followed in July by mixing of sufficient magnitude to upwell the filaments from the deeper water back into the epilimnion (Fig. 18). Thus, interannual variability of success of O. bourellyi can be determined by physical stability. If

conditions of high stability and little mixing are sufficiently long for the alga to settle below the thermocline then it may be effectively lost for that year.

The gas-vacuolate species Oscillatoria agardhii and O. agardhii var. isothrix formed small populations in both basins and years (Fig. 17). O. limnetica (Fig. 19) attained a greater filament length than these species but represents a small biomass due to its narrow diameter (c. 2 μm) compared to that of other species of Oscillatoria (diameter c. 6-9 μm) in the lake. During 1989 a red form of Oscillatoria, possibly O. rubescens, has reached appreciable quantities in both basins.

Growth of the potential surface bloom-forming species of Anabaena (Fig. 20) were low. However, levels of Aphanizomenon flos-aquae (Fig. 19) are now becoming appreciable, probably as a result of lake enrichment and input of inocula from Blelham Tarn to the North Basin and Esthwaite Water to the South Basin. That these lakes may be important as sources of inocula to Windermere is suggested from their periodicities given for corresponding years in Canter et al. (1990).

5(c) Stratification of major species

Coarse indices of the vertical distribution of O. bourrellyi as mm ml^{-1} and of the presence of other algal species below the upper mixed layer ranked on a relative scale from rare to dominant are given in Figs 21 and 22 respectively.

Fig. 21 shows that O. bourrellyi can sediment into the deeper layers of both basins during periods of calm weather (e.g. South Basin, June 1988) and at the end of the population growth cycle. Microscopic examination shows that as filaments enter the deep aphotic zones they generally break up into much shorter pieces. This filament breakage resulting from necrotic cells in the hypolimnion will lead to increased oxygen consumption in this zone.

The presence of other algal forms in deeper waters in terms of ranked abundance (Fig. 22) shows that besides O. bourrellyi, the gas-vacuolate blue-green algae Aphanizomenon flos-aquae f. gracile, Anabaena flos-aquae/A. circinalis complex and Gomphosphaeria naegeliana, the diatoms Asterionella formosa, Fragilaria crotonensis, Melosira italica subsp. subarctica and Tabellaria flocculosa could be occasional or common. With the exception of the dinoflagellate Gymnodinium and the green alga Eutetramorus other taxa were generally rare.

7. CHARR

7(a) The biology of the Windermere charr stocks

i) Stock structure

Earlier work by Winifred Frost (1965) and recent investigations by Partington & Mills (1988), Mills (1988) and Mills (1989) demonstrate that Windermere contains both a spring-spawning and an autumn-spawning race of charr. The differences between these races are both genetic and morphological. The latter include differences in both the mean number and the mean length of the gill rakers. By using a combination of the number and the length of gill rakers, it is now possible, by means of a discriminant function, to predict with more than 95% accuracy whether an individual charr is a spring or autumn-spawner. There are also differences, principally in growth rates, between fish in the two basins (Table 3). North Basin autumn spawners grow relatively slowly, North Basin spring spawners and South Basin autumn spawners are intermediate and South Basin spring spawners are by far the fastest-growing charr in any Cumbrian lake. Adult charr are known to return to the same spawning site each year (Le Cren & Kipling, 1963), there are consistent variations in growth rates between basins and both spring and autumn spawners have at least one spawning site in each basin. Consequently, each basin must be considered to hold separate stocks of the two principal races. It may even

be that each of the separate spawning sites comprises a separate stock but this would depend on the extent to which juveniles imprint to a particular site within the lake.

Using plumb-line tackle anglers generally catch fish at depths ranging from about a metre to perhaps 20 metres. Both fish bought from anglers and fish caught in gill nets set along the bottom in deep water at over 30 metres contained an extremely high proportion (at least 95%) of the autumn-spawning race of charr. This was true for both basins of the lake.

ii) Age structure

The mean ages of spawning charr from the four main stocks caught between 1986 and 1988 are surprisingly high. The mean age of females is always greater than that of males and that of spring-spawners is generally greater than that of autumn spawners. However, there is no large difference between basins (Fig. 24). The differences between the ages of male and female spawners arise because most male charr mature at five years-of-age (though a few mature precociously as young as 2 years old). Few females mature until they are six or more years old but they are clearly longer-lived than males (Fig. 24). Seventy eight percent of charr between 9 and 14 years old were female. Male and female charr grow at the same rate (Fig. 24). The presence of quite a high proportion of old charr in both basins of the lake indicates that mortality through angling cannot be very great or few fish would survive to reach such ages (unless a proportion behave in such a way that they are not vulnerable to angling).

It should be noted that earlier studies on Windermere charr which relied on scales rather than otoliths for ageing almost certainly under-aged many fish, particularly the larger ones.

Frost (1965) illustrates 9 sites where the autumn race spawns and 4 sites for spring spawners (Fig. 23). Our recent netting surveys have demonstrated that spawning still occurs on at least seven of the autumn sites. Spring

spawners could be readily caught at the two North Basin sites but were only found in very small numbers on the South Basin sites in 1987 and 1988. Males were particularly scarce (Fig. 24) and females had the highest mean age (9.2 years) of any group (Fig. 24). Attempts to locate spawning fish from this race elsewhere in the South Basin were unsuccessful despite setting nets at several sites and night-time searches with an echo-sounder.

During spring 1989, however, the picture changed. Catch rates south of Rawlinson's Nab remained low compared with other spawning sites but most of the fish caught (40 out of 55) were males aged 4 or 5. Only 10 females were caught of which 5 were aged 10 or over. It looks as though there were successful spawnings 4 or 5 years ago and that by next year females from these spawning's may also reach maturity on reaching 6 years of age.

iii) Parasitic infestation

Almost all Windermere charr over three years of age contain cysts of the intermediate stage of the tapeworms Diphyllbothrium dendriticum and D. ditremum. The parasites enter the charr in infected copepods and burrow through the stomach or intestine wall. They usually encyst on the stomach or other internal organs or, less often, on the abdominal wall. Of the two species D. dendriticum is the more invasive and the encysted worm can reach 100 mm in length compared with 30 mm for D. ditremum. The normal final hosts are gulls for D. ditremum and probably ducks and cormorants for D. dendriticum though the latter species can infect a variety of mammals including man (Curtis 1984).

In Windermere the parasite burden increases with size and age with some large, old charr containing 50 D. dendriticum and several hundred D. ditremum. Details of infection rates are given in Mills (1990). Most charr caught by anglers probably contain between 1 and 10 cysts of D. dendriticum but cleaning the fish will remove almost all the cysts and cooking will kill the remainder so they are unlikely to cause a threat to health.

(b) The levels of the Charr stocks

i) Long-term records

The IFE has catch per unit effort (CPUE) data for autumn-spawning charr from the Low Wray Bay spawning site from 1939 to 1973. Due to interference with the gill nets used for this work, the monitoring site was changed to another autumn site in the North Basin at North Thompson Holme where data collection has continued from 1975 to the present (Fig. 25). These results show a steady increase in catches from around 1944 when the FBA started to cull the larger pike in the lake. Between 1945 and the mid 1960's this reduced the biomass of large pike in the North Basin by around 65% (Fig. 25) and in the South Basin by around 50%. Since that time, the biomass of large pike has been kept at around 20-25% of the pre-cull level, and the charr spawning site CPUE data have shown considerable oscillations but around a much higher mean (Fig. 25).

ii) Anglers catch data

This pattern of increased catches, followed by relative stability, is very well echoed by changes in anglers CPUE (Fig. 26).

Between 1927 and 1942 the average catch per hour on charr tackle was 0.47 charr per hour (range 0.15 - 0.56) (Fig. 26), and 0.06 trout (range 0.03 - 0.11). From 1965-1972 catches of charr were much higher, averaging 2.58 fish per hour (range 1.65 - 3.50), but more similar for trout at 0.088 per hour (range 0.043 - 0.158). Data from 2 anglers for most years between 1975 and the present shows that overall catches of charr have continued at around these increased levels (Fig. 26). Spawning charr form the main winter diet for the Windermere pike population and the decrease in stocks of larger pike is almost certainly the principal factor behind the increase in charr stocks (Kipling, 1984) (Fig. 25).

Though there have been considerable variations in angling success both within and between years the catches of both angler 2 and 3 tend to be greatest in May and decline to a low point in September (Table 4). Further analysis of the data from these anglers shows that up to 1984 mean catches were slightly higher in the South Basin than in North (Table 5). Between 1984 and 1988 catches by both anglers showed a slight, though not significant, increase over the earlier years in the North Basin. However, catches by both anglers in the South Basin showed a large and significant fall to a half or less of the pre-1984 levels (Table 5, Fig. 26). The reductions in annual catch rate in the South Basin began in 1984, some years after the present series of blooms of O. bourrellyi. However the possibility that there is a direct physical effect due to interference with anglers gear from filaments of O. bourrellyi and/or reductions in visibility due to high algal biomass was tested by analysing daily catch rates by angler 2 in the South Basin from 1981 to 1987. These years span the decline in catch rates and most had blooms. June, July and August data was used as these are months when mean catch rates show little overall variation. Between 1981 and 1987 54 sessions averaging around 8 hours were fished at an overall catch rate of 2.29 charr h⁻¹. This represents a total catch of close to 1000 South Basin charr. The majority of the sessions (41) took place at low levels of O. bourrellyi (0-7 m layer) of between 0 and 40 mm ml⁻¹ (mean 6.3 mm ml⁻¹) but the remainder occurred during blooms where there were between 120 and 230 mm ml⁻¹ (mean 169.3 mm ml⁻¹). The mean catch rate during blooms of 2.32 fish h⁻¹ was virtually identical to the rate of 2.28 fish h⁻¹ during non bloom periods. There was a slight negative correlation (r = -0.193 53 d.f.) between mean chlorophyll a concentration (0-7 m layer) and catch rate but this fell well below the 5% level of significance (r = 0.279, 50 d.f.). Thus there is no statistical evidence that catch decline is related to interference with the fishing process itself. Nevertheless, this does not preclude the possibility that deep maxima of O. bourrellyi (Fig. 18)

may interfere with the functioning of charr tackle. The most likely explanation of the recent decrease in CPUE is that there has been a real decline in the South Basin charr stocks.

iii) Variations in reproductive success

Anglers claims that the charr in both basins are increasing in size are certainly borne out by our results. However this phenomenon is not confined to the South Basin as analysis of the size and age of the spawning stock of charr from North Thompson Holme confirms anglers reports that fish size has increased in the North Basin over the past few years. Fig. 27 shows the change from 1983 to 1987. This change has resulted from a change in the age-structure of the spawning stock, not from a change in growth rate. It is likely that there were very successful spawnings 8 and possibly 9 years ago followed by much less successful ones 5, 6 and 7 years ago. Thus large, older fish formed a greater than usual proportion of the spawners in 1987. There is evidence that this type of change in the spawning stock has occurred several times over the 50 years that the FBA has monitored a North Basin autumn spawning site (Fig. 28) and thus pre-dates severe oxygen depletion. The reappearance this year (1989) of young adult males on the spring spawning site south of Rawlinson's Nab indicates that the same processes occur in this basin as well though the fluctuation here seems particularly extreme.

The factors that make some spawnings so much more successful than others is not yet understood. This is partly because of the lack of reliable age data for earlier years. The IFE has sufficient otolith material to produce age structures going back to the mid-1970's for North Basin autumn spawning charr and this work is now underway.

iv) Populations estimates

It has been estimated (Mills, 1988) that Windermere probably contains around 140,000 adult charr of which most (132,000) are of the autumn spawning race. These would have a biomass of 30-35 Mg (tonnes). Some individual

anglers catches can exceed 1000 fish per annum but the total catch is probably between 12,000 and 20,000 fish per annum. Of these 50-60% are adults and the remainder juveniles. This is because the minimum takeable size is 203 mm but few charr mature until they are 5 or 6 years old and around 250 mm in length. Thus anglers may catch 7-12000 adults per annum totalling 5 to 8% of the estimated adult stock. This relatively low level of exploitation is consistent with the considerable age reached by many of the adult charr in the lake (Fig. 24).

An independent source of information on the numbers of charr in the lake, and of the relative numbers in each basin is given by the results of our echo survey work. These surveys pick up individual fish in mid-water but not those either very close to the surface or the lake bottom. The surveys were made over a fixed course in the deeper waters of the lake (Fig. 29). The results must be interpreted with caution as not all the echos will come from charr, though perch and pike tend to be restricted to the uppermost layer of water and to the shallower parts of the lake. In addition the echos do not provide information on the size distribution of the fish surveyed and the estimates will not include charr feeding on the bottom of the lake. It is clear from our netting surveys that charr, particularly juveniles, are present close to the bottom at all times, except in the deeper areas of the South Basin when they become anoxic.

The surveys found very few mid-water echo traces during the winter but considerable numbers by April, the numbers falling off again in November. This is coincident with spawning by the dominant autumn spawning race when the adults move into the shallows to lay their eggs and thus out of the surveyed region. In 1986 a series of surveys between May and October gave estimates of 3288 to 12,617 echos in the South Basin (mean 6223) and 22,524 to 64,308 in the North (mean 36,481). A survey in October 1987 gave estimates of 20,928 in the South and 52,656 in the North. A series of surveys in 1988 gave estimates of

11,413 to 42,447 in the South (mean 30,658) and 33,718 to 104,379 in the North (mean 60,442). Overall the surveys show two or more times as many echos from the North than from the South though the difference is greater in 1986 than 1987. This may in part be accounted for by the great increase in the number of brown trout feeding in mid water in the South Basin in 1988. Normally where brown trout and charr occur together the charr occupy the central and deeper waters, feeding on zooplankton and benthos, whereas the trout occupy a shallower and more littoral niche, feeding on surface insects and littoral invertebrates. In the past all charr anglers records have supported this theory, with trout catches never forming more than a small fraction of the total catch made on charr fishing gear. However, 1987 and 1988 saw an unprecedented rise in the proportion of trout in the South Basin catches. Fig. 30 shows this for angler 2 who actually caught trout at a slightly higher rate than charr in 1988. Examination of samples of trout caught on charr gear in 1988 showed that they were feeding on zooplankton like the angler-caught charr. They were mainly fish from the 1984 and 1985 year classes and between 260 and 320 mm fork length. There was a slight increase in the rate of capture of trout in the North Basin in 1988 but not in 1987 and certainly nothing comparable to the massive increase in the South (Fig. 30).

Whether this change in the South Basin was due to a change in habits by the trout due to a reduction in charr density or by an increase in the overall number of trout is uncertain. 1985 was a good spawning year for trout in the streams but in 1984 there was a severe drought with poor conditions for young trout. Early indications for 1989 are that trout catches are down and that charr catches have increased somewhat in the South Basin. The consequence for the echo trace results of the increased trout numbers is that in 1987 and particularly 1988 the South Basin totals probably include a considerable proportion of trout as well as charr whilst those from the North Basin will not. Thus despite the various provisos the North Basin certainly does seem to

contain more than twice as many mid-water feeding charr than does the South Basin. What we do not know, except for anglers catch data, is the pre-1984 situation.

The IFE is at present engaged in commissioning a much more sophisticated computer-linked echo sounding system that will provide information both on echo numbers and on the size of the fish producing the echos and we hope to use this in the future to obtain more detailed information from the two basins.

(c) Possible threats to the charr population

i) Eutrophication

Eutrophication or nutrient enrichment is not harmful to charr per se; charr grow very slowly in nutrient-poor lakes such as Wastwater (Table 3). Indeed the deliberate fertilisation of extremely oligotrophic lakes is used as a management strategy in some Scandinavian countries to increase the food supply for the charr and to combat acidification (Milbrink & Holmgness, 1984). However there is evidence from several Alpine lakes that any benefits of increasing eutrophication are soon outweighed by low oxygen concentrations, siltation of spawning sites and increased competition, especially from cyprinids. For example, the charr population of Lake Constance is now only maintained by continual restocking (Hartmann, 1984), catches in Lake Zug have fallen by 98% (Ruhl , 1984), and charr became extinct in Lake Neuch tel in 1970 (Pedroli, 1983).

The present situation in Windermere is clearly not as serious as this. There has not been any obvious increase in cyprinid populations and the shallow gravel areas where the autumn spawners lay their eggs appear reasonably silt free. Unfortunately our attempts to examine the physical structure of the deep Rawlinson's Nab site in the South Basin during the February spawning season have been frustrated by poor weather and visibility. Earlier diver observations at the spring spawning site in the North Basin at Holbeck point

found the site to be gravel and large stones arranged in a 'tongue' about 14 to 18 m wide which extended from a depth of 9.5 to 28 m. This is much smaller than the autumn sites that have been well characterised (Frost 1965). Given the low numbers of spawning charr caught at this site in successive years it would be desirable to obtain more information on the quality of the bed material and survival of eggs. Tipping clean gravel on badly-silted charr spawning sites has proved a successful technique for improving spawning success in other lakes (Ruhlé, 1984).

Reduced oxygen levels will force the charr to alter their behaviour. Exactly what levels these are is not clear for this species though there is information for various related salmonids. Trout Salmo trutta, start to show distress at levels of oxygen below $125 \mu \text{ moles l}^{-1}$ and die at levels below $90 \mu \text{ moles l}^{-1}$. However the brook trout (or brook charr) Salvelinus fontinalis is more tolerant and can survive levels down to $55 \mu \text{ moles l}^{-1}$. It is likely that the minimum levels for charr lie somewhere between 100 and $50 \mu \text{ moles l}^{-1}$. In a year like 1988 this will exclude them from the deeper waters of the South Basin for a considerable period (Fig. 31). Evidence from echo traces does indicate that during the period of oxygen depletion in 1988 the mean depth of echos in the South Basin (from charr and other species) was consistently shallower than in the North (Fig. 32). This was not the case in 1986, a year when there was no bloom of O. bourellyi and no severe deoxygenation (Fig. 32). The young 1 and 2 year old charr that were located by netting in the deeper parts of both basins in 1988 were displaced by the deoxygenation. Catches ceased in the deep parts of the South Basin after the start of September when oxygen levels fell below $100 \mu \text{ moles l}^{-1}$ (Fig. 31) whereas in the better oxygenated North Basins catches continued throughout September.

ii) Temperature

The Arctic charr has a preferred temperature range of between 5 and 16°C. This compares with 4-19°C for brown trout, 6-20°C for salmon and 8-26°C for most of Britain's non-salmonid species (Elliott, 1981). Experimental studies on young Windermere charr found good growth rates between 8 and 16°C but a dramatic fall at higher temperatures. Evidence from echo sounding shows that the mean depth of pelagic echos, principally from charr, increases as the temperature of the epilimnion rises. This change in charr distribution may put more fish beyond the reach of anglers and be partially responsible for the drop in catch rates towards the end of the season though in 1986 the fish also had a greater mean depth in the spring (Fig. 32).

In warm years such as 1984 the top 10-12 m of the lake can be above the charr's optimum temperature range (Fig. 31). Such years will become more common with predictions of increases in mean temperature of up to 2°C in summer and 4°C in winter (George, 1988). However, even in an extreme year such as 1976 only the top couple of metres reached water temperatures in the range that can be directly lethal to the charr (22-27°C). Nevertheless, as Fig. 31 illustrates the trend towards increasing anoxia in combination with more warm summers may result in some future years with only a relatively narrow band of water that is both well-oxygenated and within the optimum temperature range.

Climatic change may also affect survival of the eggs. These are extremely sensitive to temperatures above 8°C, especially during the first few days of development and again close to hatching (Swift, 1965). Analysis of IFE's long-term CPUE data for autumn spawning charr in the North Basin over the period 1959-1987 shows that almost all spawning occurs in November. Mean temperatures in this month have ranged from 7.6 to 10.3°C, indicating that substantial mortality could occur in some years. Water temperatures fall considerably during the month so the data was further analysed to detect whether the charr tend to delay spawning in warmer years. This was done by plotting the November date when half the years catch of spawning fish had been

made against mean October and November temperatures. This mean spawning data ranged from 5th to the 22nd of the month (mean 16th).

Warm water temperatures had a significant but very minor role in delaying spawning, accounting for 12% of the variance in a multiple correlation using both October and November water temperatures. This suggests that spawning time is principally governed by day length and that the time of spawning is not very flexible. This is supported by information on the river spawning Ennerdale charr population which spawns between November 10th and 16th (Frost, 1970).

Consequently a rise in winter temperatures of up to 4°C (George, 1989) could have serious consequences for the survival of the eggs of autumn spawning charr during November. Temperatures over the remainder of the incubation period to hatching in February should remain sufficiently low to avoid further mortality. Eggs of spring spawners will not face temperature problems at spawning time in February but could possibly encounter temperatures above 8°C by hatching time in May or early June.

8. SUMMARY

8.1 This Report provides additional information on Windermere to that contained in the commissioned Reports to NWW from FBA by Atkinson *et al.* (1986), Heaney & Talling (1988) and Mills (1988). Results are given of the annual changes in major limnological variables during 1987 and 1988, a more detailed appraisal of critical phosphorus loading to the lake, and an investigation of the biology and population structure of the charr stocks.

8.2 Both 1987 and 1988 had relatively warm winters, periods of rapid warming during spring (1987) and June (1988), but generally cool summers. Levels of deoxygenation in both basins varied between years and between basins. In the South Basin near-anoxic conditions did not develop until November during 1987. However, during 1988 anoxia was observed for a prolonged period between the end

of September and mid-November extending upwards to a depth of about 25 m. In the North Basin oxygen concentrations remained above 45% saturation throughout 1987 but fell to less than 20% saturation below 30 m depth during the first half of November 1988. Oxygen depletions in both basins during 1988 were the most severe on record and were associated with the sedimentation of large populations of the blue-green alga Oscillatoria bourrellyi.

8.3 Plant nutrient levels in 1987 and 1988 did not differ markedly from those found in the 1980's generally. Both $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ accumulate in the hypolimnion of the South Basin but not in the North Basin. During autumnal mixing this accumulation increases the winter concentrations of these nutrients in the South Basin although $\text{NH}_4\text{-N}$ quickly declines. The winter concentration of $\text{PO}_4\text{-P}$ in the South Basin is approximately twice that in the North Basin. Nitrate-nitrogen fell to lower concentrations in the South Basin than in the North during late summer of both years.

8.4 The phytoplankton dynamics of both basins produced two main pulses of biomass; a spring growth of diatoms (mainly Asterionella formosa) and a summer growth of blue-green algae (mainly Oscillatoria bourrellyi). The growth of O. bourrellyi was delayed during 1987, presumably due to a reduced level of overwintering inoculum. In 1988 the biomass of O. bourrellyi in the South Basin reached the highest level recorded to date (614 mg ml^{-1}). Noteworthy floristic changes in both basins were the appearance in appreciable quantities of Melosira islandica and a red gas-vacuolate blue-green alga similar to Oscillatoria rubescens.

There is evidence which shows that growing populations of O. bourrellyi sediment from the upper layers of the lake during calm weather. If prolonged, this can lead to elimination of the alga from the plankton for the rest of the year. Such conditions of enhanced stability in nutrient enriched waters could

well encourage the growth of buoyant gas vacuolate blue-green algae which are fortunately rare at present.

8.5 Using the mean depth and discharge data available for 1984 (a year of relatively low discharge); 1987, a year whose discharge equals the long-term average for Windermere (Reynolds in Atkinson et al. 1986); and 1988, a moderately wet year, the annual critical loadings for total phosphorus to Windermere and its basins were calculated according to the equation of Vollenweider (1976). This equation when applied to phosphorus controlled lakes describes the transition range between oligotrophy and eutrophy. The lower limit of critical phosphorus loading for these three years were calculated as $558 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (whole lake) $890 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (North Basin), and $980 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (South Basin), which are much lower than the present total P loadings calculated to be 1040, 1100 and $1670 \text{ mg P m}^{-2} \text{ yr}^{-1}$ respectively.

Removal of 80% of the phosphorus from the effluents of Tower Wood and Ambleside sewage works would reduce the phosphorus loadings to $609 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (whole lake), $760 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (North Basin), and $840 \text{ mg P m}^{-2} \text{ yr}^{-1}$ (South Basin). Such action is likely to lead in time to an improvement of water quality with a reduction of algal biomass, particularly in the South Basin, and a reduction in the level of oxygen depletion in the hypolimnia of both basins. It would not preclude the possible development of small populations of surface-bloom forming blue-green algae which could be concentrated by gentle winds into bays.

8.6 The long-term management policies of the FBA have greatly increased stocks of charr and anglers catch rates by limiting the numbers of larger (> 550 mm) pike in the lake.

8.7 At the present level of fishing effort anglers catches reflect rather than control the abundance of charr.

8.8 Since the mid-1960's charr numbers and anglers catch rates have remained relatively constant in the North Basin, though average fish size has fluctuated. Up to 1984 anglers catch rates were slightly higher in the South Basin than in the North, but from 1984-1988 have fallen to only half of the level of those in the North Basin.

8.9 There is no statistical evidence that this decline is due to physical interference with the angling process by filaments of the blue-green alga O. bourrellyi. Nevertheless, as populations of the alga may at times settle and concentrate in the region of the thermocline, and mean filament length can vary during the growth cycle, the correlation between CPUE and biomass of the alga in the 0-7 m layer may not be a simple one. The most likely explanation for the reduced catch rates in the South Basin, which is supported by echo survey results, is that there are fewer charr present. During late summer and autumn (August to October), this could result from the exclusion of young charr from deeper waters by low oxygen concentrations. In the case of the deep-spawning spring race, increased organic deposition on the spawning gravel could impair recruitment.

8.10 The charr populations face the twin threat of increasing anoxia in the deeper waters, and from the increased summer water temperatures resulting from predicted climate change. Experience from nutrient-enriched lakes elsewhere, including lakes deeper than Windermere, suggests that eutrophication alone may endanger the species. In addition, the predicted 4°C increase in mean winter temperature could have serious consequences for the survival of eggs of the autumn-spawning race of charr.

9. RECOMMENDATIONS

9.1 There should be a removal of 80% of the phosphorus from the sewage effluents of the Tower Wood and Ambleside sewage works. This should eventually lead to a reduction of algal biomass and prevent oxygen concentrations in the deeper waters falling to below about 50% of the saturation values. The removal of phosphate will only result in a gradual improvement of water quality because the lake sediments will discharge their accumulated phosphorus in appreciable quantities for some years. Should phosphorus removal from sewage effluents be undertaken, it is recommended that the rate of loss of phosphorus from the sediments be measured. This would provide valuable data for determining the rate of recovery of the lake and its optimum management to provide a water productive enough for good fish production without environmental stress.

9.2 On conservation and aesthetic grounds the Windermere fish populations should continue to be managed to optimize charr numbers. This would involve the continued removal of 30-50% of the pike > 550 mm each year.

9.3 The charr populations in both basins of the lake should be monitored, preferably by a mark-recapture exercise followed by regular echo sounding surveys.

9.4 Measures should be considered to ensure that there can be no major increase in the present, acceptable, level of fishing pressure. These could include limiting the number of licences issued and raising the takeable size from 203 to 254 mm (8-10 inches) to reduce the removal of juvenile charr. It would be extremely helpful, but perhaps impractical, for detailed catch returns to be obtained from licence holders.

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Table 3 Mean lengths and numbers (n) of aged charr from eleven Lake District and one Welsh populations.

	Age	2	n	3	n	4	n	5	n	6	n	7	n	8	n	9	n	10	n	11	n	12	n	13	n	14	n
Buttermere		139	1	221	2	242	5	271	5	300	9	301	6	304	3			326	2								
Coniston				151	1	207	4	254	12	272	19	288	17	296	18	299	3	299	2	329	1						
Crummock				116	4	160	8	187	19	227	4	251	8	261	1	260	1										
Cwellyn		113	1	164	3	182	7	200	7	218	1	219	3					241	1								
Ennerdale								270	2	288	20	304	41	317	19	339	3	392	1								
Haweswater		138	1	155	1	217	7	236	19	251	4	270	4	252	1												
Thirlmere		122	4	162	14	182	6	209	7	225	6	235	3	234	4	239	2	238	2			248	1				
Wastwater		117	16	140	15	171	4	185	7	187	1																
Windermere North Basin Autumn sp				204	4	236	8	248	30	212	34	283	33	289	21	301	26	307	2	321	10	311	1				
Windermere North Basin Spring sp						254	1	254	14	289	10	300	14	318	35	329	31	342	23	353	11	348	3	338	1		
Windermere South Basin Autumn sp		168	3	219	1	247	3	282	17	300	46	320	35	331	35	341	22	346	17	343	8	359	8	355	3		
Windermere South Basin Spring sp		167	1					303	5	318	5	325	8	343	24	351	22	360	6	361	7	380	8	378	3	367	1

Table 4 Monthly angling success by two charr anglers. Catch rates expressed as catch per boat per hour (CPUE)

Angler 2 - data from 1966 - 72 and 1978 - 88

	South Basin		North Basin	
	n	CPUE	n	CPUE
May	18	3.23	15	3.52
June	14	2.72	17	2.57
July	13	2.26	18	2.91
August	12	2.05	18	2.82
September	15	1.67	17	1.59

Angler 3 - data from 1975 - 88 (except 1980 and 82)

	South Basin		North Basin	
	n	CPUE	n	CPUE
April	7	2.33	2	1.38
May	11	2.14	12	1.98
June	3	0	12	1.79
July	5	1.60	11	1.53
August	5	0.89	10	1.70
September	3	0.55	9	1.53

Table 5 Anglers catch rates (CPUE) for charr before and after 1984.

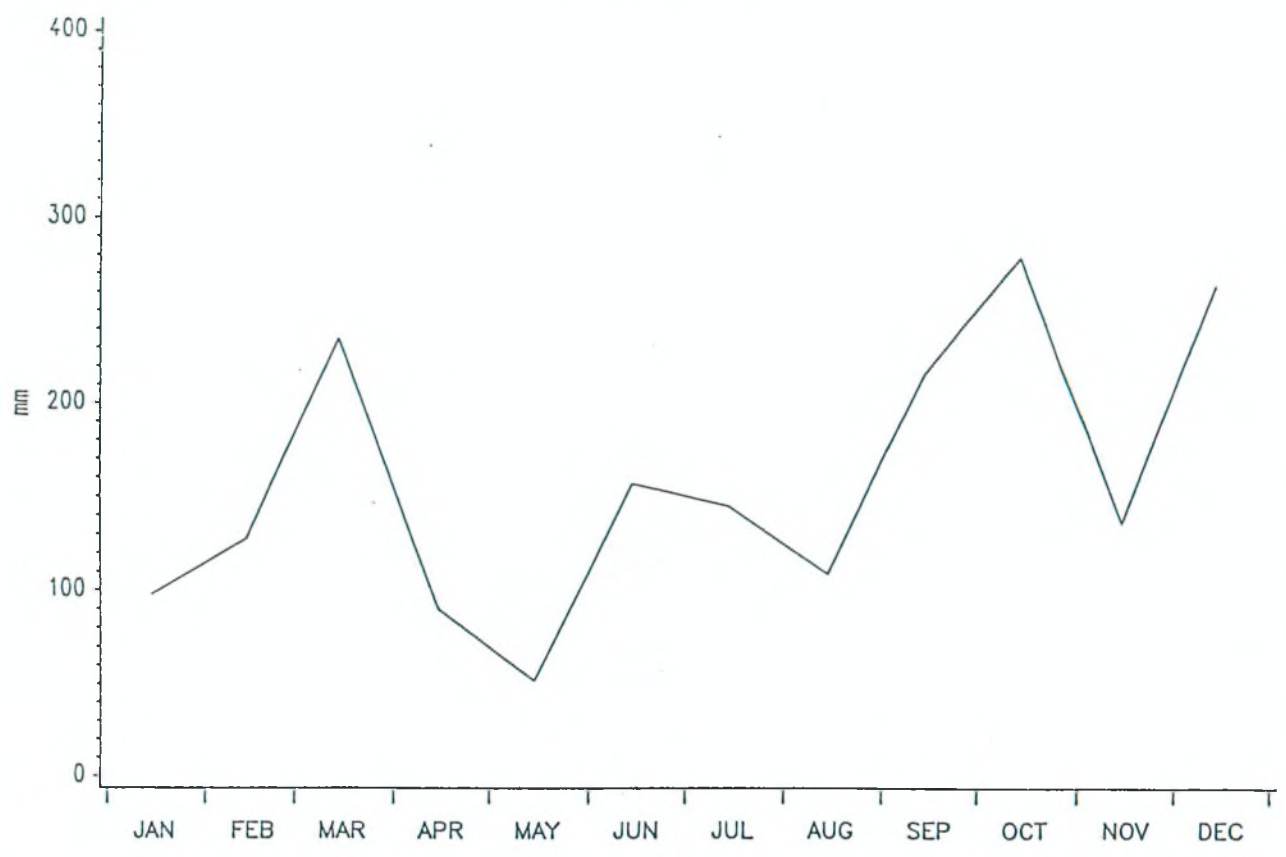
Angler 2 - data from 1966-72 and 1978-88

	South Basin			North Basin		
	months			months		
	fished	CPUE		fished	CPUE	
pre 1984	56	2.74) F = 9.86	63	2.51) F = 2.39
) SIG)
1984-88	16	1.37) P < 0.01	22	3.11) NS

Angler 3 - data from 1975-88 (except 1980 and 82)

	South Basin			North Basin		
	months			months		
	fished	CPUE		fished	CPUE	
pre 1984	16	2.26) F = 7.34	32	1.59) F = 2.23
) SIG)
1984-88	18	0.99) P < 0.01	24	1.86) NS

RAINFALL 1987



RAINFALL 1988

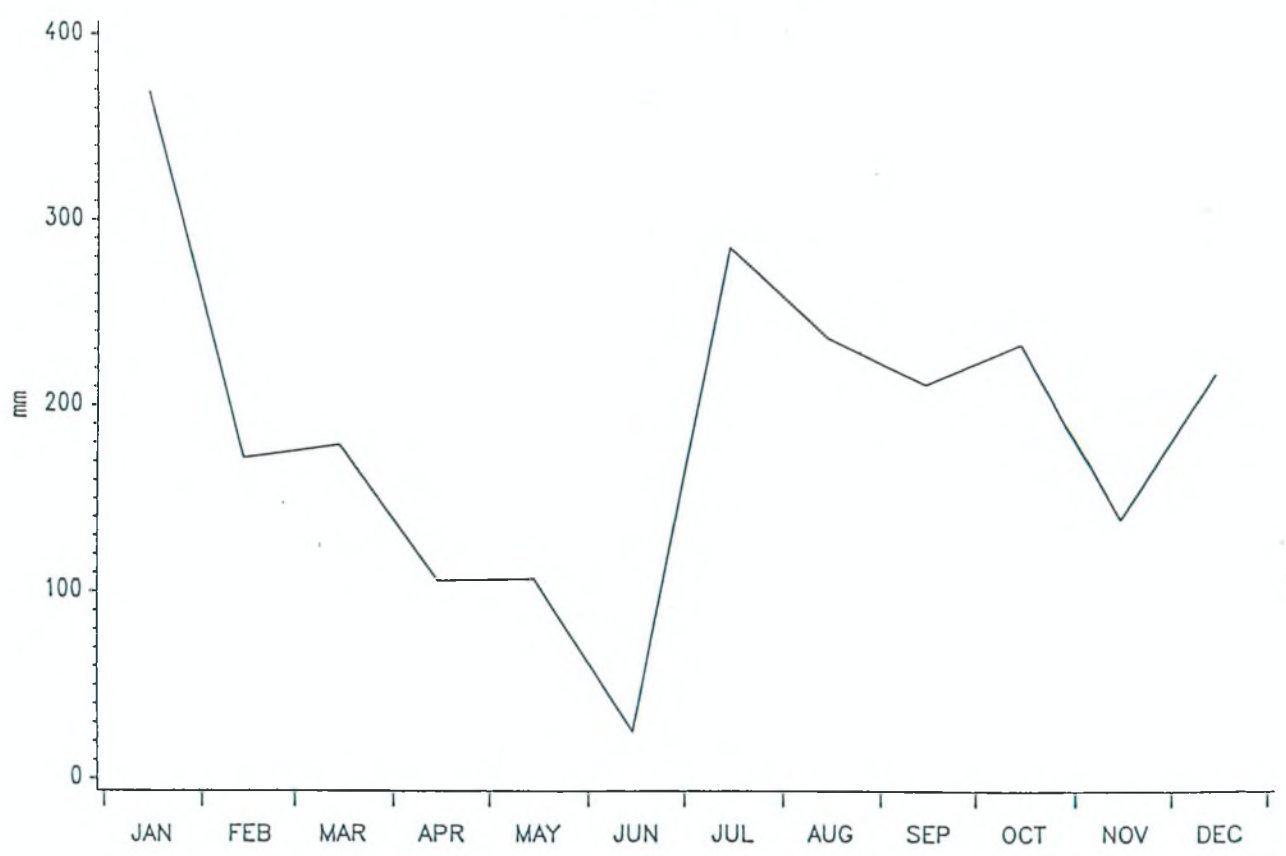


Figure 1. Total monthly rainfall (mm) measured at Ambleside.

WINDERMERE

Monthly Mean Levels & Discharges

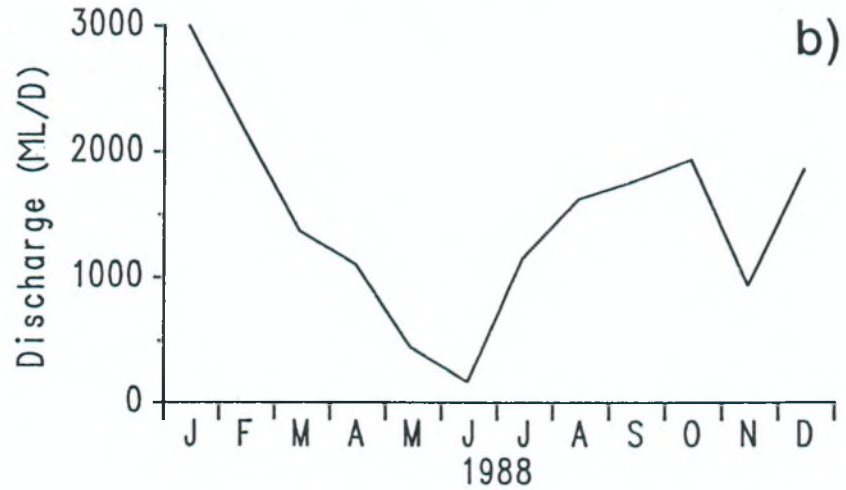
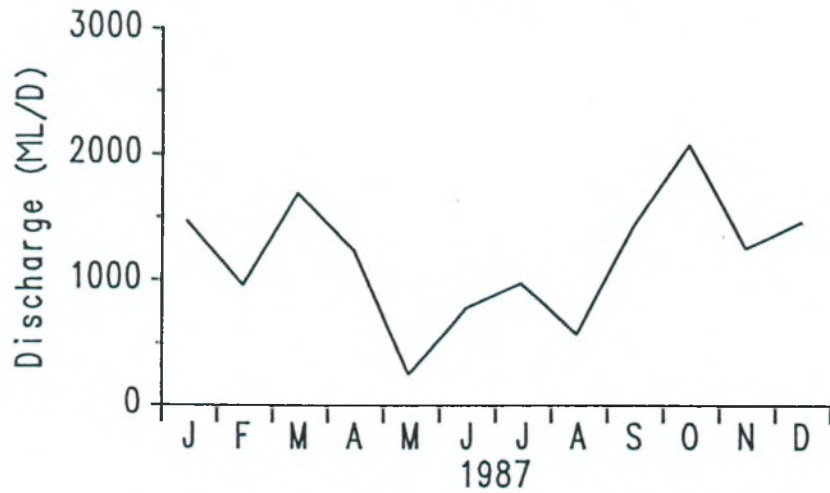
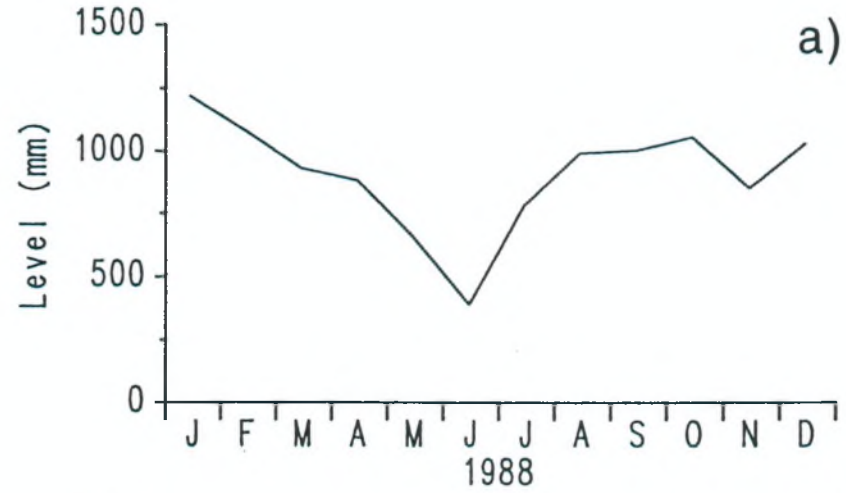
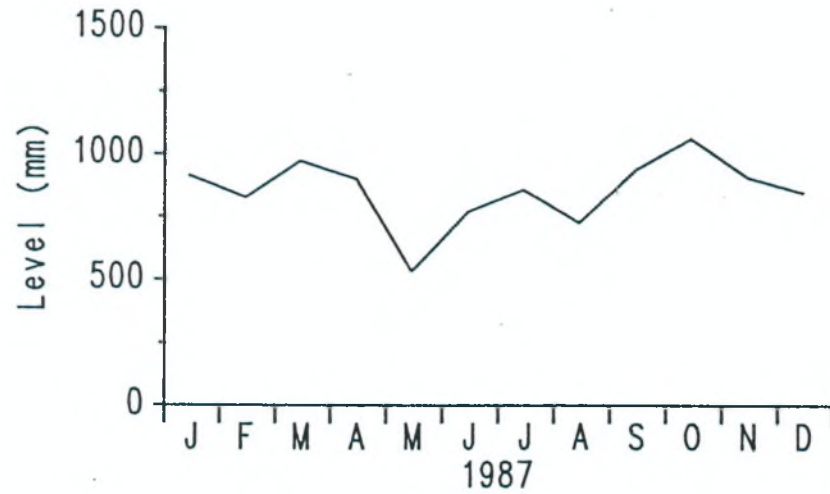
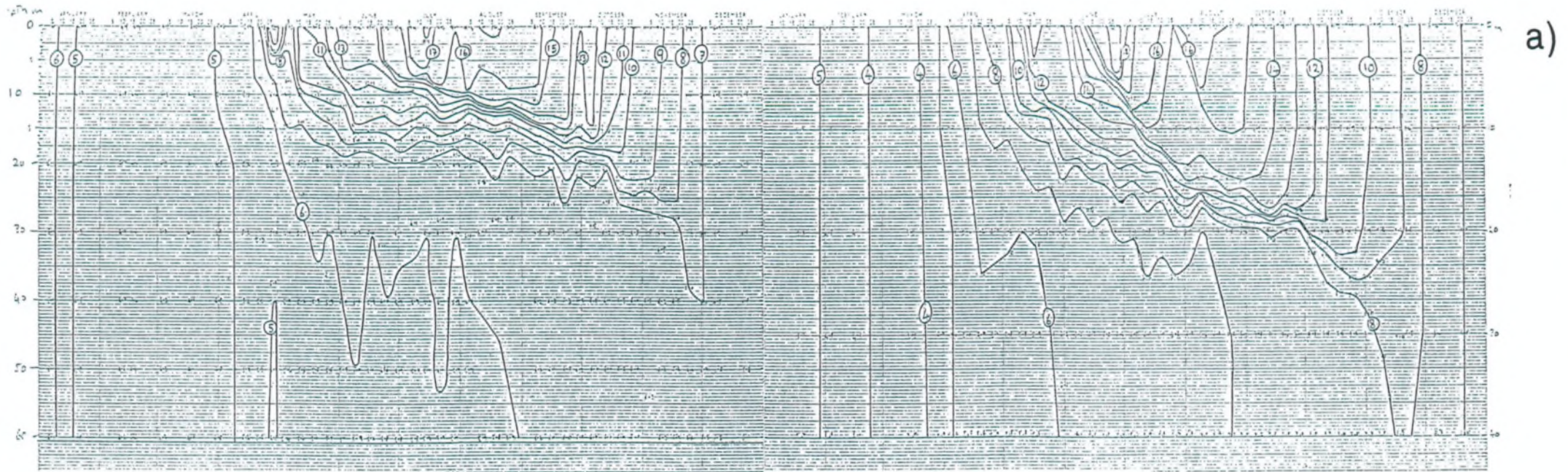
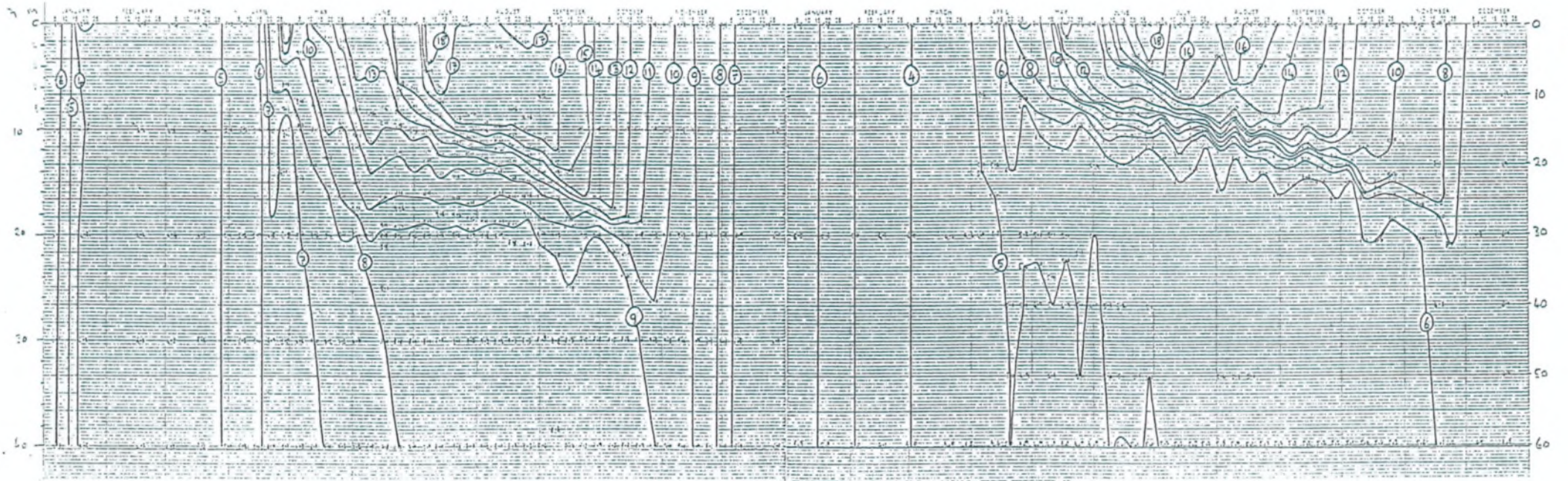


Figure 2. Mean monthly lake levels (mm) measured at Newby Bridge, and mean monthly discharge as megalitres per day (ML/D) from Windermere for 1987 and 1988.



a)



b)

Figure 3. Depth-time distribution of temperature (isotherms in °C) during 1987 and 1988 in (a) North and (b) South Basin.

FIG.3

WINDERMERE SECCHI DISC & CHLOROPHYLL a

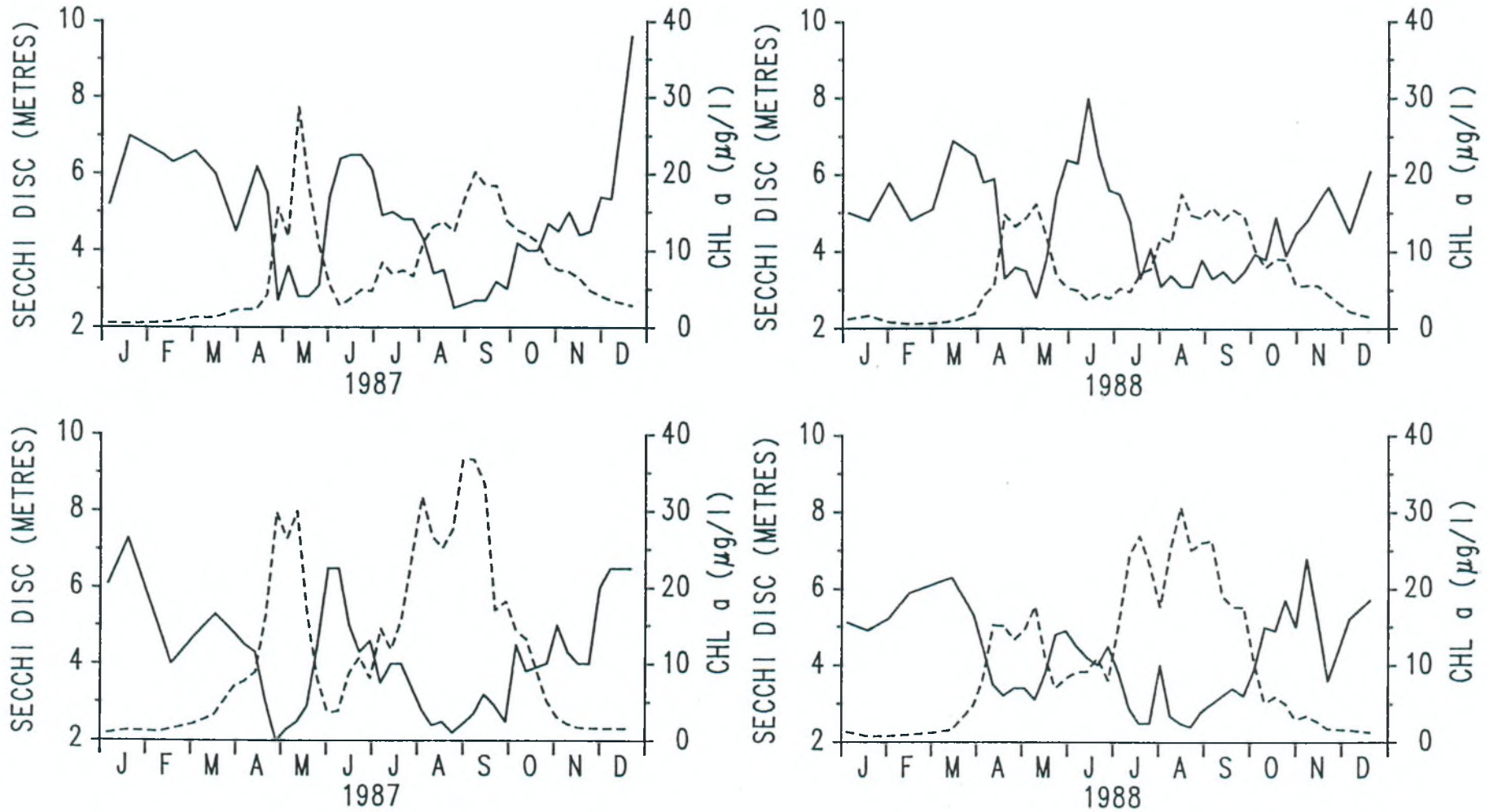


Figure 4. Variation of transparency(—) (Secchi-disc (m)) and the mean concentration of chlorophyll a (---) ($\mu\text{g l}^{-1}$) in the 0-7 m layer, 1987 and 1988.

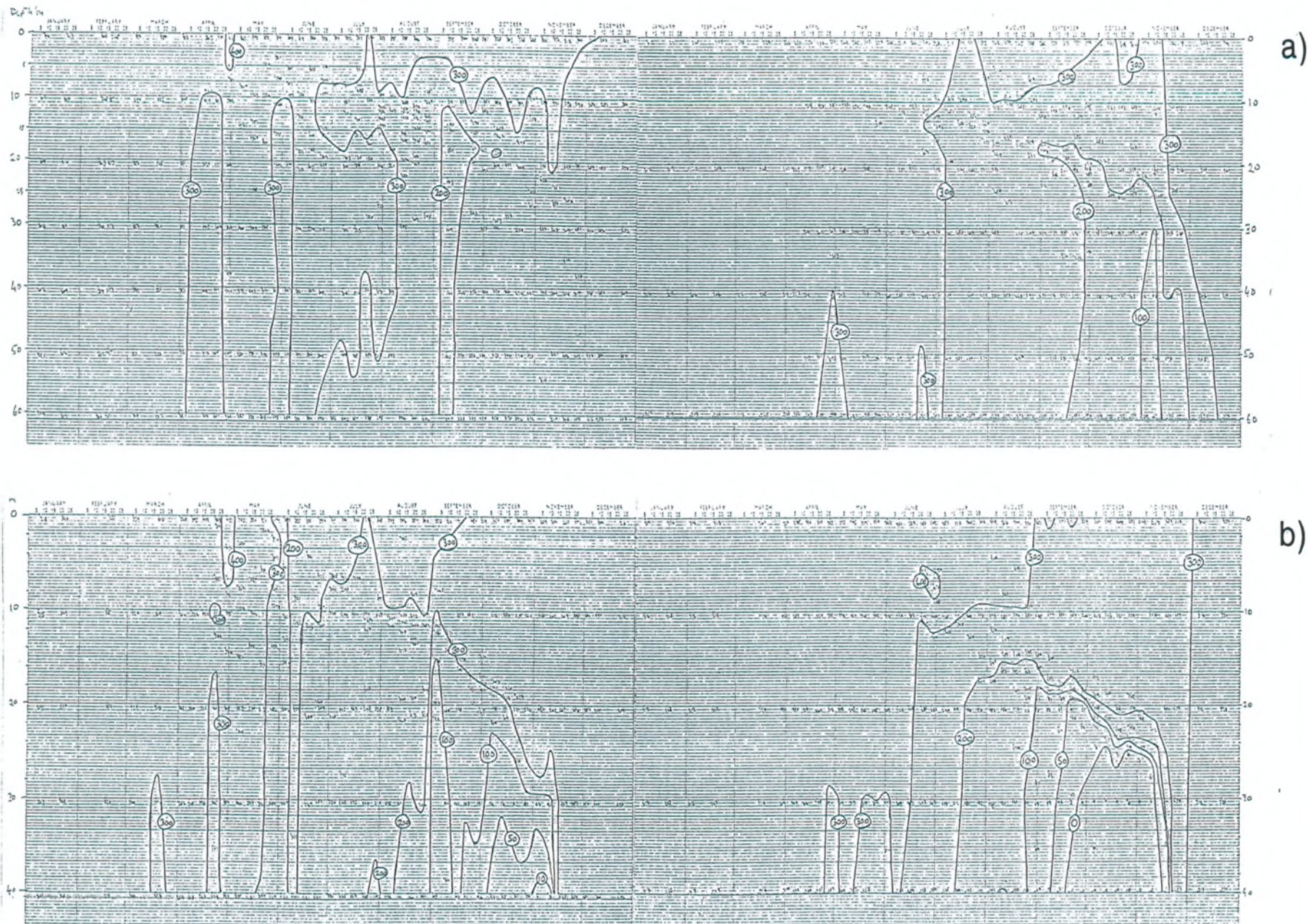


Figure 5. Depth-time distribution of dissolved oxygen (isopleths in μ moles l^{-1}) during 1987 and 1988 in (a) North and (b) South Basin.

WINDERMERE – ALKALINITY

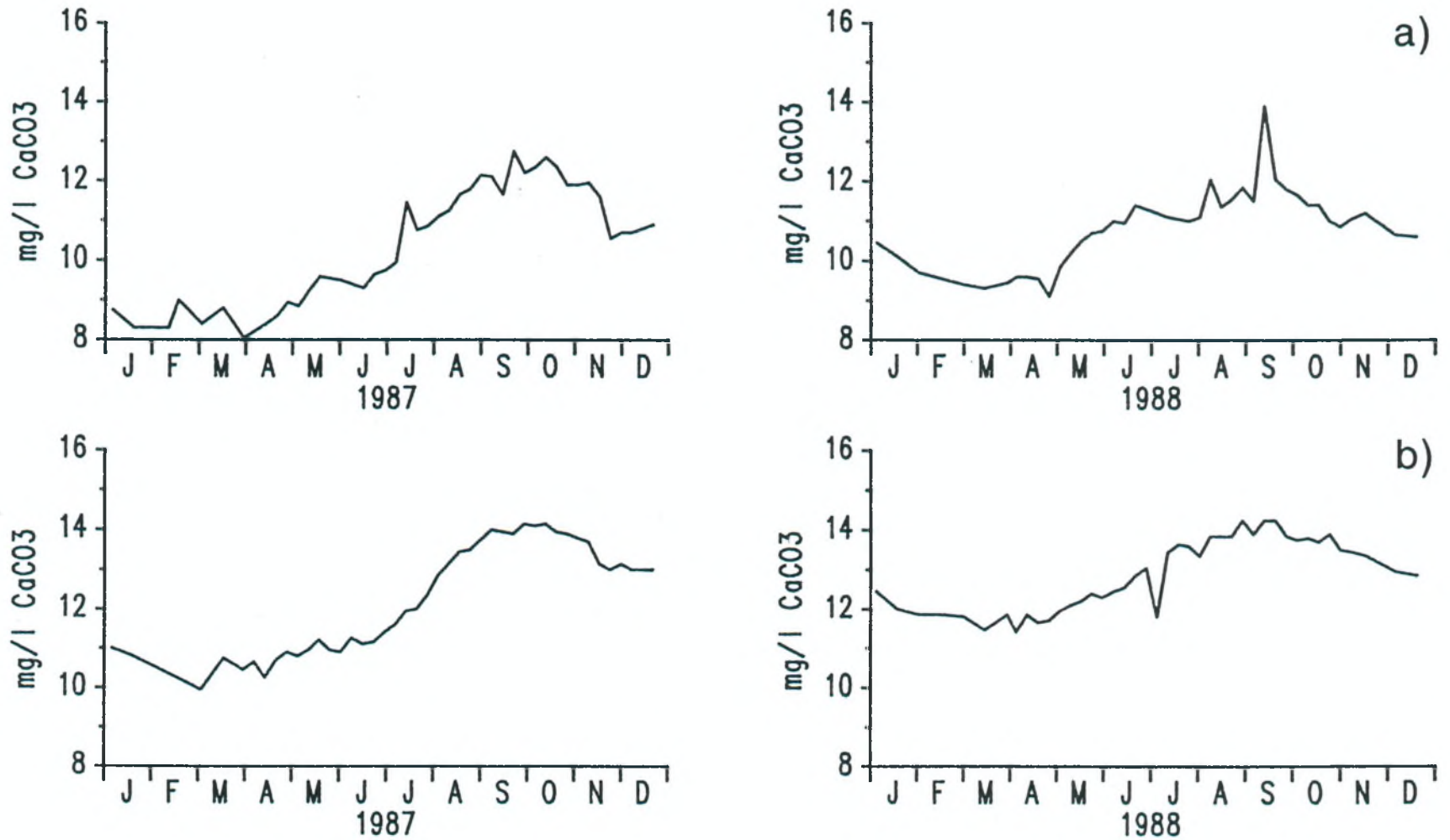


Figure 6. Seasonal variation of alkalinity expressed as mg CaCO₃ l⁻¹ in surface water of (a) North and (b) South Basin, 1987 and 1988.

WINDERMERE - pH

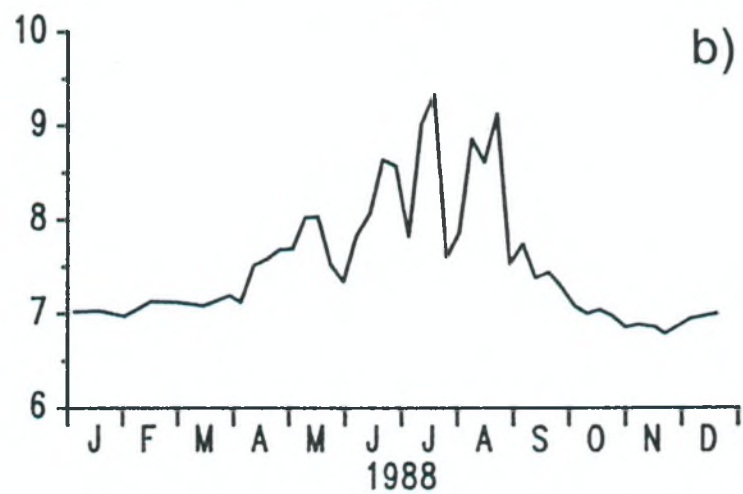
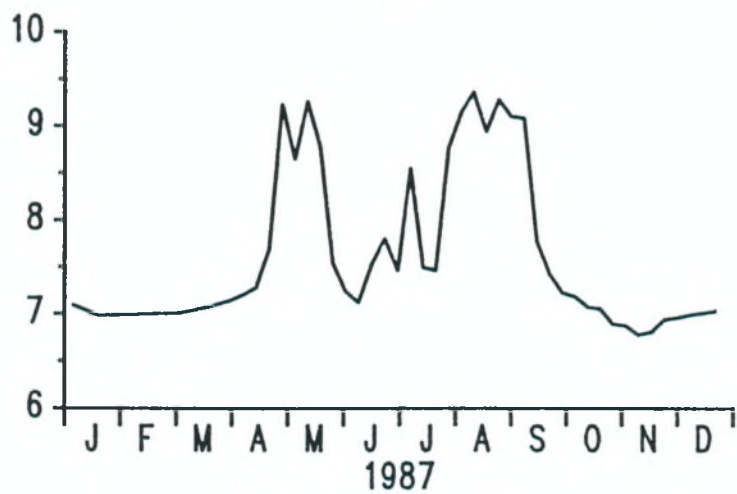
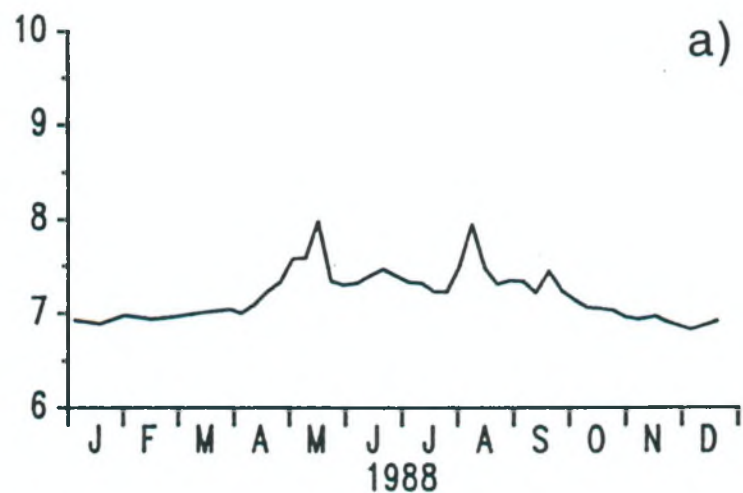
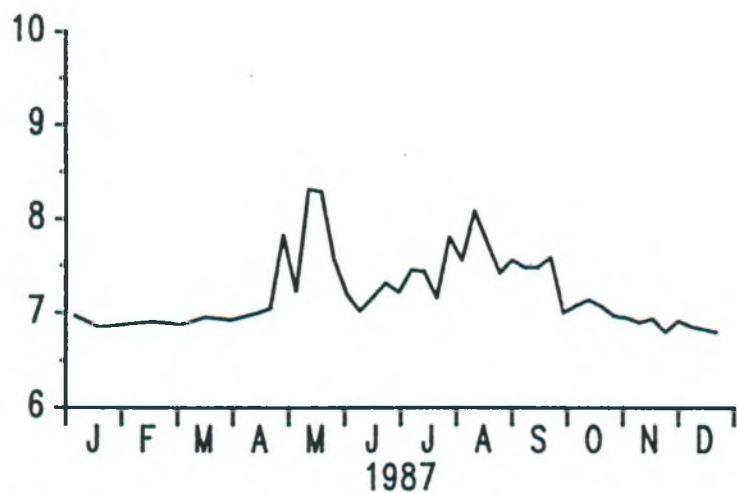


Figure 7. Seasonal variation of pH in surface water of (a) North and (b) South Basin, 1987 and 1988.

WINDERMERE PHOSPHORUS & SILICA

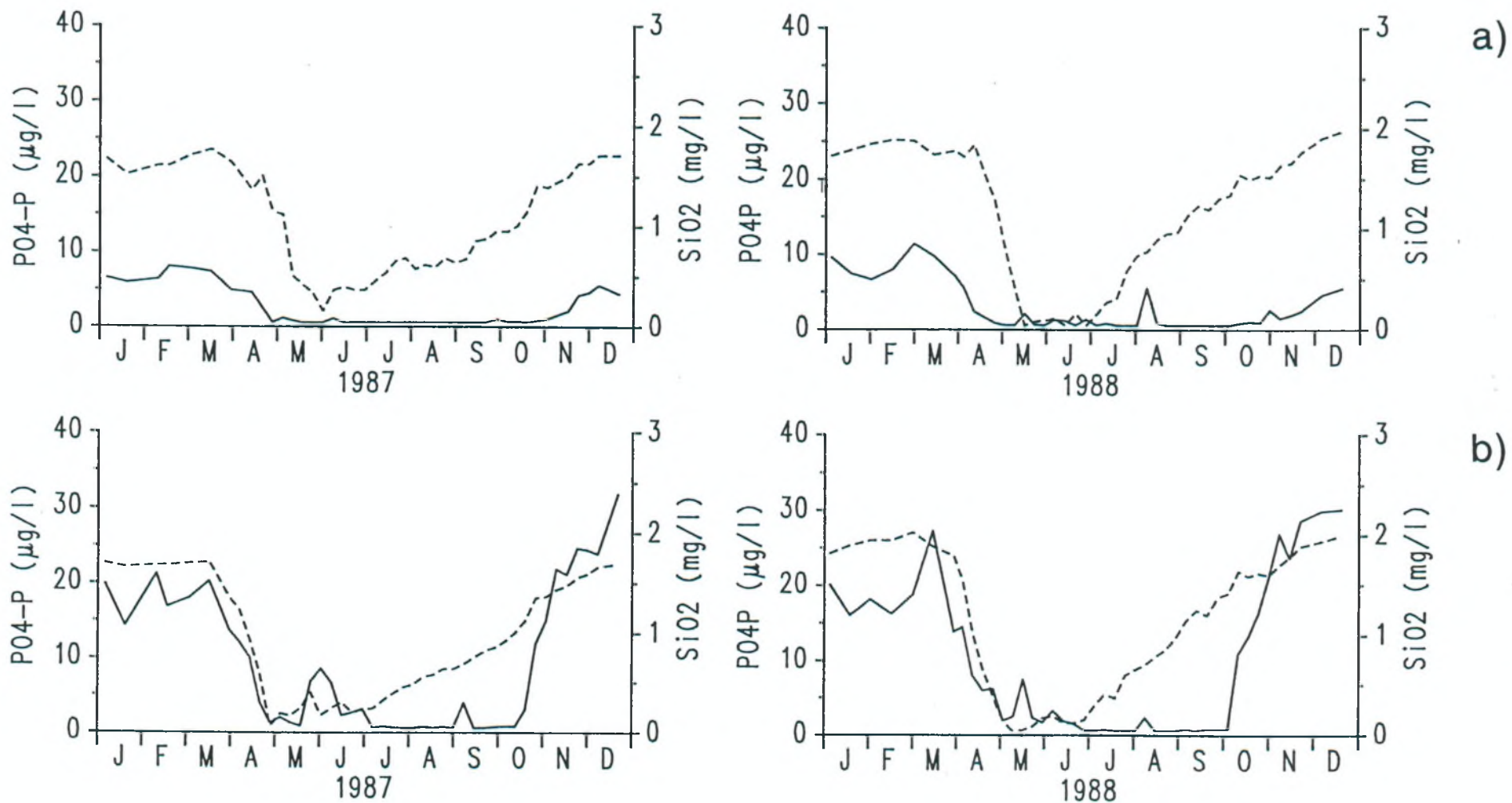


Figure 8. Variation of the mean concentration of dissolved silicon (---) as mg SiO₂ l⁻¹ and soluble reactive phosphorus (—) (µg l⁻¹) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988.

WINDERMERE NITRATE (NO₃-N)

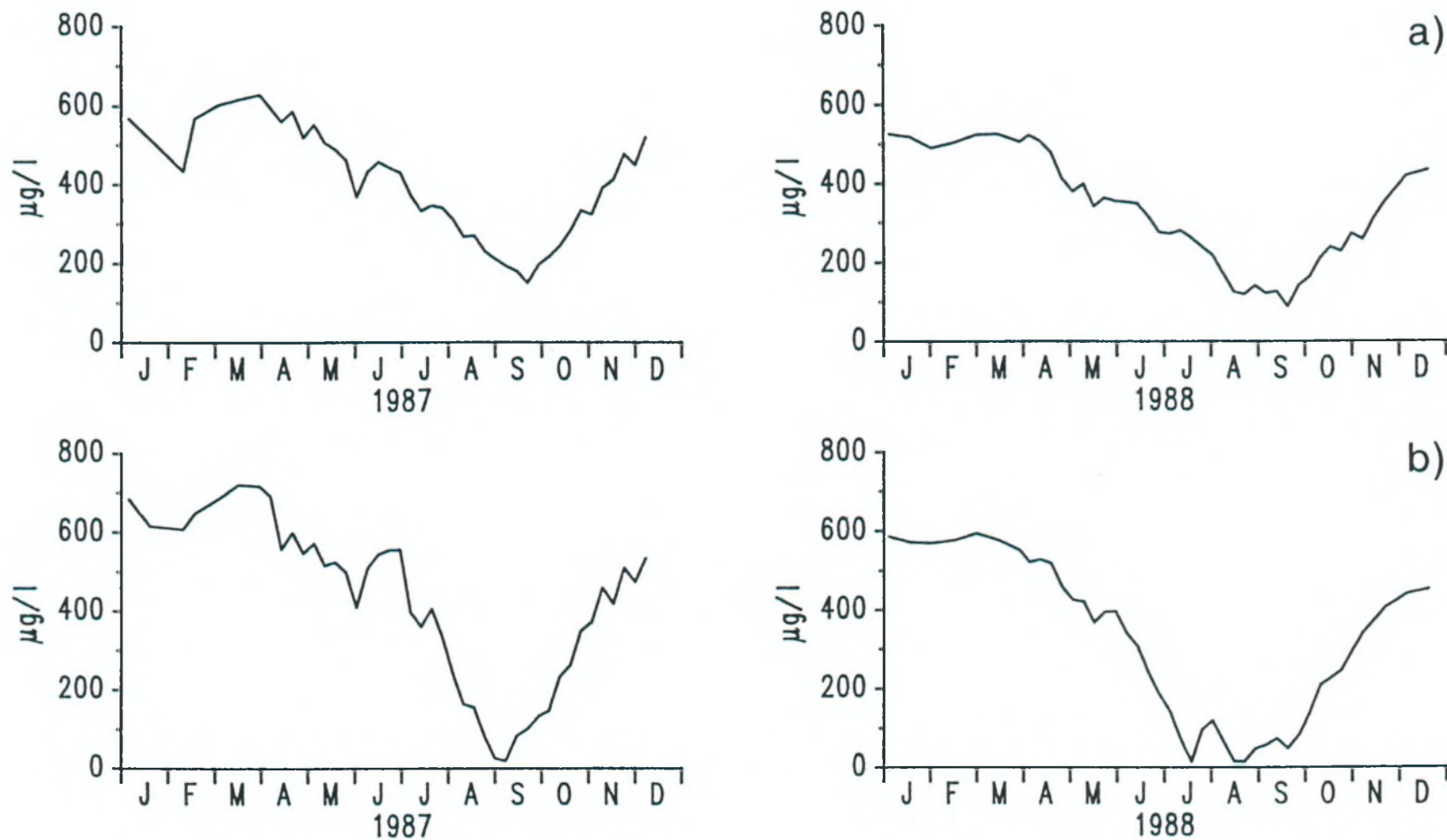


Figure 9. Variation of the mean concentration of nitrate nitrogen ($\mu\text{g l}^{-1}$) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988.

WINDERMERE AMMONIUM (NH₄-N)

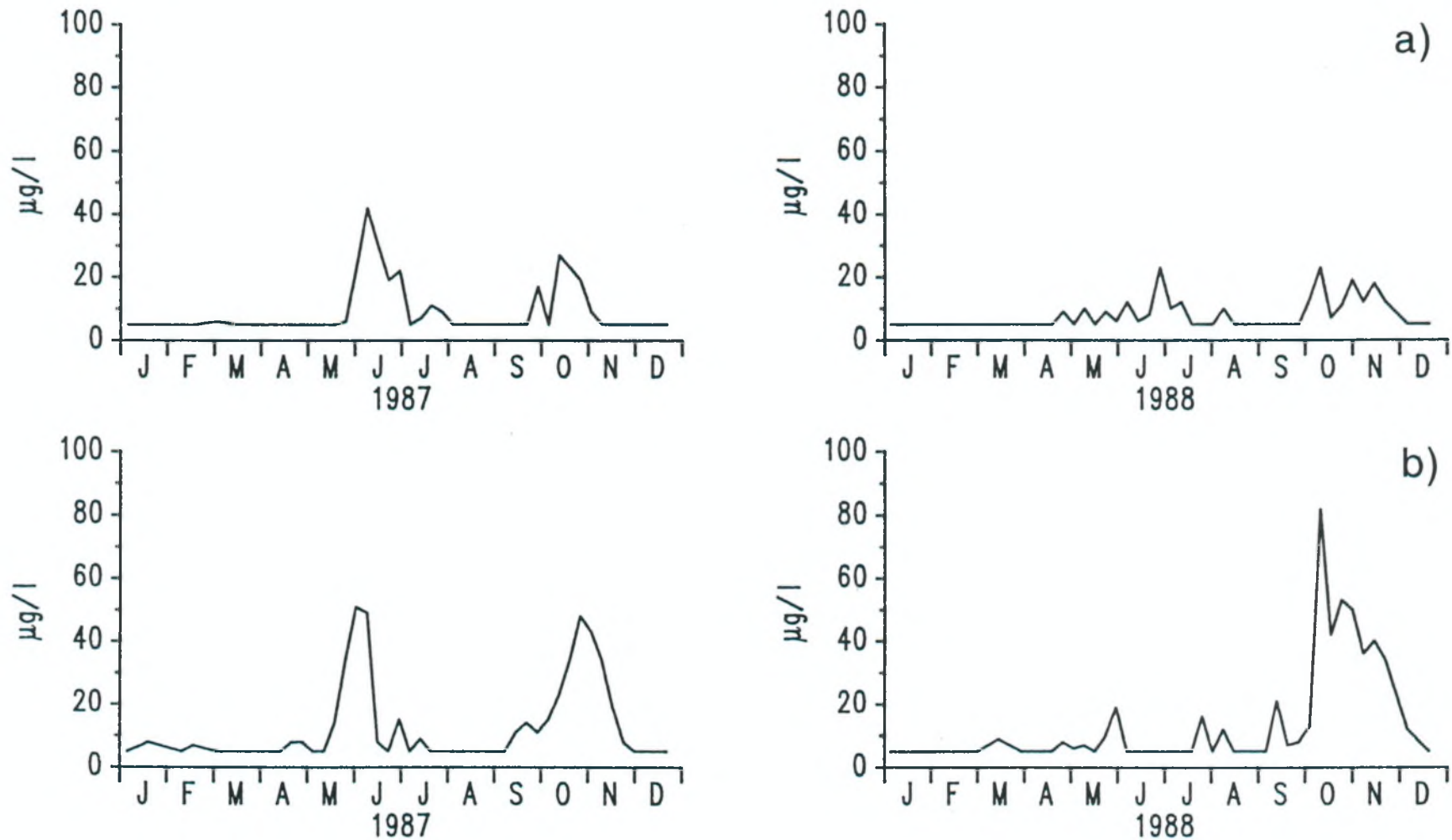


Figure 10. Variation of the mean concentration of ammonium nitrogen ($\mu\text{g l}^{-1}$) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988.

WINDERMERE TOTAL PHOSPHORUS

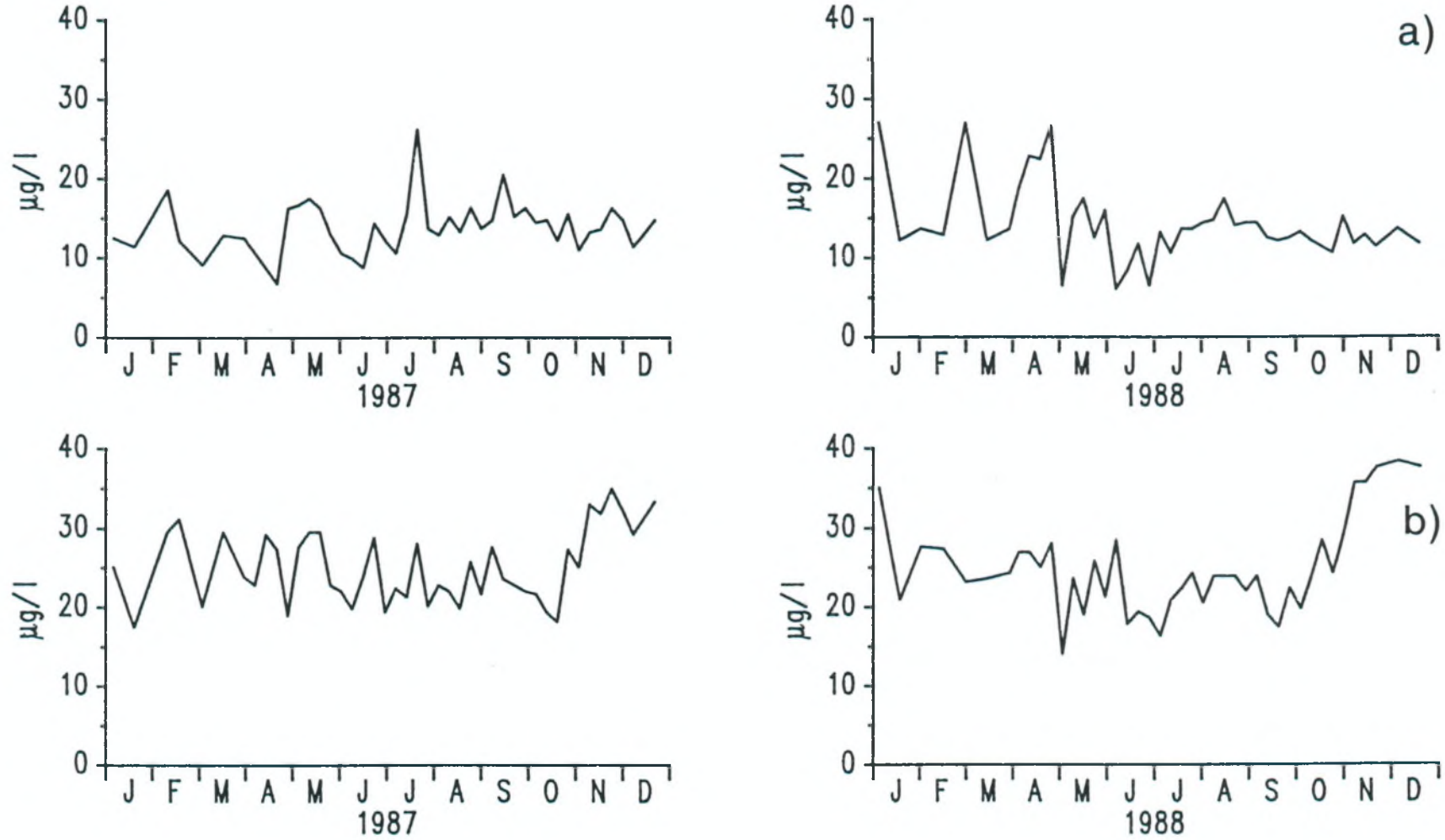


Figure 11. Variation of the mean concentration of total phosphorus ($\mu\text{g l}^{-1}$) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988.

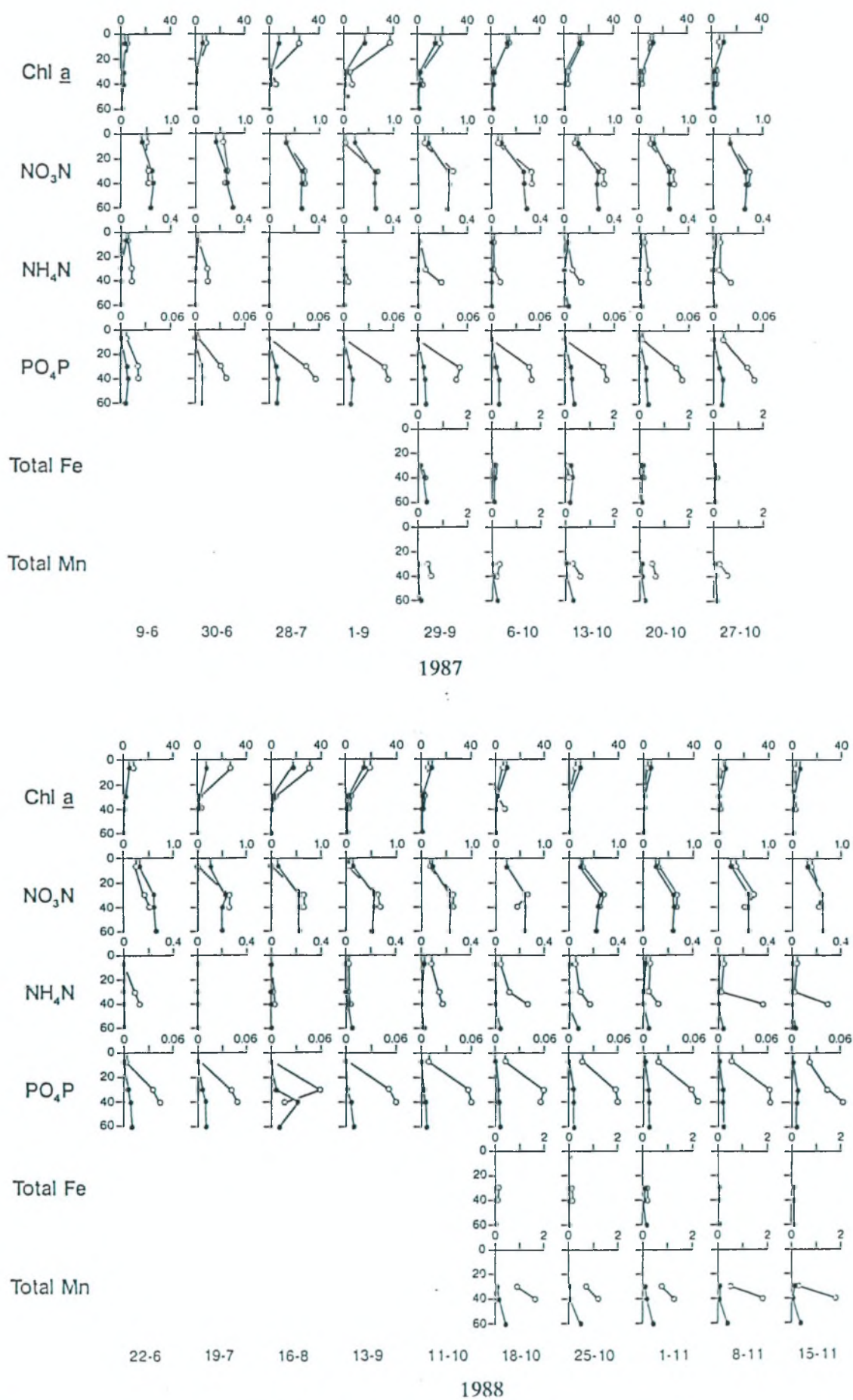


Figure 12. Vertical distribution of chlorophyll *a*, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, total Fe and total Mn (all as $\mu\text{g l}^{-1}$) in North Basin (●) and South Basin (○) between June and October in 1987 and June and November in 1988.

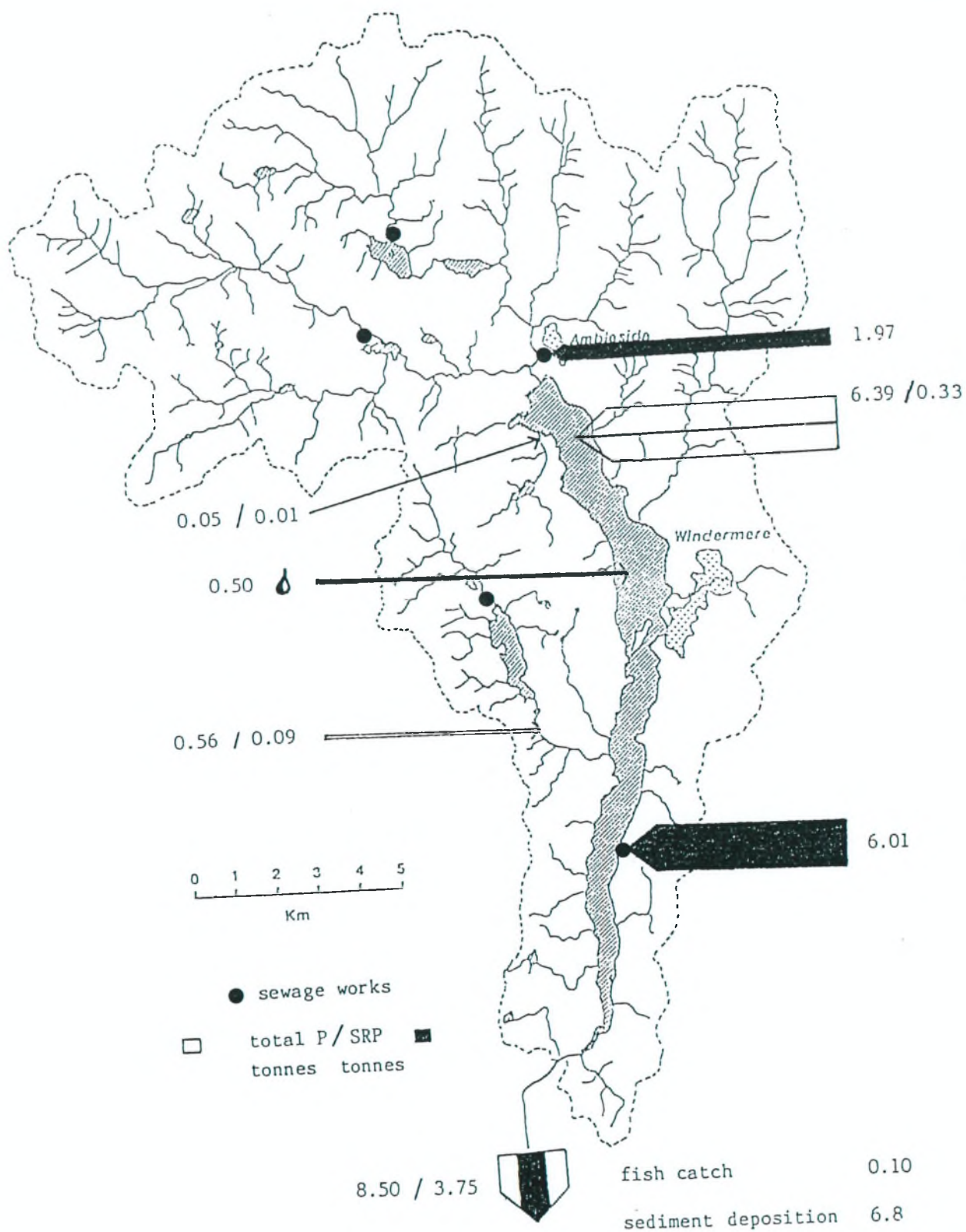


Figure 13. Inputs to and discharge from Windermere of total \square and soluble reactive \blacksquare ($\text{PO}_4\text{-P}$) phosphorus as determined in Table 1; \bullet sewage works, ☼ phosphorus in rainfall.

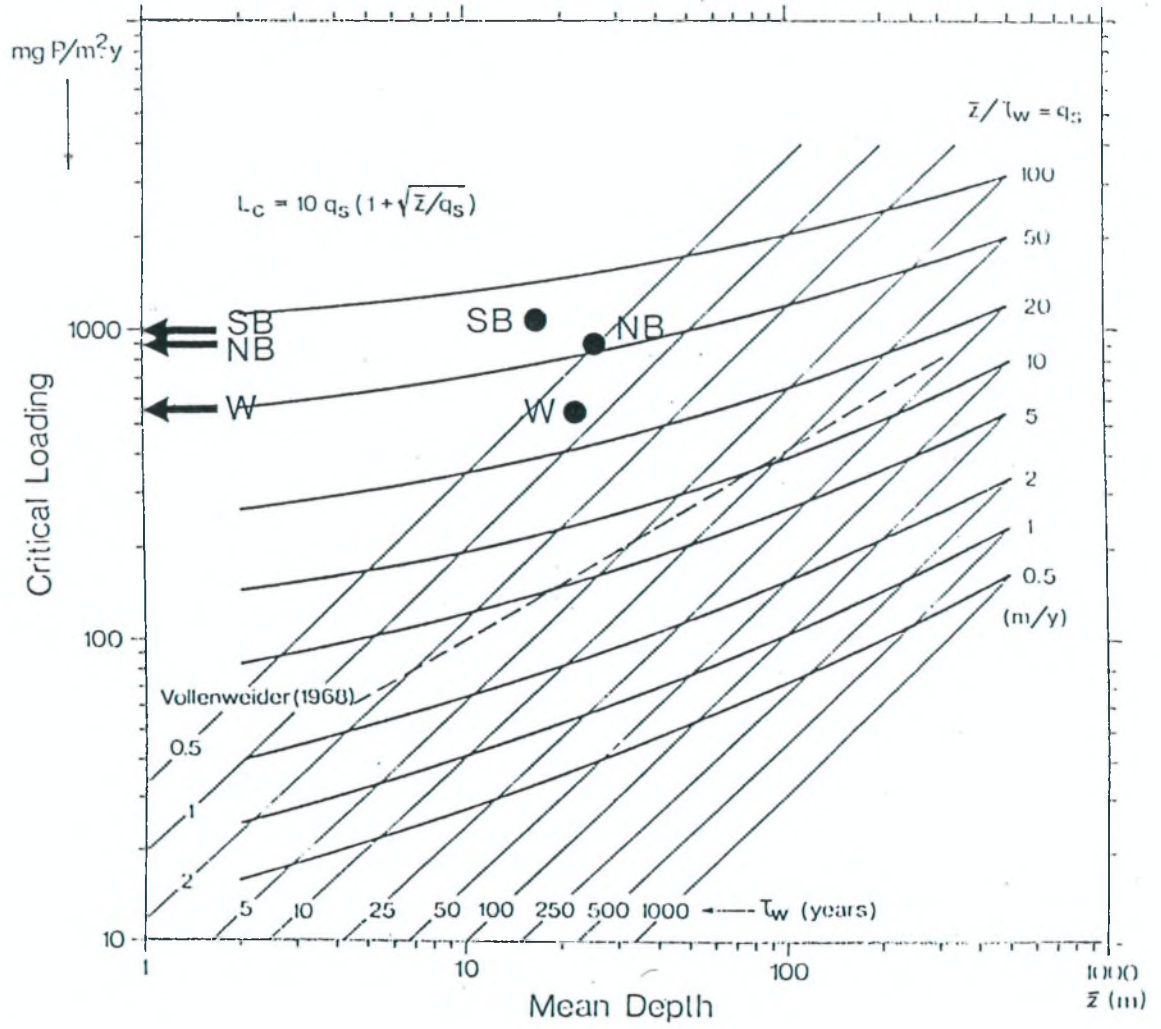


Figure 14. Critical loading (lower limit) for total phosphorus to Windermere (W) and its basins (NB and SB) as determined using Fig. 5 of Vollenweider (1976); q_s , the hydraulic load, is calculated from mean lake discharge values from 1984, 1987 and 1988.

WINDERMERE
Asterionella formosa & *Melosira* spp.

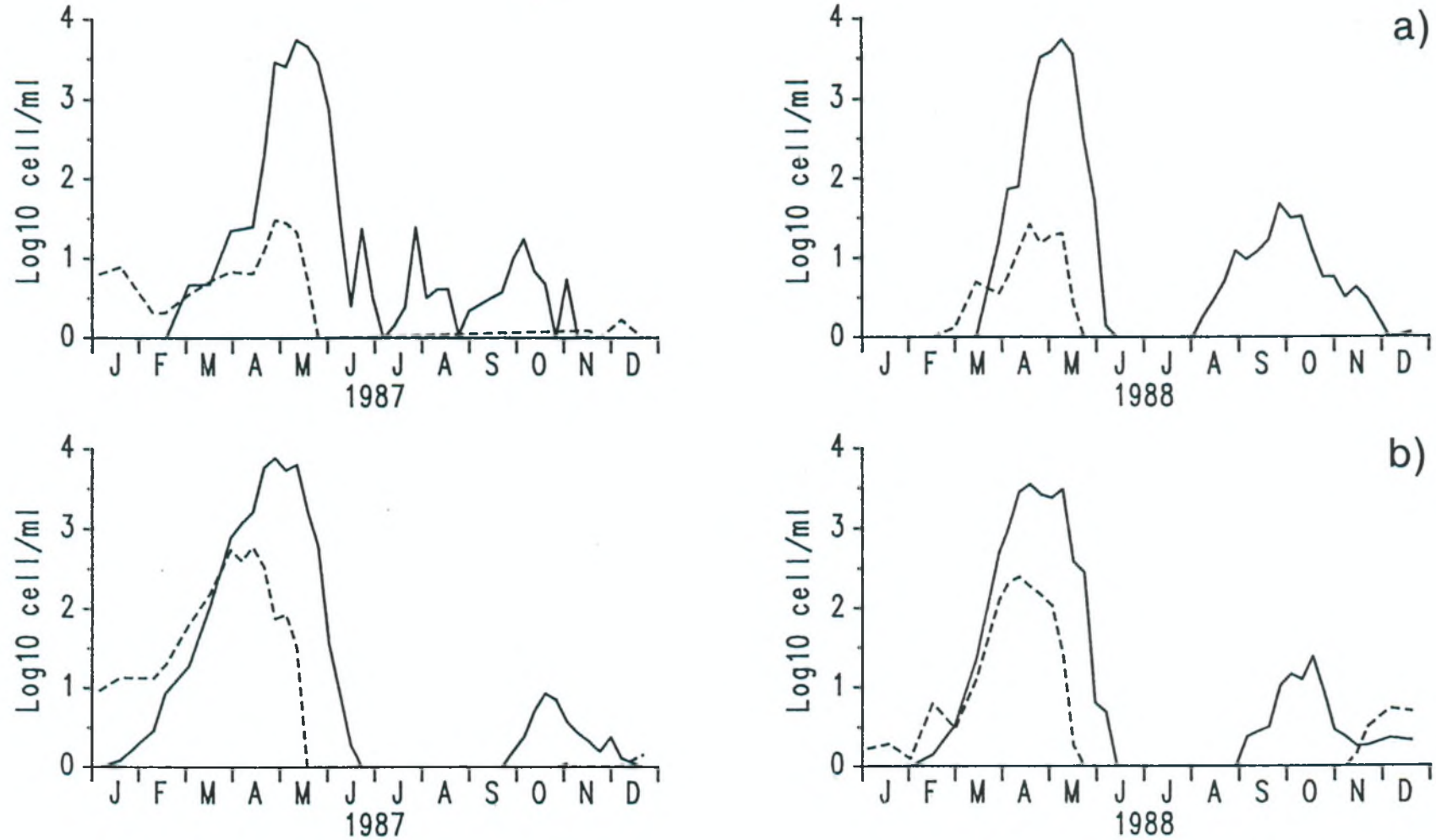


Figure 15. Variation of the numbers, as cells ml⁻¹, of *Asterionella formosa* (—) and *Melosira italica* subsp. *subarctica* + *Melosira islandica* (---) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988; note zero values represent cell numbers of 1 ml⁻¹ or less.

WINDERMERE
Fragilaria crotonensis & *Tabellaria* spp.

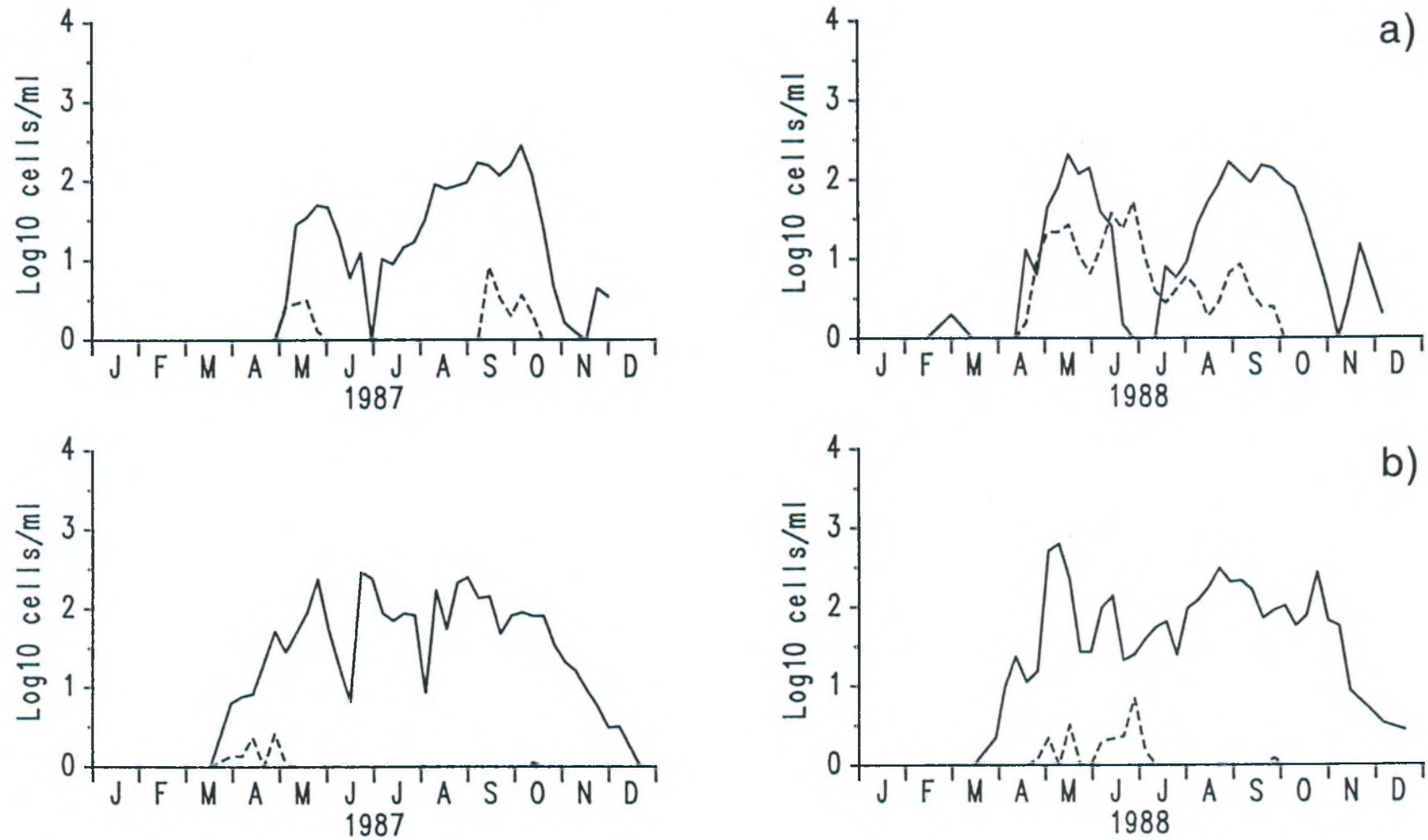


Figure 16. Variation of the numbers, as cells ml⁻¹, of *Fragilaria crotonensis* (—) and *Tabellaria flocculosa* var. *asterionelloides* + *Tabellaria fenestrata* (----) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988; note zero values represent cell numbers 1 ml⁻¹ or less.

WINDERMERE
Oscillatoria bourrellyi & *Oscillatoria aghardii*

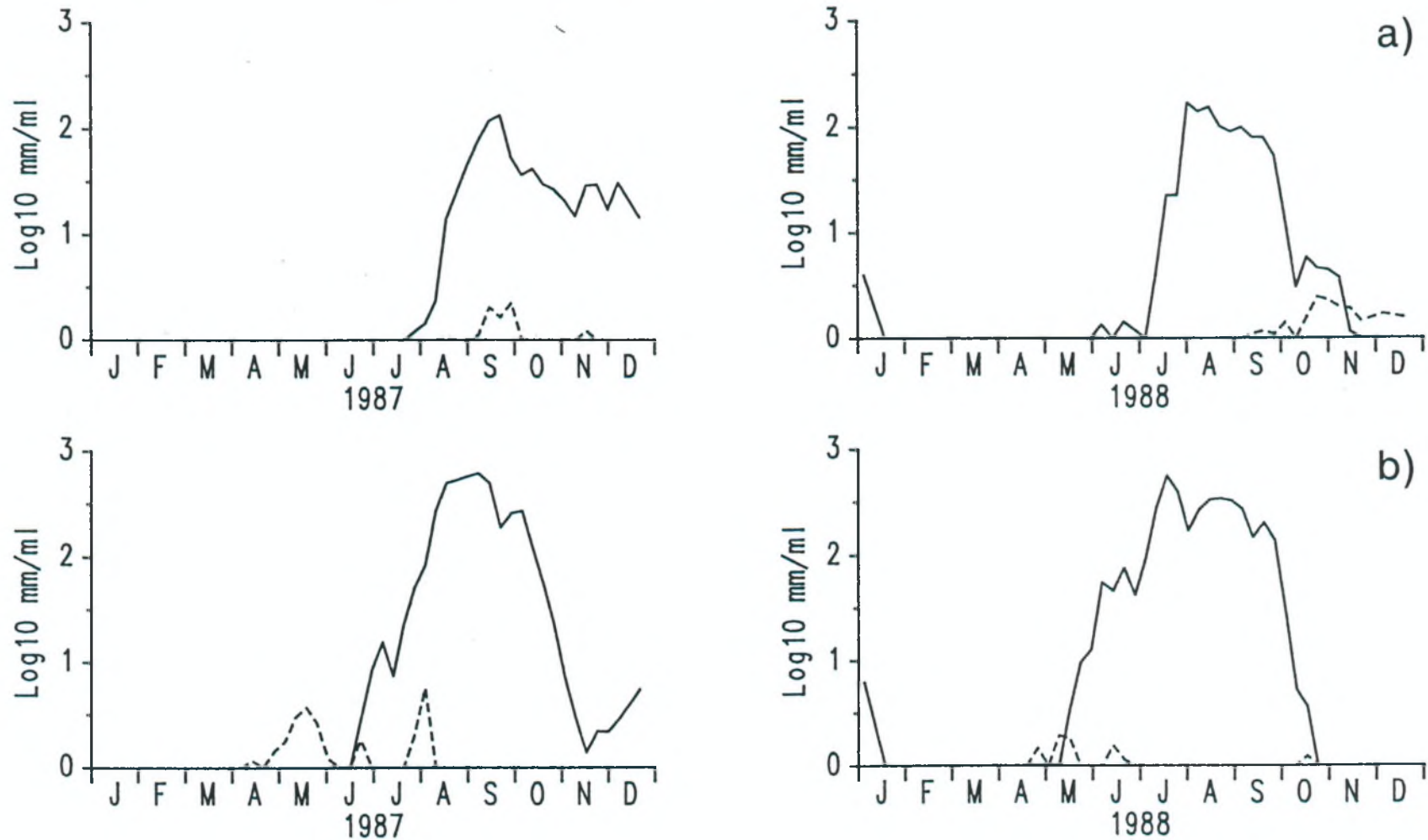


Figure 17. Variation of the abundance, as mm ml^{-1} filament length, of *Oscillatoria bourrellyi* (—) and *Oscillatoria aghardii* + *Oscillatoria aghardii* var *isothrix* (----) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988; note zero values represent biomass of 1 mm ml^{-1} filament length or less.

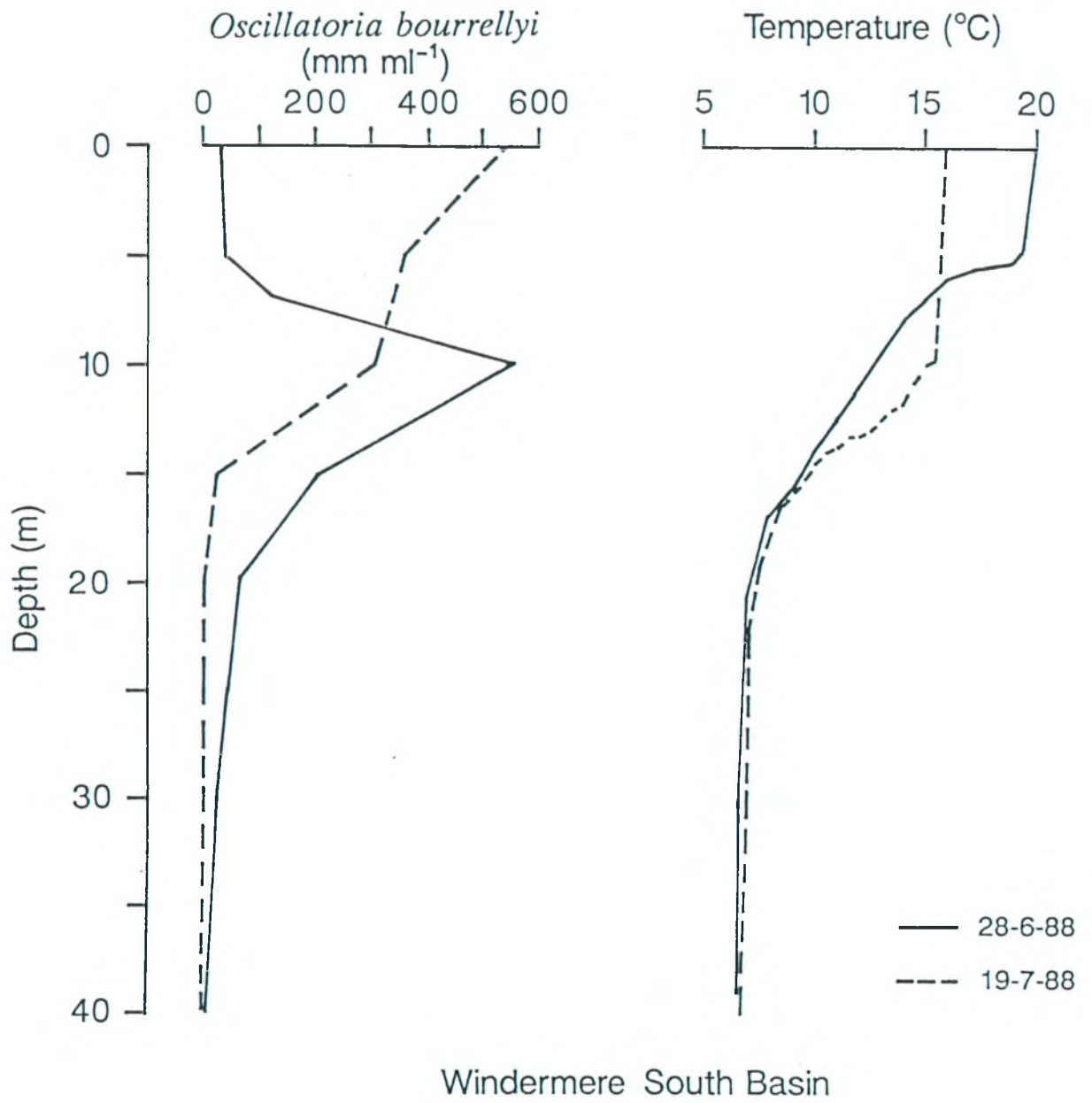


Figure 18. Vertical distribution of *Oscillatoria bourellyi* in the South Basin showing a well-developed sub-surface layer after a period of calm weather (28 June 1988) and its subsequent mixing into the upper layer after strong winds (19 July 1988); the vertical temperature structure is also given for these dates.

WINDERMERE
Oscillatoria limnetica & *Aphanizomenon flos-aquae*

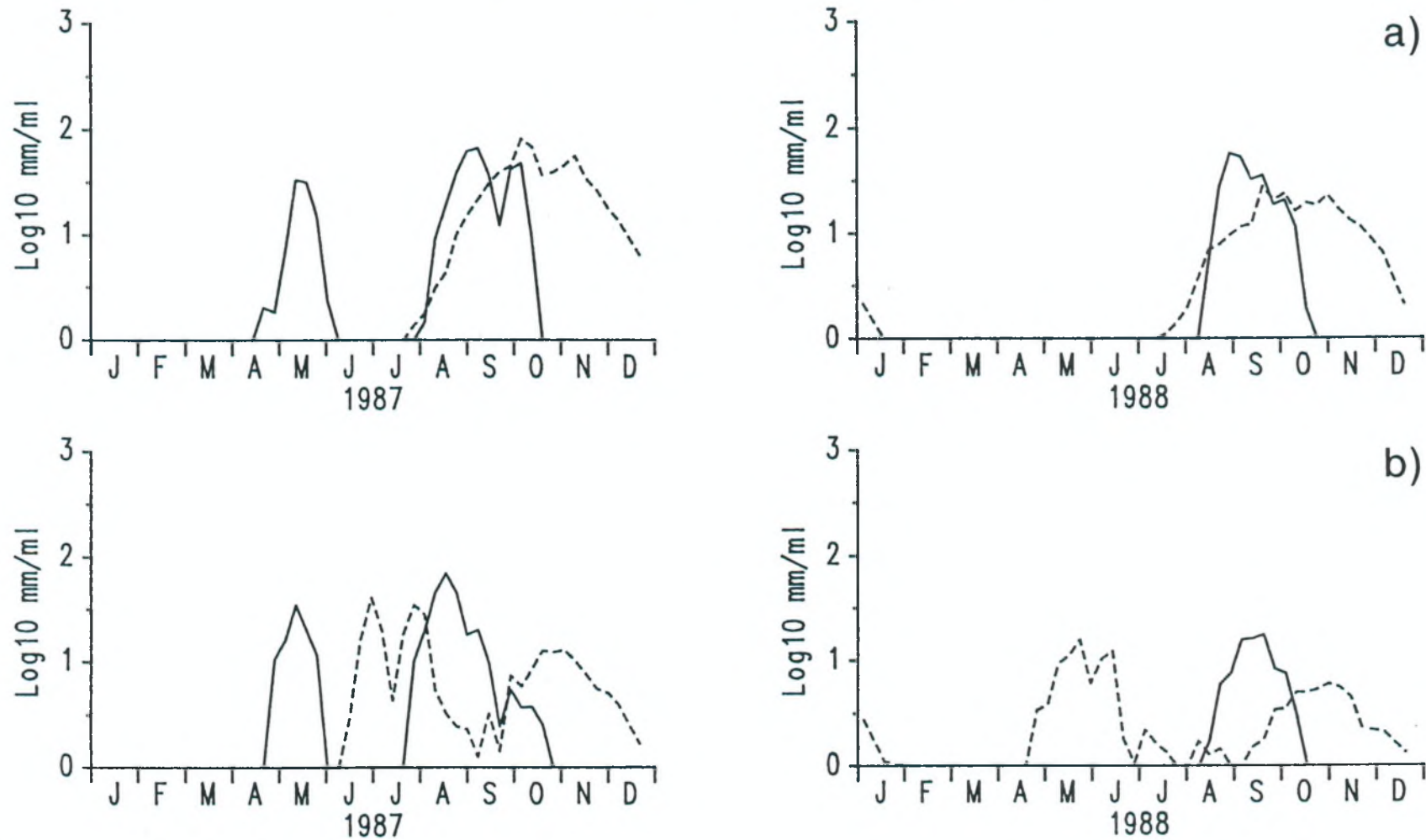


Figure 19. Variation of the abundance, as mm ml^{-1} filament length, of *Oscillatoria limnetica* (—) and *Aphanizomenon flos-aquae* (----) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988; note zero values represent biomass of 1 mm ml^{-1} filament length or less.

WINDERMERE
Anabaena flos-aquae⁺ & *Anabaena solitaria*

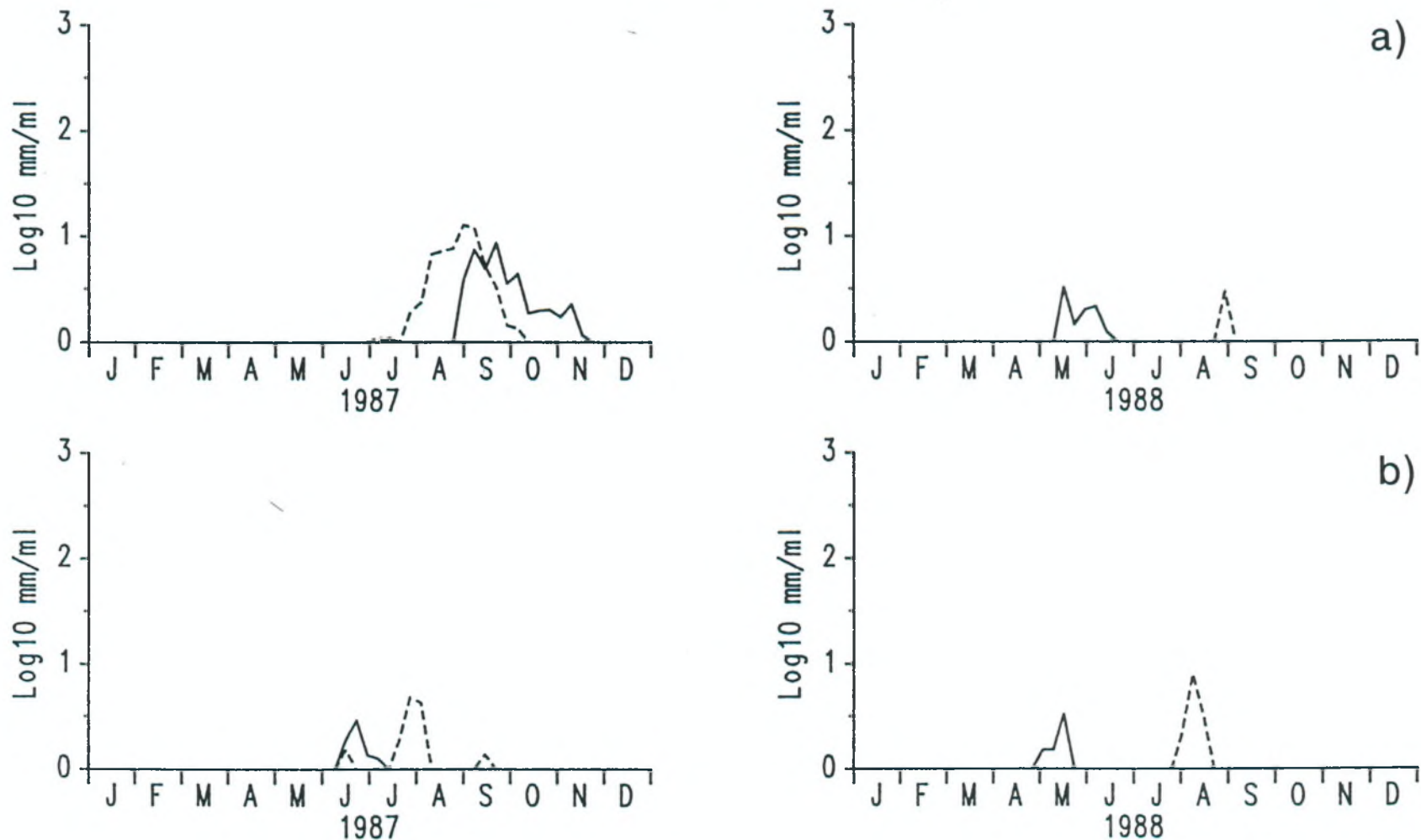


Figure 20. Variation of the abundance, as mm ml^{-1} filament length, of the *Anabaena flos-aquae*/*Anabaena circinalis* complex + (—) and *Anabaena solitaria* (---) in the 0-7 m layer of (a) North and (b) South Basin, 1987 and 1988; note zero values represent biomass of 1 mm ml^{-1} filament length or less.

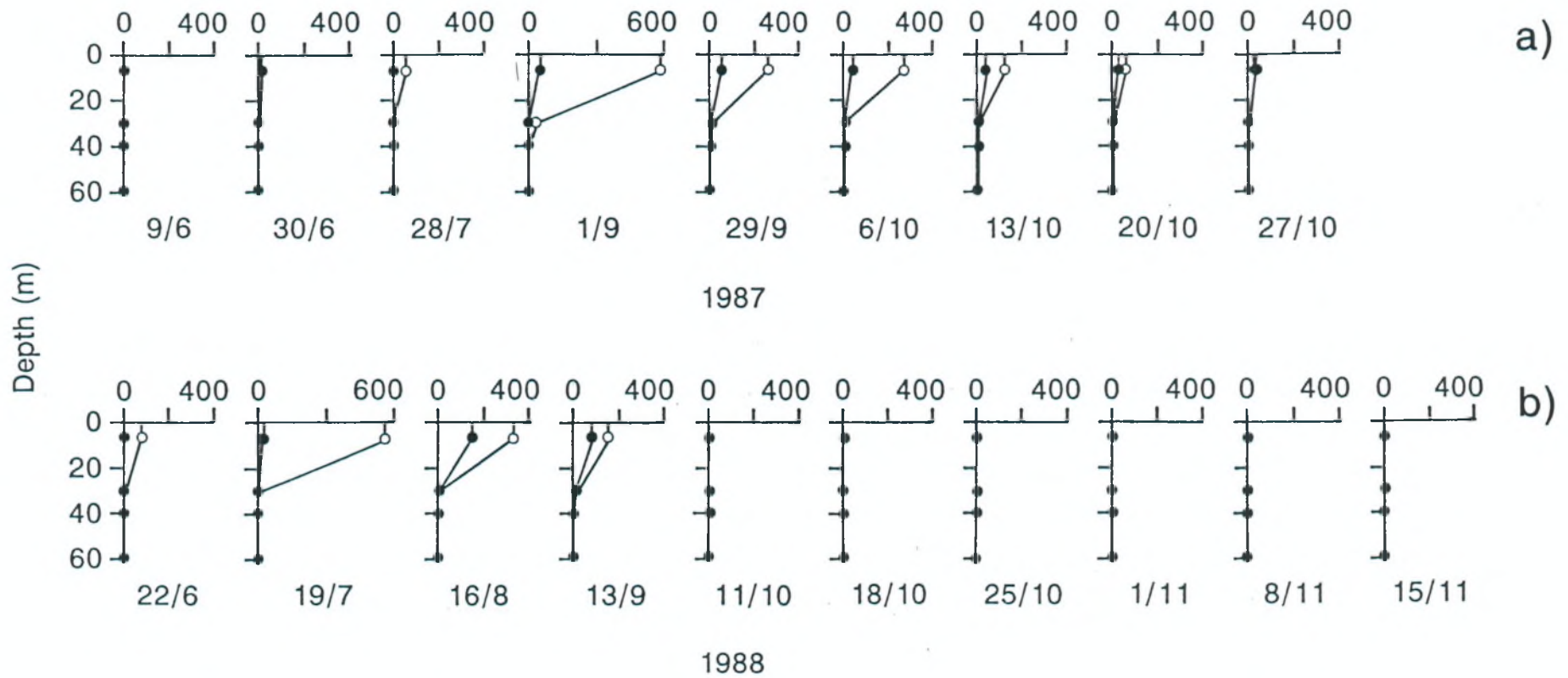


Figure 21. Vertical distribution of *Oscillatoria bourrellyi* as mm ml⁻¹ filament length in North (●) and South Basin (○) between (a) June and October in 1987 and (b) June and November in 1988.

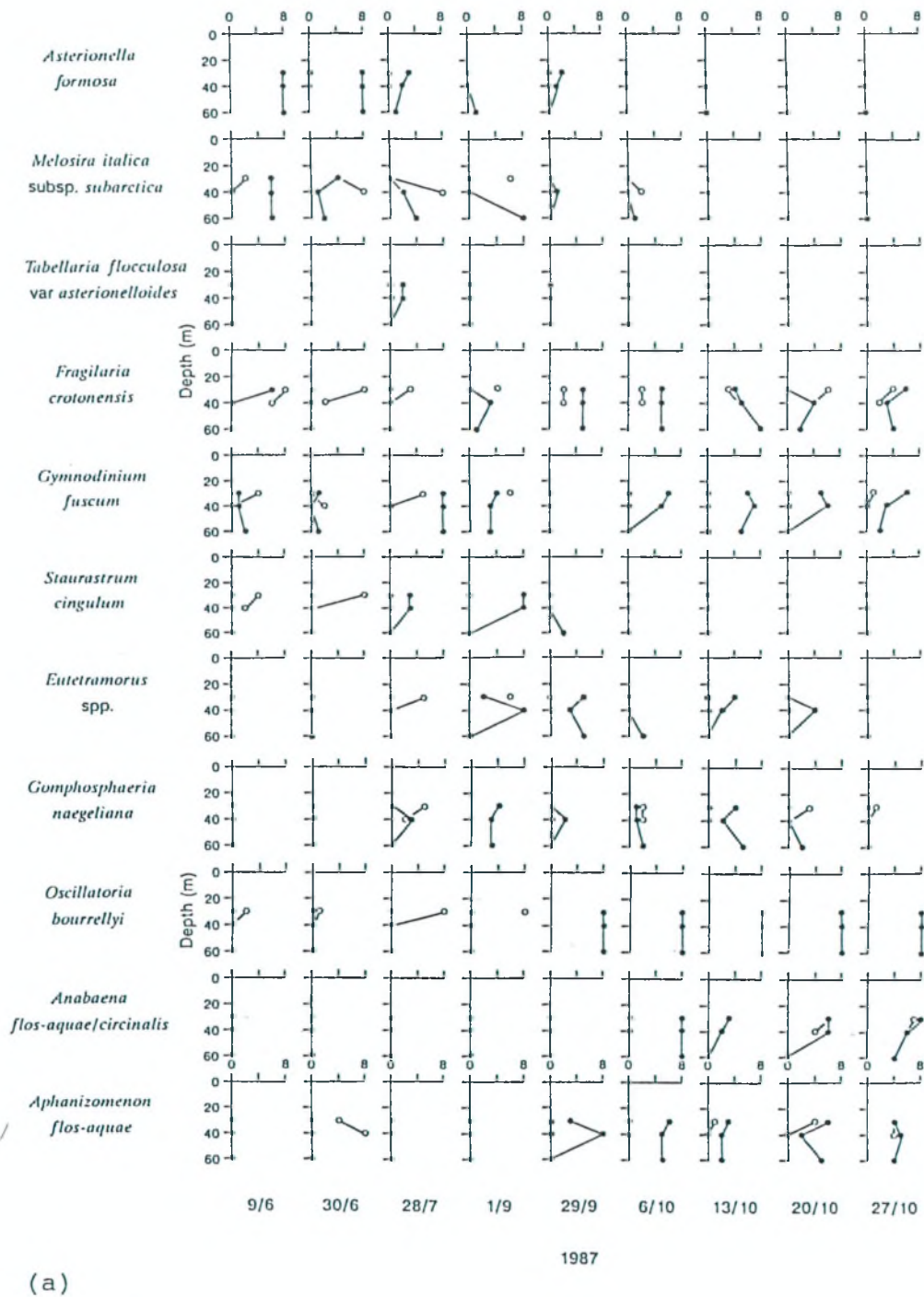
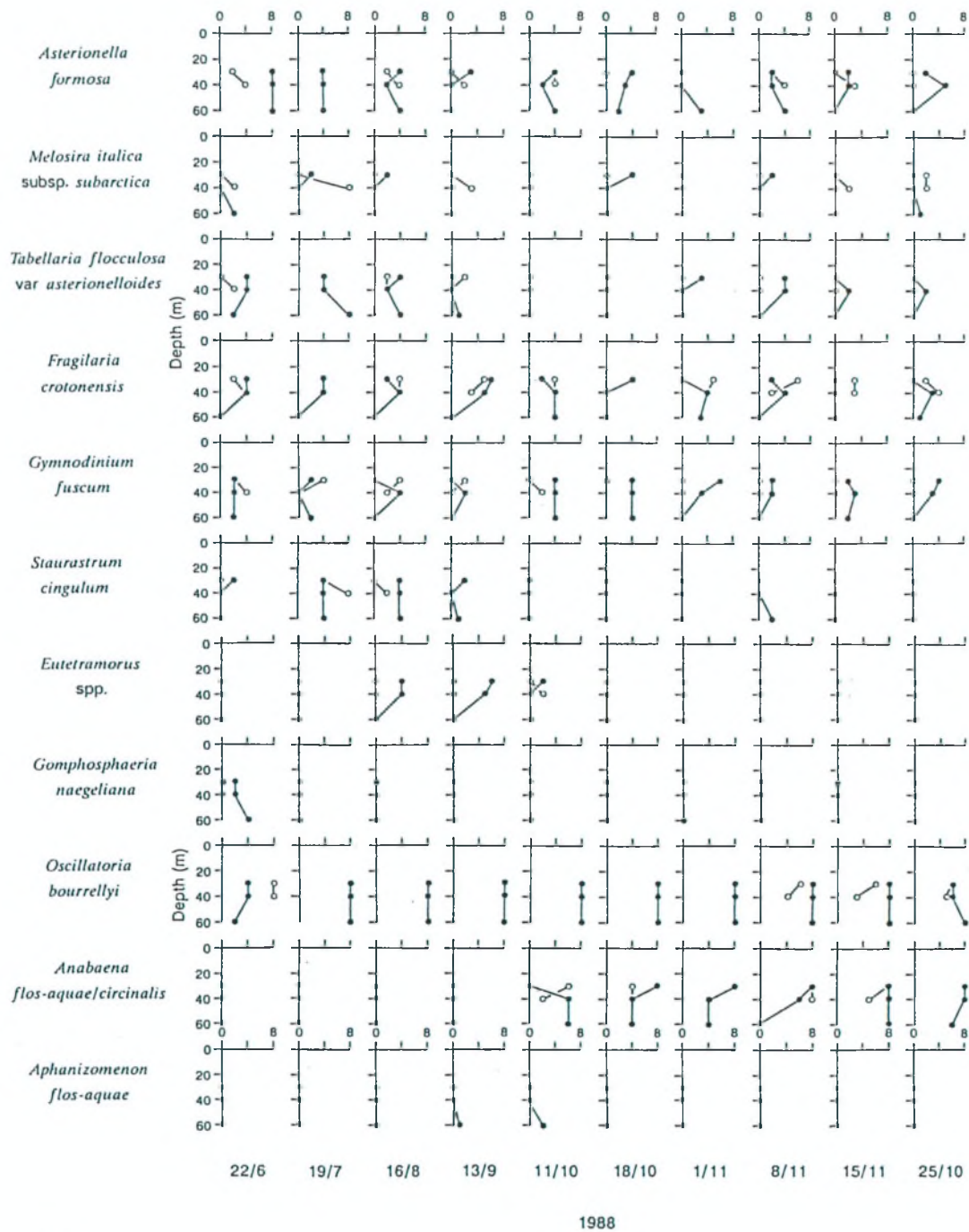


Figure 22. Vertical distribution in the relative proportions of major algal species in North (●) and South Basin (○) expressed on a 4-point scale (dominant = 8, common = 6, occasional = 4, rare = 2) between (a) June and October 1987.



(b)

Figure 22b. As 22. (b) June and November 1988

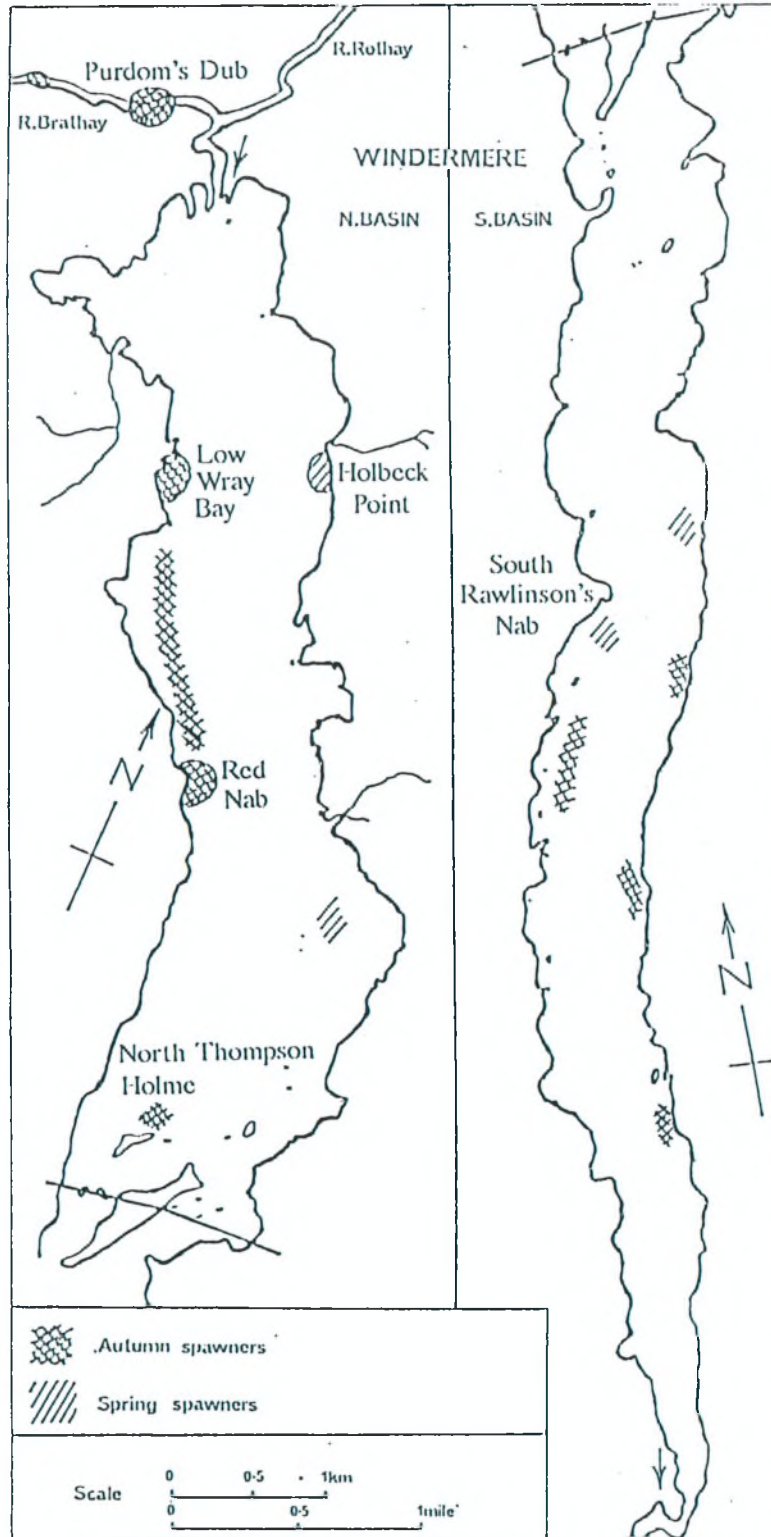


Figure 23. Spawning sites of charr in Windermere (adapted from Frost 1965).

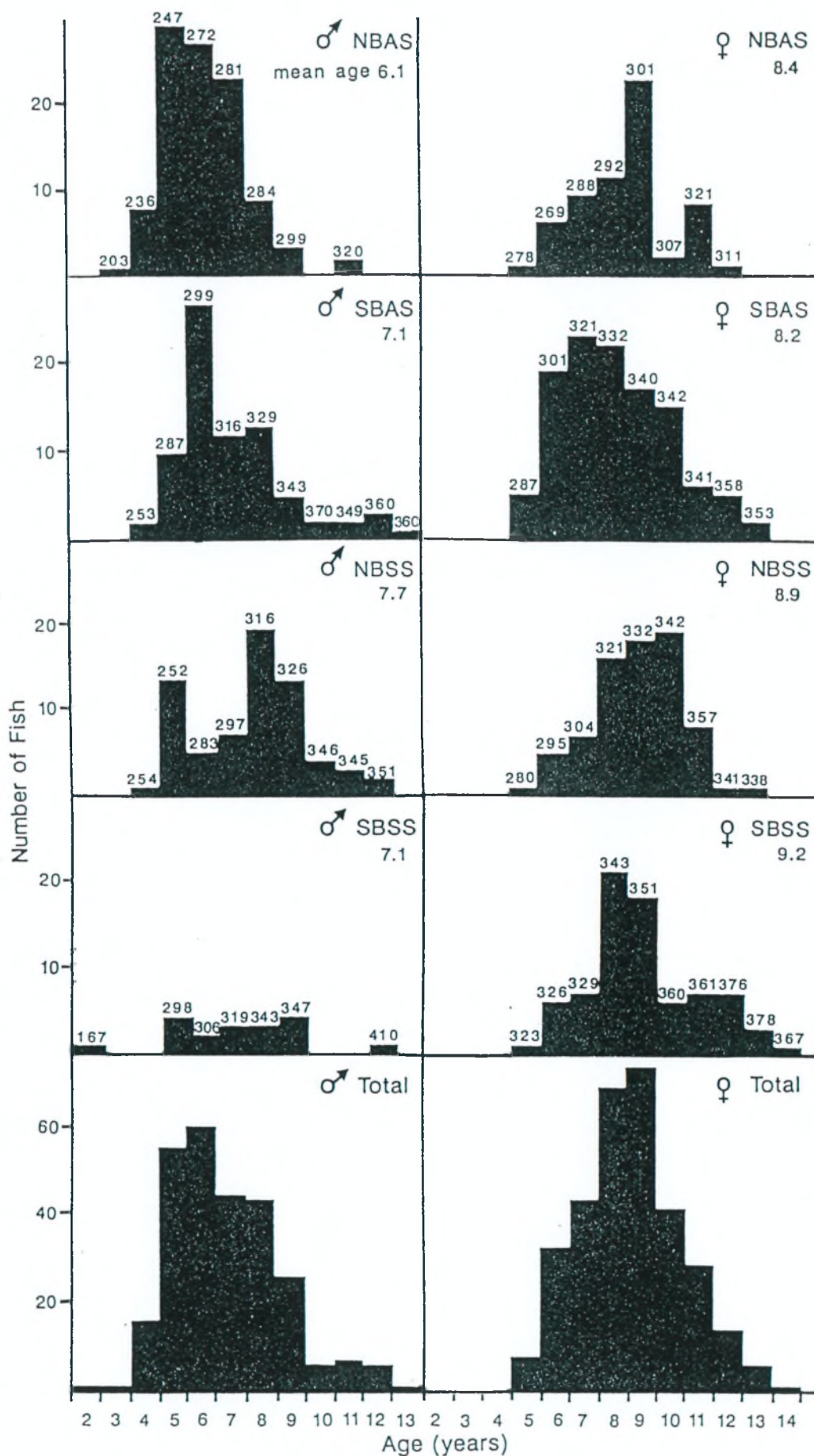


Figure 24. The age-structure of mature charr from the principal Windermere spawning groups. The figures above the histogram bars denote mean lengths. NBAS-North basin autumn spawners; NBSS-North basin spring spawners; SBAS-South basin autumn spawners; SBSS-South basin spring spawners.

Long-term changes in the number of autumn-spawning charr caught at North Basin spawning sites and in the biomass of larger pike (males >3yrs, females >2yrs).

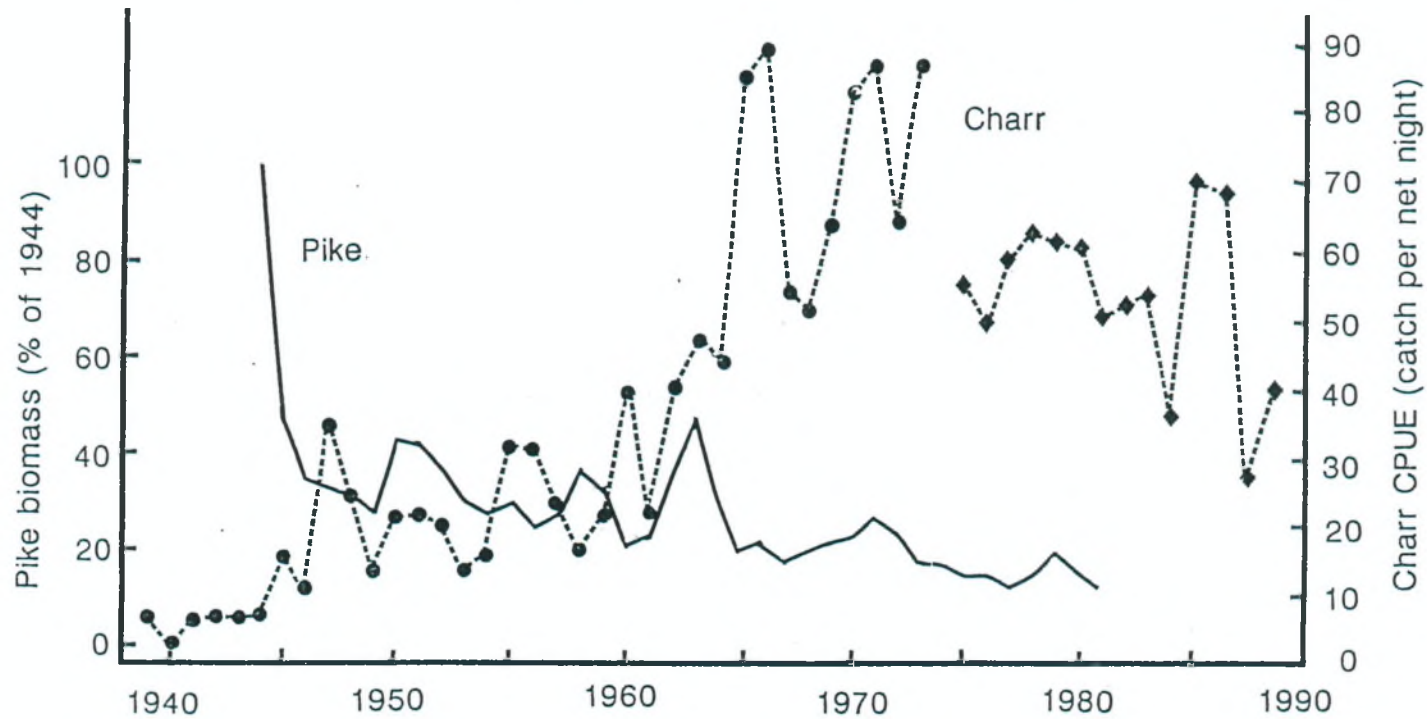


Figure 25. Changes in the estimated biomass of larger pike (males > 3 years, females > 2 years) as a percentage of the pre-fishery level (solid line) and in the catch per 32 mm gill net per day in November (CPUE) of autumn spawning charr in the North Basin of Windermere. The circles denote catches at Low Wray Bay, the diamonds denote those at North Thompson Holme; data from Kipling (1984a), Mills (in press) and from unpublished sources.

Long-term changes in catch rate by
three Windermere charr anglers

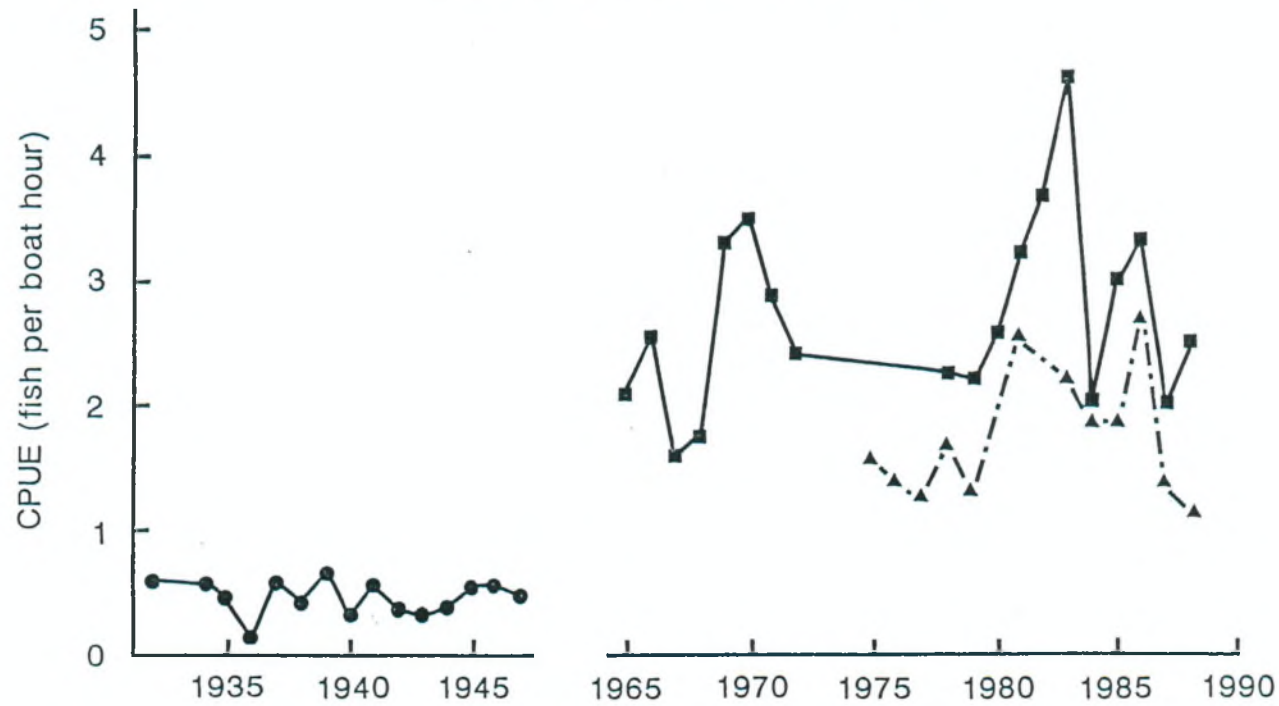


Figure 26. The number of charr caught per boat per hour (CPUE) in each fishing season by 3 anglers. Angler 1 - circles, angler 2 - squares, angler 3 - triangles

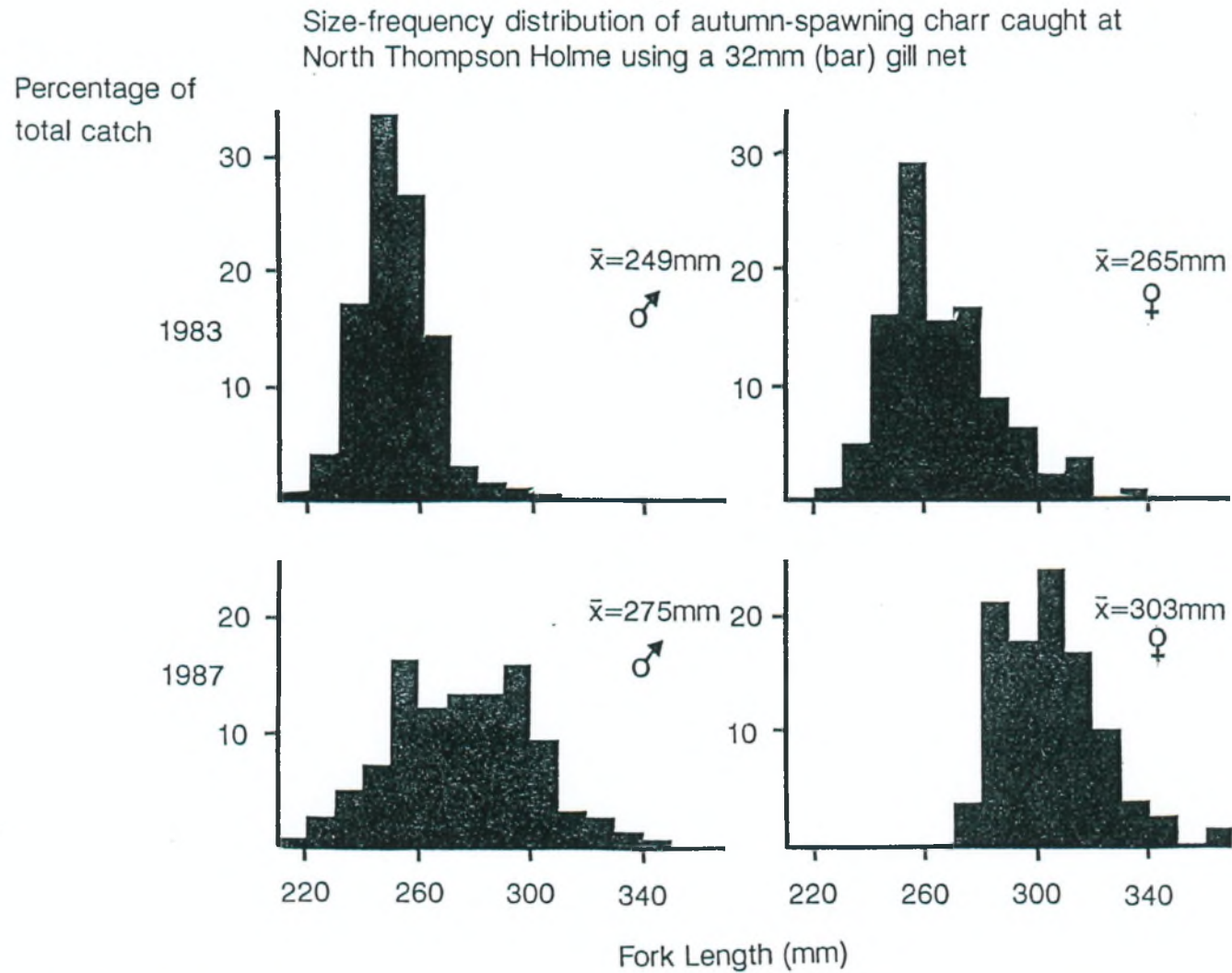


Figure 27. Length-frequency histograms for male and female autumn spawning charr captured at the North Thompson Holme spawning site in 1983 and 1987.

Length Changes in Autumn Spawning Charr

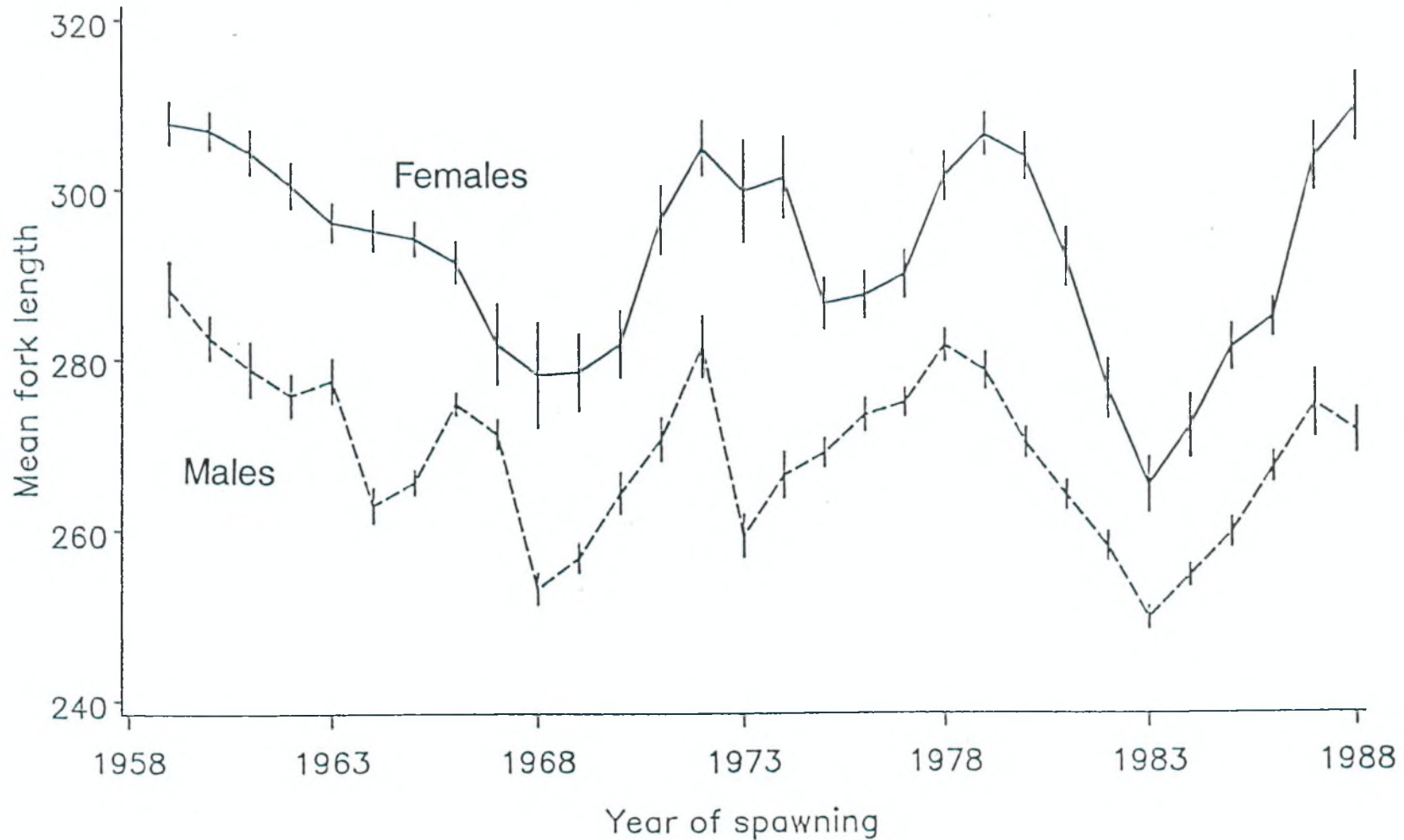


Figure 28. Changes in the mean lengths of male (dashed line) and female (solid line) autumn spawning charr captured at the North Basin spawning sites described in Fig. 4.

FIGURE 1. Survey Routes on Lake Windermere.

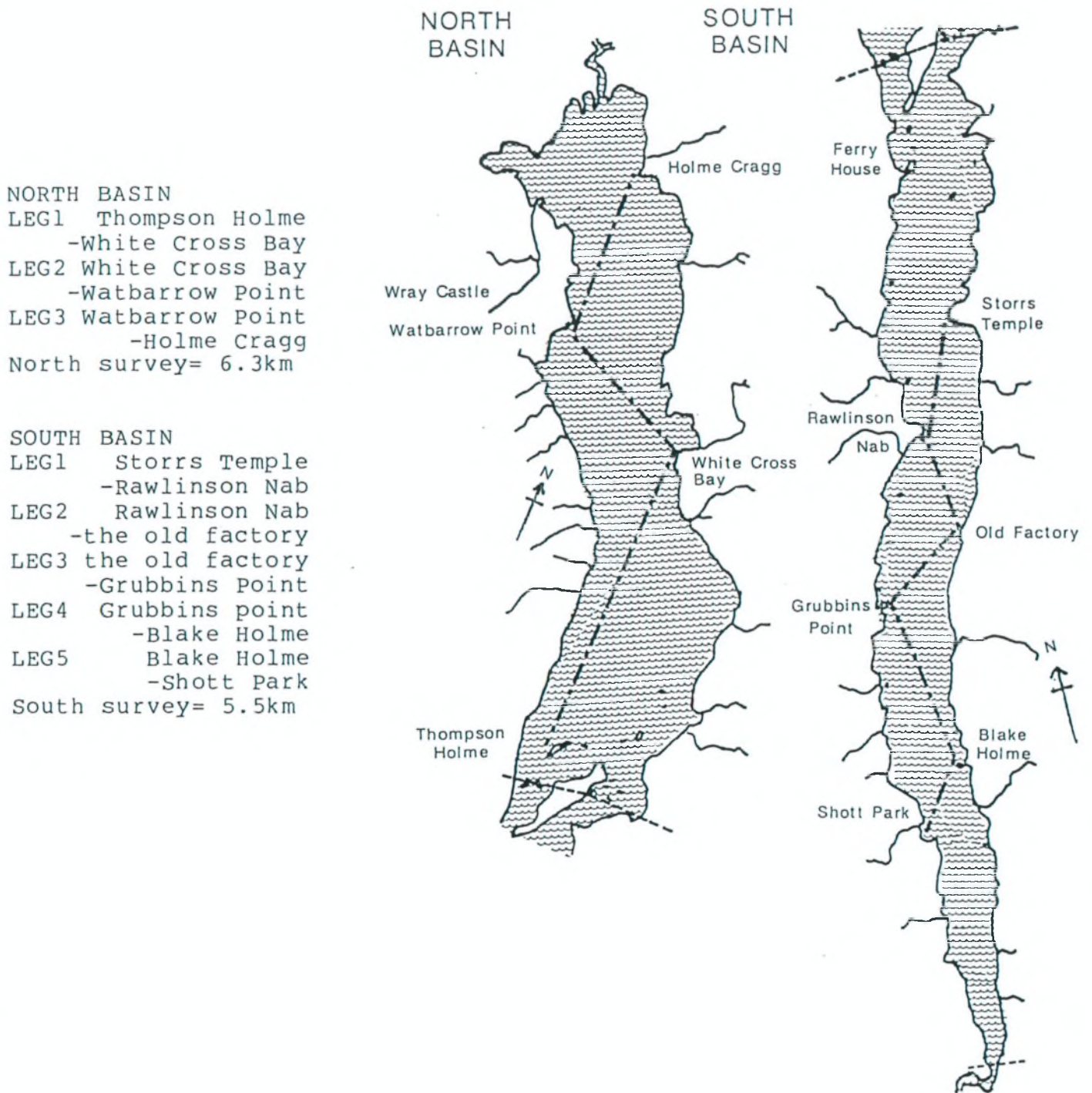


Figure 29. Echo survey routes used in estimating the number of fish in the pelagic zone of Windermere.

Annual catch rates for charr (squares)
and trout (triangles) on charr tackle

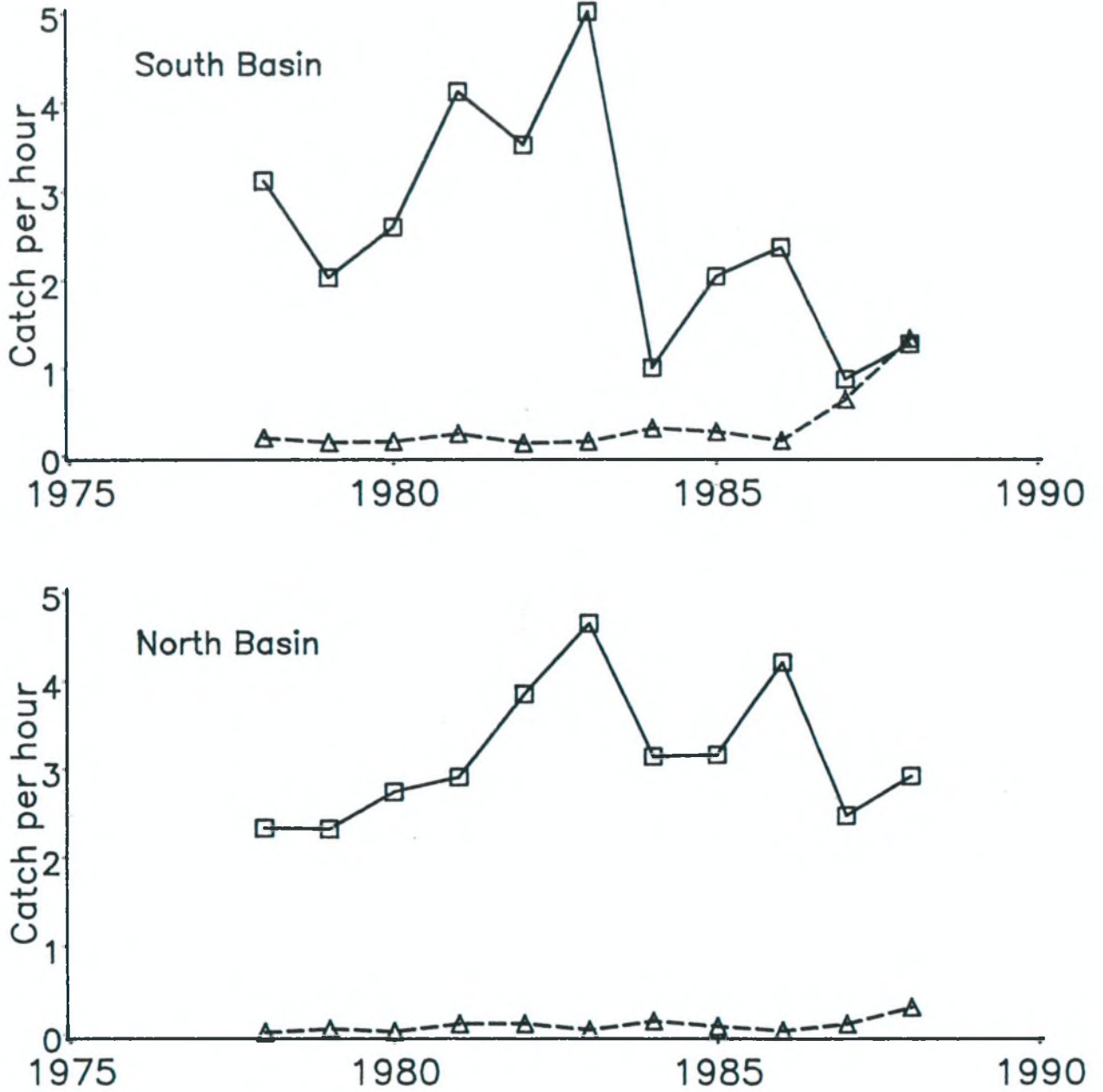


Figure 30. A comparison of an angler's catch rates for charr (squares) and trout (triangles) on charr tackle in the two basins of Windermere.

Windermere South Basin

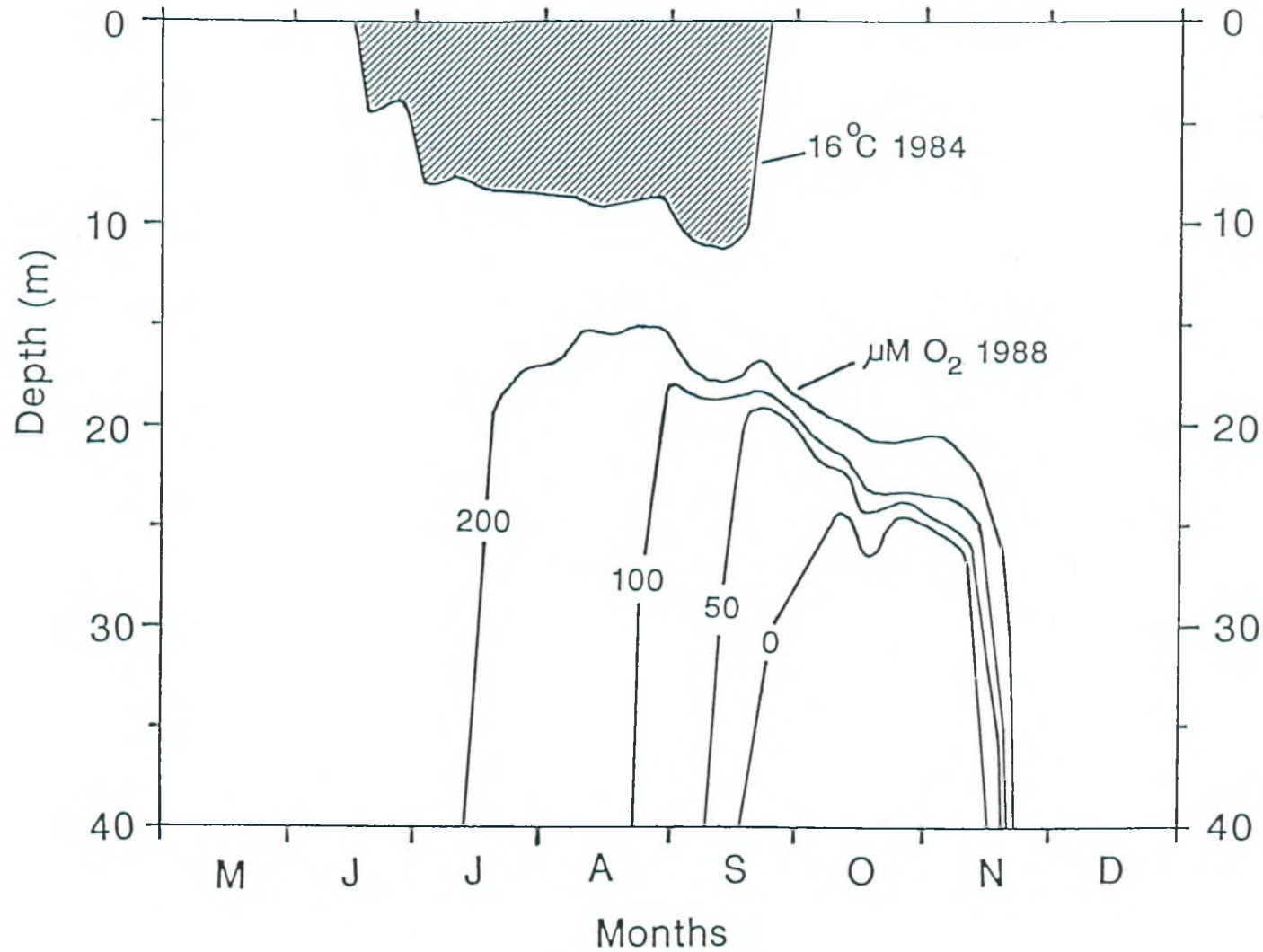


Figure 31. A depth-time plot for the South Basin of Windermere using depth profile data taken at the deepest point. The plot illustrates the extent to which temperature exceeded the charr's preferred maximum in a recent warm year (1984) together with the extent of a recent substantial deoxygenation (1988).

Mean echo depth in the North Basin (squares) and South Basin (triangles) of Windermere

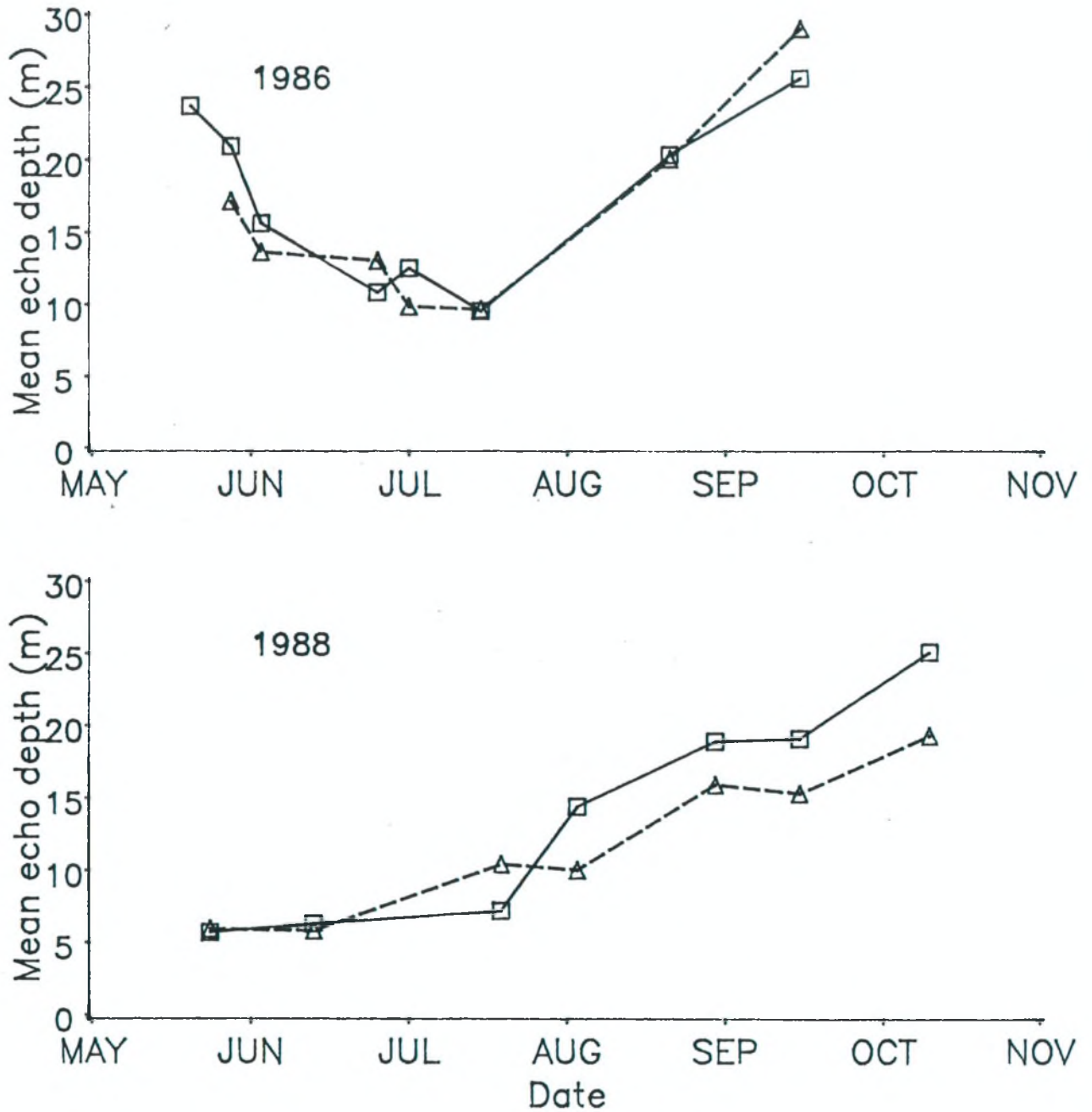


Figure 32. The mean depths of echo traces taken in the North Basin (squares) and South Basin (triangles) of Windermere in two recent years.

Appendix 1.

North West Water

Contract agreement : Windermere Water Quality

Interim report on limnological changes in Windermere for the period
April 1987 - March 1988

Introduction

This is a summary of the main limnological changes in Windermere over the last year. This interim report should be seen in context of the report by the Freshwater Biological Association for NWW on 'A general assessment of environmental and biological features of Windermere and their susceptibility to change' Atkinson *et al* (1986) and the current data from Windermere sent by FBA to NWW over the past year.

Windermere is essentially composed of two deep basins, North Basin (NB) and South Basin (SB), separated by a region of shallow water and islands. Similarities and differences between the basins are highlighted below.

Physics

The spring of 1987 was warm giving rise to early stratification, but the summer was cool. These general weather features were reflected in cool temperature within the epilimnia (maximum both basins 18.6°C) and hypolimnia (7.4°C NB; 9.5°C SB). The temperatures of the hypolimnia were c. 2°C cooler than in 1986.

Underwater light penetration as measured by Secchi disc showed minimum values for 1987 appreciably lower (2.5 m NB; 2.0 m SB) than for 1986 (3.4 m NB; 3.2 m SB).

Chemistry

Minimum percentage oxygen saturation recorded for the NB was 45%, slightly higher than for 1986 (42%). For the SB the lowest value was 1% at the beginning of November just before overturn compared to 12% during mid-October in 1986.

The summer maxima of pH in NB and SB were 8.3 and 9.4 respectively. It should be noted that the maximum value of pH in SB was 7.9 in 1986.

The maximum values of alkalinity in NB and SB were 12.75 and 14.15 mg $\text{CaCO}_3 \text{ l}^{-1}$ respectively.

Of the major plant nutrients the availability of silicon almost certainly restricts the maximum population density of the spring diatom bloom. Nevertheless in the NB the minimum value of 0.16 mg SiO_2 indicates the possibility of other factors, possibly sedimentation, controlling the size of the diatom population in 1987. In the SB silicon was more completely utilized and the minimum value of SiO_2 was 0.06 mg l^{-1} .

The winter maxima of soluble reactive phosphorus (SRP) (0-7 m layer) in NB and SB were 0.0081 and 0.0318 mg l^{-1} respectively indicating the high level

of SRP loading to the SB. Maximum values of total P in the SB 0.035 mg l^{-1} are now approaching those of Esthwaite Water.

In both basins the summer minima of $\text{NO}_3\text{-N}$ (0-7 m layer) were markedly lower than during 1986. This correlates with more extensive growths of blue-green algae in 1987.

Epilimnetic maxima of $\text{NH}_4\text{-N}$ in NB and SB were 0.042 and 0.052 mg l^{-1} , appreciably lower than for Esthwaite Water (0.263 mg l^{-1}).

Chemical analysis of samples within the hypolimnia of both basins show that redox cycling of Mn and Fe is now apparent to a limited extent.

Phytoplankton

The major features of algal succession, periodicity and long-term trends in Windermere are given in Atkinson et al. (1986) Here the increasing importance of the blue-green alga Oscillatoria bourrellyi in both basins was shown as well as the mass-death of the alga in 1986. Also indicated was the correlation of low concentrations of $\text{NO}_3\text{-N}$ in the epilimnion and anoxia in the hypolimnion of the SB in years of large populations of the alga. In spite of the decline of O. bourrellyi during 1986, the alga grew to large populations in both basins in 1987. The SB population in 1987 was the largest on record with a population density of 614 mm ml^{-1} (previous record 561 mm ml^{-1} in 1985). The NB population reached a density of 135 mm ml^{-1} . Other blue-green algae, including in particular Aphanizomenon flos-aquae, Anabaena flos-aquae, Gomphosphaeria năgeliana and G. lacustris, showed notable population densities in both basins.

The spring chlorophyll a maximum in the SB was 30 mg m^{-3} and in the NB it was unusually high at 29 mg m^{-3} . Summer maxima of chlorophyll a in NB and SB were 20 and 40 mg m^{-3} respectively.

Summary

The results of 1987 show that the water quality in Windermere is continuing to be influenced by the development of large populations of O. bourrellyi. It is interesting to note that the record population in the SB was delayed a month later than usual and that the epilimnetic exhaustion of $\text{NO}_3\text{-N}$ and hypolimnetic depletion of oxygen were also lagged by c. 1 month. Had the O. bourrellyi population maximum been achieved a month or more earlier then conditions of severe anoxia could have developed within the SB. A further consideration requiring investigation is the effect of deposition of sedimented O. bourrellyi onto fish spawning regions and the longevity of such "algal fluff" on the sediments.

S.I. Heaney

April 1988

This report includes data obtained by Dr J.F. Talling and Dr C.S. Reynolds