

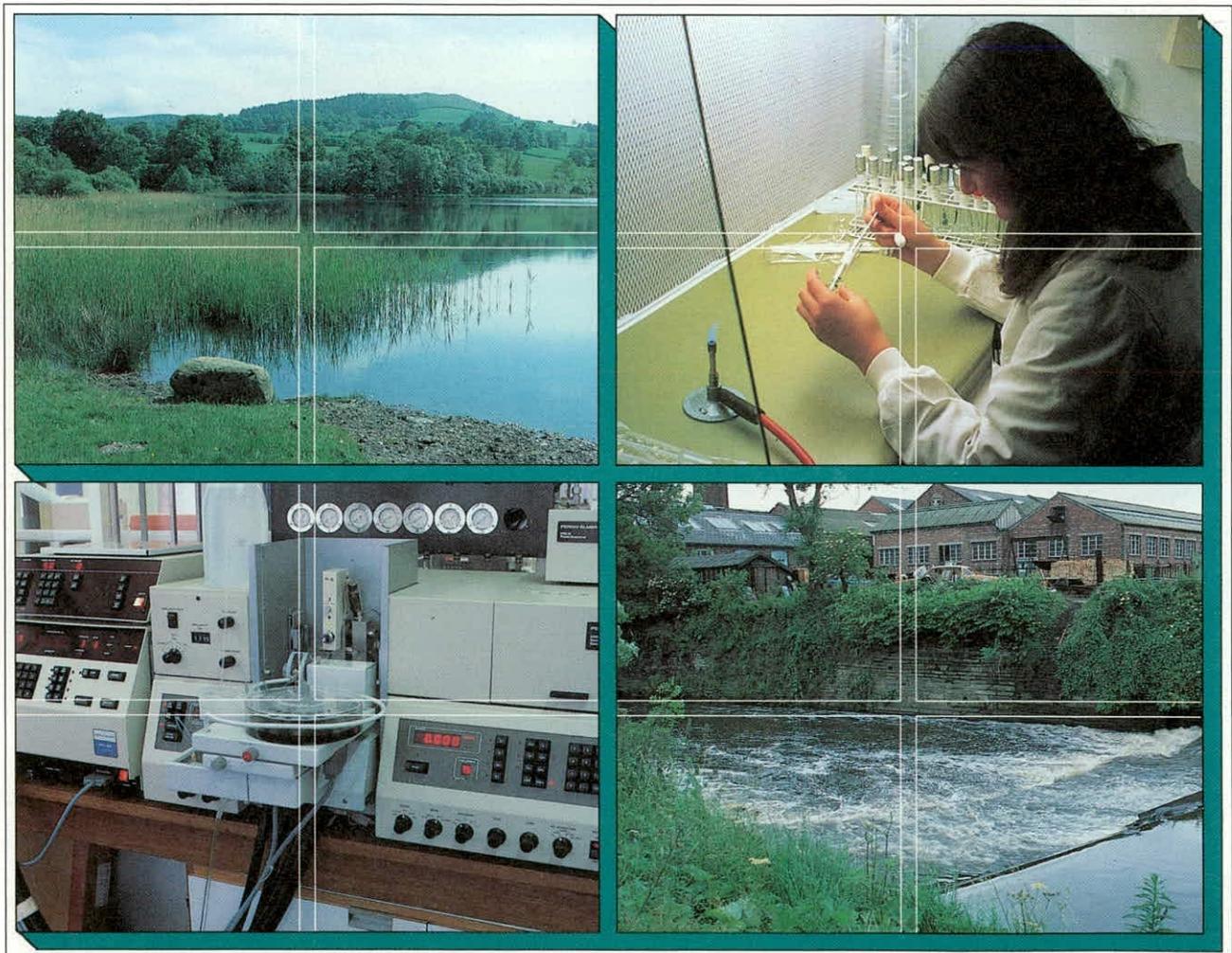


**Institute of  
Freshwater  
Ecology**

## **INSTITUTE OF FRESHWATER ECOLOGY**

### **MANAGEMENT AND ECOLOGY OF ARCTIC CHARR POPULATIONS IN WINDERMERE**

**Principal Investigator: J.M. Elliott, BSc, PhD, DSc, CBiol, FIBiol**





NERC INSTITUTE OF FRESHWATER ECOLOGY  
THE WINDERMERE LABORATORY  
AMBLESIDE, CUMBRIA LA22 OLP

**MANAGEMENT AND ECOLOGY OF ARCTIC CHARR  
POPULATIONS IN WINDERMERE**

Principal Investigator: J.M. Elliott, BSc, PhD, DSc, CBiol FIBiol

Project Leader: J.M. Elliott  
Contract Start Date: 1 April 1990  
Report Date: April 1991 (interim report)  
Report To: North West Water Limited  
TFS Project No: T11050n5  
IFE Report Ref No: W1/T11050n5/1

This is an unpublished report and should not be cited without permission, which should be sought through the Director of the Institute of Freshwater Ecology in the first instance.

## CONTENTS

## PAGE

Summary	1
1. Introduction	3
1.1. Origins of present investigation	
1.2. Ecology of Windermere charr	
2. Methods	7
2.1. Echo sounding	
2.2. Gill netting and angler's catches	
2.3. Laboratory experiments	
3. Results	11
3.1. Echo sounding	
3.2. Gill netting and angler's catches	
3.3. Laboratory experiments	
4. Discussion	15
5. Acknowledgments	18
6. References	19

## SUMMARY

1. This interim report summarises the origins of the present investigation from previous work on the effects of enrichment on the water quality of Windermere, and especially on the population of Arctic charr in the lake. Previous work on the ecology of Windermere charr is also summarised. There are at least four races of charr in the lake with the north and south basins each containing two distinct races that spawn in spring and autumn respectively. Most of the charr are autumn spawners (94 - 96% of adult population).
2. The present investigation commenced on 1 April 1990 and is a two-year study with the following objectives:
  - (i) To provide an adequate basis for comparison between spring and autumn races of charr in the north and south basins of Windermere, and to survey their spawning sites.
  - (ii) To investigate, experimentally, the sensitivity of juvenile stages of the different races to reduced oxygen concentrations and to elevated temperatures.
  - (iii) To integrate this information for the purposes of the future management of the Windermere charr fishery.
3. The methods used to obtain field data are:
  - (i) Echo sounding to survey both basins every two weeks throughout most of the year.
  - (ii) Gill netting at the long-term site for autumn spawners in the north basin (annual records from 1939 to present), and at other autumn and spring spawning sites in the north and south basins of the lake.

- (iii) Angler's catches from both basins (records from 1966 to present).
4. Tolerance and resistance to thermal stress are being investigated in the laboratory, using different life stages (alevins, fry, parr) for the four races. Tolerance and resistance to low oxygen levels are also being investigated in the laboratory, but on a more limited scale than the work on thermal stress.
  5. Results from the echo sounder show that the total number of fish in the open water varies considerably through the year. Estimates of the total number of fish in both basins varied from 6,437 to 310,495 for the north basin and 7,927 to 188,541 for the south basin. Although these results can only be regarded as preliminary they do indicate that fish movements between depth layers are extensive and complex.
  6. The gill-net catch in the north basin was higher in 1990 than in the three previous years. This increase was also seen in the angler's mean catch per unit effort for the whole lake. The ratio of angler's catches in the north and south basins showed that catches have been relatively low in the south basin from 1984 to 1988. There was a clear improvement in 1989 but the return in 1990 to a low value indicated that the improvement was temporary, not permanent.
  7. Results from the experiments on thermal tolerance and resistance do not appear to be significantly different between the four races. The upper temperature limits for charr are about 2-3°C and 5-6°C lower than values obtained for brown trout and salmon respectively. The experimental work should be completed in the near future.
  8. Some general points are discussed but as the work is still progressing, it would be premature to discuss the results in detail.

## 1. INTRODUCTION

### 1.1. Origins of present investigation

Windermere is the largest natural lake in England and is a Site of Special Scientific Interest situated in a National Park. The lake provides part of the water supply to North West England and is a focus for tourism and recreation. Windermere is divided by shallows and islands into a north basin (area 8.1 km<sup>2</sup>) and a south basin (area 6.7 km<sup>2</sup>).

Since 1945, regular measurements from both basins have shown that the lake has become nutrient enriched (Lund 1972, Sutcliffe *et al.* 1982, Heaney *et al.* 1988, Talling & Heaney 1988). The Freshwater Biological Association (FBA, now Institute of Freshwater Ecology, IFE) was commissioned by North West Water to provide a general assessment of environmental and biological features of Windermere and their susceptibility to change. The unpublished report (Atkinson *et al.* 1986) showed that since 1945 there has been a c.20-fold increase in the mean winter concentration of soluble reactive phosphorus in the south basin, rising to more than 20 µg l<sup>-1</sup>, but smaller increases have occurred in the north basin, rising to less than 10 µg l<sup>-1</sup>. The report also highlighted hypolimnetic deoxygenation during summer and autumn in the south basin, first recorded during 1981. It was indicated that the charr population 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 final report (Heaney, Mills & Corry 1989) showed that hypolimnetic deoxygenation was particularly severe during 1988. In the south basin, anoxia occurred for a prolonged

period between the end of September and mid-November, and extended upwards to a depth of about 25 m. Complete anoxia does not occur in the north basin, but oxygen concentration fell to less than 20% saturation below 30 m depth during the first half of November 1988, this being the most severe on record.

Although nutrient enrichment is not directly harmful to charr, the associated anoxia will restrict the water volume available to the charr and this will be reduced further in hot summers when surface temperatures may be higher than the preferred values for the charr. It is also possible that summer water temperatures will increase as a result of climate change. Evidence from other European lakes indicates that increasing enrichment can lead to a reduction and eventual extinction of charr populations (Mills *et al.* 1990).

Following the IFE report, North West Water started work to reduce phosphate discharged in treated sewage from the Windermere and Ambleside sewage works. The new sewage treatment plants should markedly reduce the quantity of phosphates entering both the north and south basins of Windermere. However, evidence from other lakes suggests that recovery may be slow (the sediments accumulate phosphorus which may be released back into the water column over many years) and it is therefore important to continue studies on the status of Windermere charr. North West Water Limited, a subsidiary of North West Water Group PLC, therefore agreed to support a two-year study (25% funding from NWW Ltd., 75% funding from NERC).

The chief objectives of this investigation are:

- (i) To provide an adequate basis for comparison between spring and autumn races of charr in the north and south basins of Windermere, and to survey their spawning sites.

- (ii) To investigate, experimentally, the sensitivity of juvenile stages of the different races to reduced oxygen concentrations and to elevated temperatures.
- (iii) To integrate this information for the purposes of the future management of the Windermere charr fishery.

## 1.2. Ecology of Windermere charr

The Arctic charr, Salvelinus alpinus (L.), is a holarctic species that is frequently anadromous in northern latitudes higher than 65°N. At lower latitudes, this species forms numerous land-locked populations. There are several populations in Ireland and Scotland, only four recorded in Wales and all the English populations are restricted to the Lake District. Charr are present in eight lakes (Buttermere, Coniston, Crummock, Ennerdale, Haweswater, Thirlmere, Wastwater, Windermere). They also used to be present in Ullswater but have now disappeared, possibly because their spawning grounds in Glenridding Beck were polluted by suspended solids and lead from mine washings.

There are at least four races of charr in Windermere with the north and south basins each containing two distinct races that spawn in spring and autumn respectively (Frost 1965, Child 1984, Partington & Mills 1988). By using a combination of the number and length of gill rakers, a discriminant function can be used to predict with more than 95% accuracy whether an individual charr is a spring or autumn spawner (Partington & Mills 1988). There are also differences in growth rates; north basin autumn spawners grow relatively slowly, north basin spring spawners and south basin autumn spawners are intermediate and south basin spring spawners grow fastest (Mills 1989).

Mark-recapture studies have shown that adults return each year to the same spawning site (Frost 1963, Le Cren & Kipling 1963). Differences in allele frequencies at esterase and malate dehydrogenase loci have been found between fish spawning at similar times but on different sites. It is therefore possible that each of the autumn and spring spawning sites could maintain separate stocks. Recent surveys have shown that spawning still occurs on at least seven of the autumn sites (3 in north basin, 4 in south basin) and four of the spring sites (2 in each basin). Most of the charr are autumn spawners with spring spawners representing less than 4-6% of the adult population (Mills 1989, Mills & Hurley 1990).

The mean age of spawning females (c. 8 years for autumn spawners, c. 9 years for spring spawners) is higher than that of spawning males (6-7 years). Most male charr mature at an age of 5 years whereas females mature at six years or older and live longer than males. About 80% of charr between 9 and 14 years old are female. There are no obvious differences in age structure between basins and male and female charr grow at similar rates. These conclusions are based on recent information (Partington & Mills 1988, Mills 1989, Mills & Hurley 1990). Comparison with earlier data is difficult because the previous use of scales for ageing (Frost 1978) led to marked underageing of older fish when compared with the use of otoliths for ageing in recent years. As there is a high proportion of old charr in both basins, mortality through angling cannot be high or few fish would survive to reach such ages.

Crude estimates of the total adult charr populations are 132,000 autumn spawners and only 8,000 spring spawners with a total biomass of 30-35 Mg (tonnes) (Mills & Hurley 1990).

## 2. METHODS

### 2.1. Echo sounding

The Simrad EY-M echo sounder was used to provide information on fish numbers, size and distribution. Surveys of both basins during daylight were performed once every two weeks throughout most of the year, and every week during the spawning seasons. A survey was postponed on some occasions because of dangerous weather or the absence of the boat during its annual refit and maintenance (the echo sounder is mounted on the hull of the boat).

The operation principle of the echo sounder can be summarised as follows. Sound waves are generated at the face of a transducer until switched off by a timer. The sound pulse travels through water away from the transducer. A target in the path of the sound pulse will return an echo to the transducer. The transducer consequently reverses its transmitting mode function. The received 'echo' is converted from pressure oscillations to electrical oscillations that are picked up by a receiver, amplified and converted into a visible sign on a display device.

The electrical oscillations picked up and displayed provide qualitative rather than quantitative information. The echo signal must be processed to provide quantitative information about fish appearing in the water column. Hardware and software supporting the hydro-acoustic data acquisition system (HADAS) provide the quantitative information required about the fish in the water column. The hardware allows for the communication between echo-sounder recordings in the field and the computer. The software allows the analysis and storage of data received from the echo-sounder. The received echo needs to be transformed to provide information on fish quantity. Fish at varying distances from the transducer produce different echo

intensities. In order to obtain echo signals depending only on the properties of the target, compensation for the decrease in sound intensity due to propagation laws is required. This is achieved by having in the echo receiver an amplifier whose effect varies with time.

Where fish are targets, the sound pulse is reflected mainly from the swim bladder, but also from the scales, flesh and bones. It is estimated that half the signal comes from the swim bladder which occupies about 5% of the volume of the fish. The signal coming from a single fish is proportional to its weight, and it is therefore possible to construct size frequency distributions for all recorded fish.

Comparisons have been made in Scandinavia between acoustic surveys using a Simrad EY-M echo sounder and a trawl (e.g. Bagenal 1981). The results were comparable but the echo sounder recorded considerably fewer fish than the trawl catch near the lake surface, and higher numbers than the trawl in deeper water. The precision of the results from the echo sounder was high with replicate estimates of fish numbers differing by only 0.4% from their mean value in deep water and by only 8.5% in surface waters (depth 4-8 m). Length frequencies for fish from the trawl catches agreed with the frequency distribution of records from the echo sounder and therefore the latter provides information on the size distributions of the fish.

The chief advantage of the echo sounder is that it provides a rapid method for estimating fish populations in a lake. The chief disadvantage is that it cannot identify fish species and therefore it must be supplemented by conventional methods of sampling, such as gill nets.

## 2.2. Gill netting and angler's catches

The long-term FBA/IFE data for autumn spawning charr in the north basin were obtained by regular gill netting with 32 mm (bar) mesh during each November from 1939 to the present. The results are expressed as catch-per-unit-effort (CPUE) which is the mean catch per gill-net day. Mature charr were all gill netted on their spawning sites using mesh sizes ranging from 19 mm to 46 mm(bar). Nettings for spring spawners were performed in deep (15-30 m) water above the spawning sites, and those for autumn spawners were performed in shallow (2-4 m) water above the spawning sites.

Charr were last commercially netted in Windermere in 1921 but they are still caught by fishermen using plumb lines (Kipling 1984). The fishery for charr in Windermere is worth at least £24 K. Anglers catch-per-unit-effort (CPUE) data were expressed as mean catch per boat per hour. Data are now available from 1966 to the present.

## 2.3. Laboratory experiments

Charr were reared from freshly fertilized eggs taken from fish caught in gill nets on the spawning sites in Windermere. Eggs were incubated and young fish reared in the IFE hatchery on the shore of the lake. Eggs and juveniles from each of the four races of charr were always kept separate so that comparisons could be made between these races.

Tolerance and resistance to thermal stress were investigated for different life stages: alevins (newly-hatched fish that are still dependent on yolk for their food), fry (newly-emerged fish that have just started to feed on external food) and juvenile parr

(older fish that are immature). The experiments were performed in constant-temperature tanks. Alevins and fry were kept in small jars containing water that was stirred and aerated by compressed air (oxygen concentration in water > 85% saturation). Juvenile parr were kept in larger aquaria through which circulated water of a constant temperature. Oxygen concentrations always remained higher than 85% saturation.

Young charr of similar size were acclimated to the same constant temperature (either 5, 10, 15 or 20°C) for 1-2 weeks. The water temperature was then raised at about 1°C/30 min to a final temperature. Records were kept of the highest temperatures, for survival over 10 min, 100 min, 1000 min and 7 days at each acclimation temperature. This methodology and protocol is basically the same as that used to investigate the effects of thermal stress on brown trout, Salmo trutta L., and Atlantic salmon, Salmo salar L. (Elliott 1981, 1991).

Tolerance and resistance to low oxygen levels have been investigated only with alevins at present. These were subjected to different oxygen levels at 5°C and 9°C. The oxygen tolerance experiments were limited because a closed system had to be used in order to prevent oxygen exchange between the low oxygen concentrations in the water and higher levels in the atmosphere. Oxygen uptake by the fish also had to be taken into account, and varied considerably between fish. A large number of replicates was therefore necessary to obtain meaningful results. Records were kept of the lowest oxygen levels for survival over 10 min, 100 min, 1000 min and 7 days at each temperature.

### 3. RESULTS

#### 3.1. Echo sounding

As the collection of data still continues, the analysis of the results is in its preliminary stages. Some estimates obtained during the day from October 1989 to July 1990 are summarised in Figs 1 to 3. Values varied markedly in both basins.

The total number of fish per hectare in the water column below a depth of 2 m (Fig. 1) and the number of single, non-shoaling fish per hectare (Fig. 2) followed a similar pattern until May when the peak for total fish in the south basin was not reflected by the number of single fish. As shown later, this discrepancy corresponded with a fish-size distribution in which 80% of the fish in the depth layer 2-10 m were small. The small size and shoaling behaviour strongly suggest that small perch were present in large numbers. This example shows that, with some careful interpretation, it is possible to discriminate between fish species and thus overcome the chief disadvantage of the methodology (see also section 2.1).

Estimates of the total number of fish in both basins varied from 6,437 to 310,495 fish in the north basin and 7,927 to 188,541 fish in the south basin. Once again, values varied markedly in both basins (Fig. 3).

One advantage of the HADAS analysis is that information can be obtained on the depth and size distribution of the fish. Examples are given for different months for both the north basin (Fig. 4) and the south basin (Fig. 5). The fish were divided into those with a length less than 20 cm (-44 to -62 dB), those between 20 and 30 cm (-32 to -43 dB) and those longer than 30 cm (-32 to -38 dB).

In the winter months from November to March, most fish were in the smallest size category in both basins. A larger proportion of the larger fish was evident in

October 1989 and from April to July 1990 in the north basin. The absence of larger fish in November could be due to the autumn spawners moving onto their spawning sites in shallow water (water depth 1-3 m). As the echo sounder cannot function adequately in shallow water, these fish would be undetected. Larger fish were present in the south basin in October and November, but did not reappear in larger numbers until June and July, and therefore later than in the north basin (cf Figs 4, 5).

Surprisingly few fish were recorded from deep water (50-60 m, 60-70 m in the north basin, 30-40 m in the south basin). The largest numbers of fish were recorded in water less than 10 m deep in six out of nine months in the north basin and seven out of nine months in the south basin. Fish in this upper layer were usually in the smallest size category. Although these results can only be regarded as preliminary, they do indicate that fish movements between depth layers are extensive and complex.

### 3.2. Gill netting and angler's catches

The gill-net catch in the north basin was higher in 1990 than in the three previous years (Fig. 6a). This increase was also seen in the angler's catch per unit effort for the whole lake; this being the highest since 1983 (Fig. 6b). The 1990 data therefore reinforced the earlier conclusion that there was good, if not excellent, agreement between the angler's catches and the gill-net catches (see also Mills *et al.* 1990).

As the angler's catches reflected changes in charr abundance, they could be used to compare population changes in the two basins of the lake. A simple, but useful, index of these changes was provided by the ratio of mean catch in the south basin to mean catch in the north basin. Values for one angler's catches from 1966 to the present showed that, prior to 1983, catches were similar in both basins or were

higher in the south basin (Fig. 7). The marked decrease in the ratio for the next five years indicated the relative decline in south basin catches from 1984 to 1988. The ratio of catches for a second angler over a shorter period (1975 to 1988) followed a similar pattern (angler B in Fig. 7). There was a clear improvement in 1989 with similar catches in both basins (ratio = 1), but the decline in 1990 to earlier values indicated that the 1989 improvement was temporary, not permanent.

Gill netting of autumn and spring spawners has confirmed that both races are present in both basins. There is no evidence to suggest that age structure and the mean age of the spawning males and females has changed significantly since the earlier surveys in 1986, 1987, 1988 (Mills 1989). The gill-net catches of autumn and spring spawners also provided eggs and sperm so that fertilised eggs could be transferred to the hatchery to rear progeny for the laboratory experiments.

### 3.3. Laboratory experiments

The experiments on temperature tolerance and resistance should be completed in the near future, but until this is accomplished, the conclusions remain tentative.

Results do not appear to be significantly different between the four races (spring and autumn spawners from the north and south basins). Some differences have been found between the different life stages (alevins, fry, parr) but it is not known if these differences are significant until the work is completed. The upper temperature tolerance limits appear to be about 2-3°C lower than those for brown trout. The lower temperature tolerance limits appear to be close to 0°C.

The experiments on tolerance and resistance to low oxygen levels at 9°C was not very successful because neither the experimental fish nor the controls survived the

7 days of the experiment. At 5°C, all controls survived and some alevins (12.5%) survived for 7 days in water with an oxygen content equivalent to 30% saturation. As % saturation increased, the number of survivors over 7 days also increased, being 25% at 50% saturation, 62.5% at 69% saturation and 100% at 75% saturation.

All alevins survived for 1000 min at oxygen levels above 17% saturation, few alevins survived below 15% saturation, and alevins survived for 10 min or less at levels below 10% saturation.

#### 4. DISCUSSION

As the work is still progressing, it would be premature to discuss results already obtained. Some general comments are, however, apt.

The echo sounding technique provides, for the first time, estimates of the total number of fish present in the open water of the lake. Previous methods all used nets or traps, and usually provided an index of abundance, most frequently of spawning adults. Such methods cannot provide estimates of absolute numbers. Echo sounding not only overcomes this problem but also provides frequent estimates of the number of fish present at different water depths and the size-frequency distribution of the fish in the water column.

The chief problem remaining to be resolved is the separation of records for charr from those for other fish species present in the water column. Shoaling fish can be recognised with the echo sounder and these are undoubtedly perch. It is therefore possible to filter out these fish from the records. Large salmon and sea-trout, that migrate through the lake on their way to their spawning grounds, are also easy to detect because of their size. Pike are probably rare in the open water of the lake. There does not appear to be an easy method for separating charr from migrating smolts of salmon and sea-trout, or from resident brown trout in the lake. The proportion of these fish in the records can be assessed only by using alternative methods such as gill nets. At present, results from the echo sounder therefore provide estimates of the total number of salmonids (charr + trout) in the north and south basins of Windermere.

The long-term records for gill-net catches are essential for the assessment of the relevance of short-term change. Low catches were obtained in 1987, 1988 and

1989, but the higher catch in 1990 demonstrates that there has been no permanent decline in catches. The 1990 value is similar to values obtained in the early 1980's (Fig. 6).

The good agreement between angler's catches and gill-net catches reinforces the conclusion that both reflect accurately the fluctuations in the number of adult charr in the lake. The ratio of angler's catches in the south and north basins of the lake clearly identifies the persistently low catches in the south basin from 1984 to 1988, and demonstrates that the improvement in 1989 was temporary, not permanent (Fig. 7). Such comparisons highlight the need for long-term records but, unfortunately, it is becoming increasingly difficult to find financial support for the collection of such records.

The laboratory investigations are essential to determine the tolerance limits of the different life stages of the charr to extremes of temperature and low levels of oxygen. It is perhaps surprising that these limits have not been determined before but there is little quantitative information on either the temperature or oxygen requirements of charr.

The upper temperature limits for charr are about 2-3°C lower than the values obtained in similar experiments on brown trout (Elliott 1981), and about 5-6°C lower than those obtained for juvenile Atlantic salmon (Elliott 1991). It is interesting that there appear to be no differences between the four races of charr in Windermere. This suggests that although they differ morphologically, meristically and genetically, their physiological response to thermal stress is similar.

The work described in this interim report will continue for at least another year and should provide greater insight into the ecology of charr stocks in Windermere.

Such information will be valuable for making future decisions on the management of the lake and its charr.

**5. ACKNOWLEDGMENTS**

I am most grateful to Mr Gordon Kidd and Mr John Cooper for supplying records of charr catches, and to the following colleagues for their assistance with this project:

P.V. Allen, E. Baroudy, P.R. Cubby, Y. Dickens, J.M. Fletcher, P.A. Tullett.

## 6. REFERENCES

- Atkinson, K.M. et al., (1986). A general assessment of environmental and biological features of Windermere and their susceptibility to change. Commissioned Report from the Freshwater Biological Association to North West Water. (Ed. J.F. Talling), 80 pp.
- Bagenal, T.B. (1981). Fishing gear experiments in Finland. Report of the Freshwater Biological Association, 49, 26-31.
- Child, A.R. (1984). Biochemical polymorphism in charr (Salvelinus alpinus L.) from three Cumbrian lakes. Heredity, 53, 249-257.
- Elliott, J.M. (1981). Some aspects of thermal stress on freshwater teleosts. In Stress and Fish (Ed. A.D. Pickering), pp. 209-245. Academic Press, London.
- Elliott, J.M. (1991). Tolerance and resistance to thermal stress in juvenile Atlantic salmon, Salmo salar. Freshwater Biology, 25, 61-70.
- Frost, W.E. (1963). The homing of Charr Salvelinus willughbii (Günther) in Windermere. Animal Behaviour, 11, 74-82.
- Frost, W.E. (1965). Breeding habits of Windermere charr, Salvelinus willughbii (Günther), and their bearing on speciation of these fish. Proceedings of the Royal Society B, 163, 232-284.
- Frost, W.E. (1978). The scales of the charr, (Salvelinus willughbii Günther), in Windermere and their use for the determination of age and growth. Journal du Conseil, 38, 208-215.
- Heaney, S.I., Lund, J.W.G., Canter, H.M. & Gray, K. (1988). Population dynamics of Ceratium spp. in three English Lakes, 1945-1985. Hydrobiologia, 161, 133-148.
- Heaney, S.I., Mills, C.A. & Corry, J.E. (1989). An assessment of changing nutrient inputs to Windermere and their influence on water quality and charr population dynamics.

Commissioned Report from the Institute of Freshwater Ecology to North West Water,

38pp.

- Kipling, C. (1984). Some observations on autumn-spawning charr, Salvelinus alpinus L., in Windermere, 1939-1982. Journal of Fish Biology, 24, 229-244.
- Le Cren, E.D. & Kipling, C. (1963). Some marking experiments on spawning populations of charr. ICNAF Special Publication No. 4, 130-139.
- Lund, J.W.G. (1972). Eutrophication. Proceedings of the Royal Society B, 180, 371-382.
- Mills, C.A. (1989). The Windermere populations of Arctic Charr, Salvelinus alpinus. Physiological Ecology, Japan, Special Vol. 1, 371-382.
- Mills, C.A., Heaney, S.I., Butterwick, C., Corry, J.E. & Elliott, J.M. (1990). Lake enrichment and the status of Windermere Charr, Salvelinus alpinus (L.) Journal of Fish Biology (Suppl. A), 37, 167-174.
- Mills, C.A. & Hurley, M.A. (1990). Long-term studies on the Windermere populations of perch (Perca fluviatilis), pike (Esox lucius) and Arctic charr (Salvelinus alpinus). Freshwater Biology, 23, 119-136.
- Partington, J.D. & Mills, C.A. (1988). An electrophoretic and biometric study of Arctic charr, Salvelinus alpinus (L.), from ten British lakes. Journal of Fish Biology, 33, 791-814.
- Sutcliffe, D.W., Carrick, T.R., Heron, J., Rigg, E., Talling, J.F., Woof, C. & Lund, J.W.G. (1982). Long-term and seasonal changes in the chemical composition of precipitation and surface waters of lakes and tarns in the English Lake District. Freshwater Biology, 12, 451-506.
- Talling, J.F. & Heaney, S.I. (1988). Long-term changes in some English (Cumbrian) lakes subjected to increased nutrient inputs. In Algae and the Aquatic Environment. (Ed. F.E. Round). Biopress Ltd., Bristol.

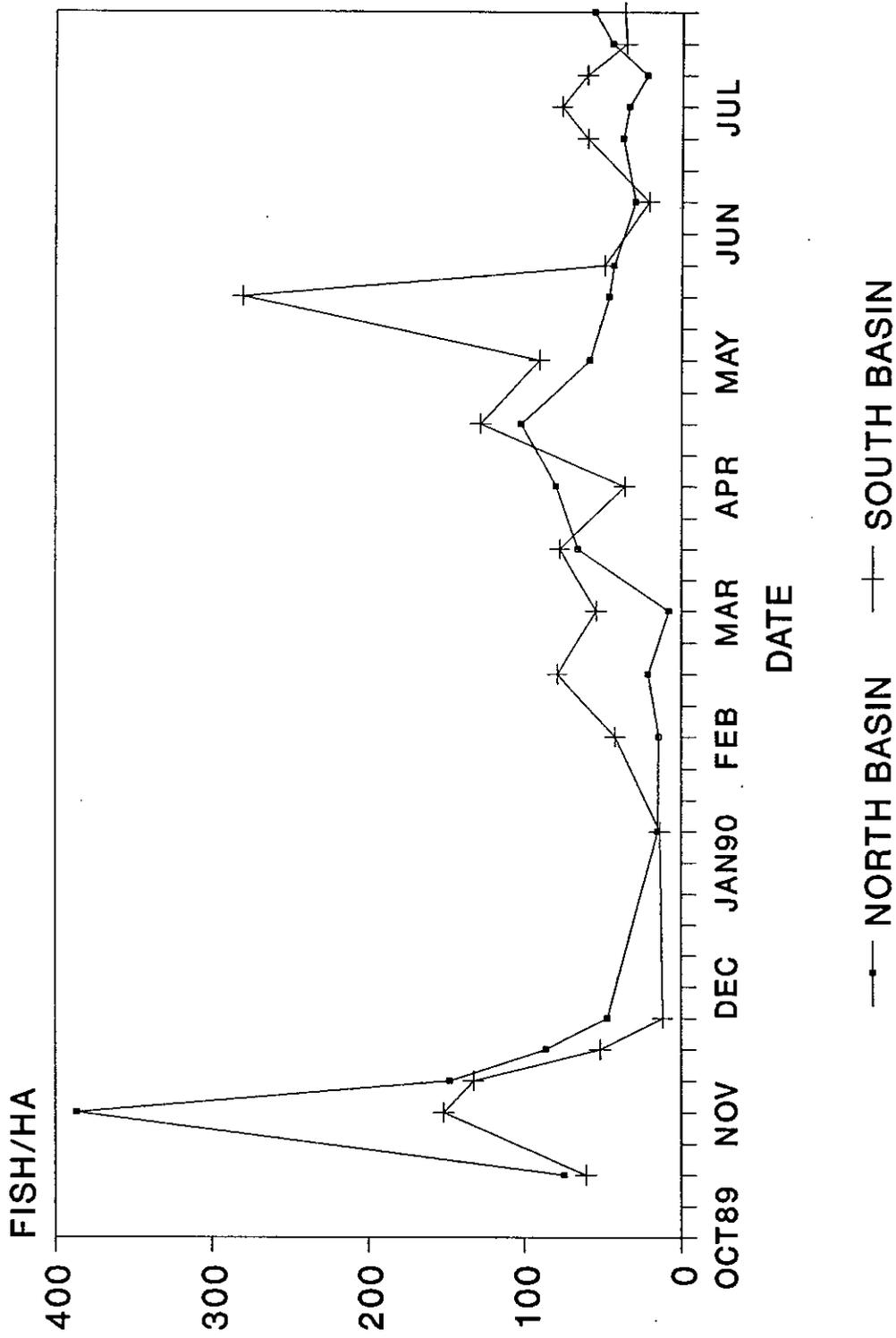


FIG. 1 TOTAL FISH ECHOES IN WINDERMERE  
(FISH PER HECTARE)

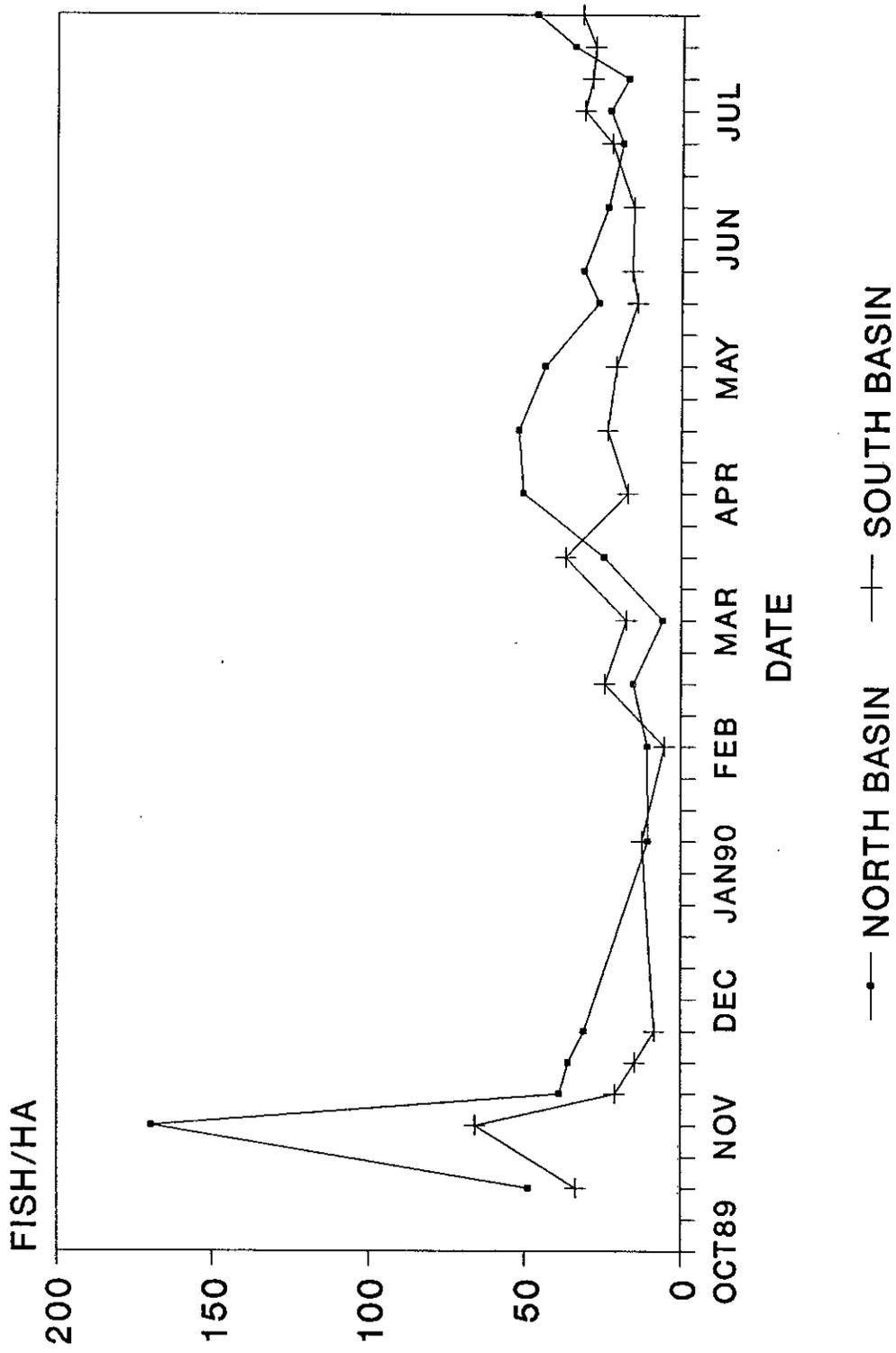


FIG. 2 SINGLE FISH ECHOES IN WINDERMERE  
(FISH PER HECTARE)

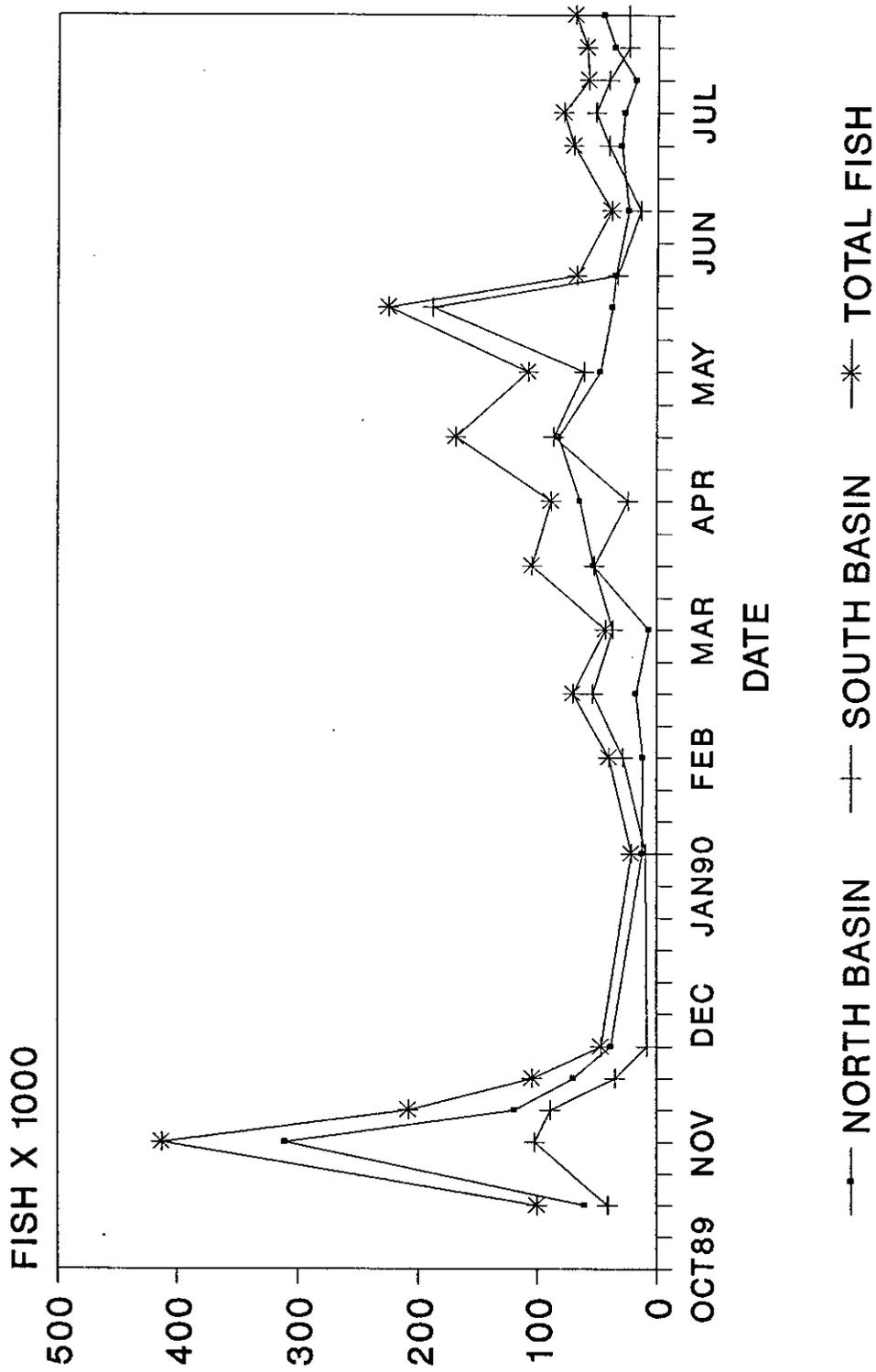


FIG. 3 FISH PER LAKE SURFACE AREA  
 (NORTH BASIN SA = 804.6 HA)  
 (SOUTH BASIN SA = 671.8 HA)

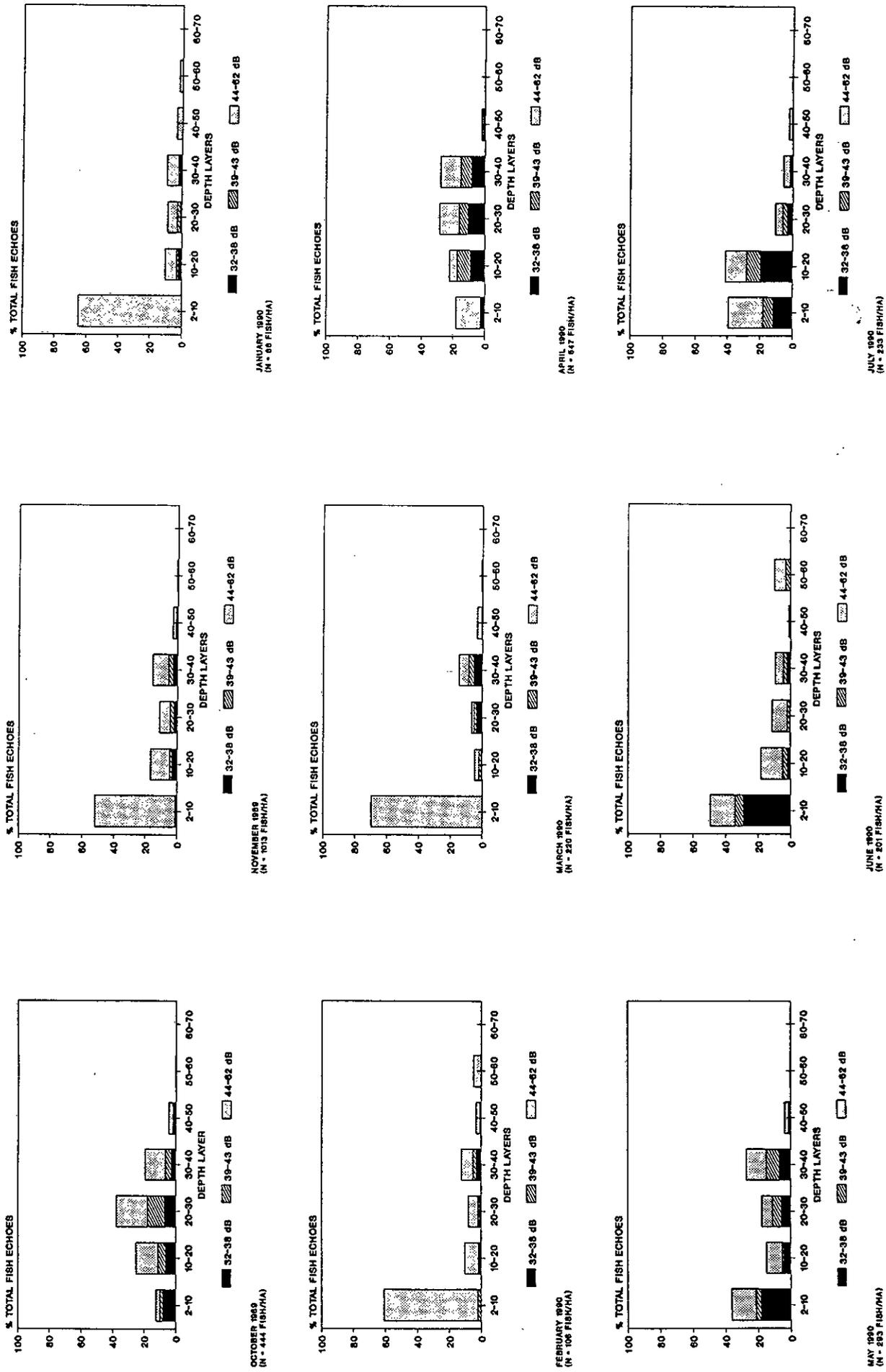


Fig. 4 Windermere fish size distribution in the North Basin.

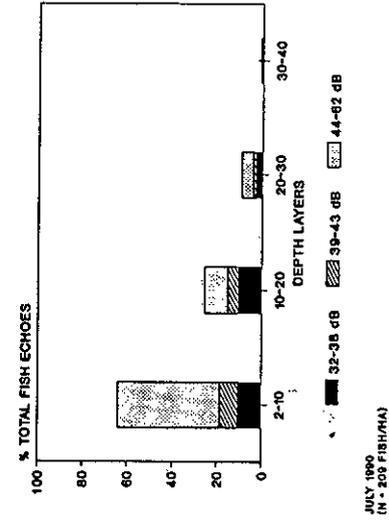
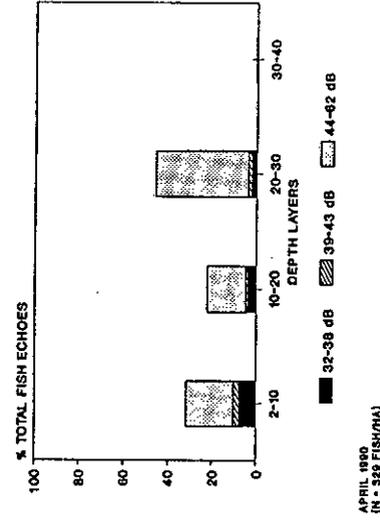
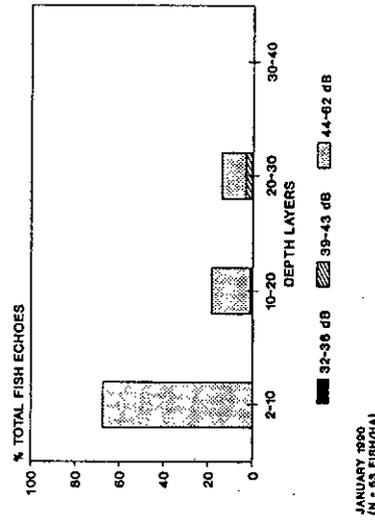
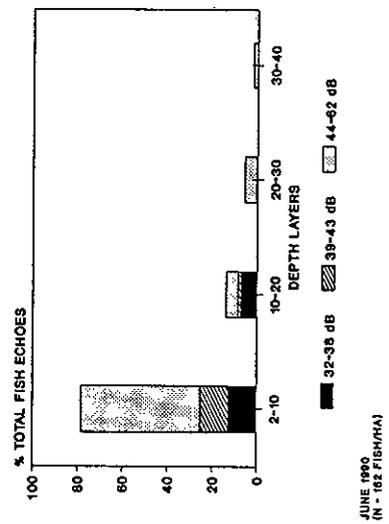
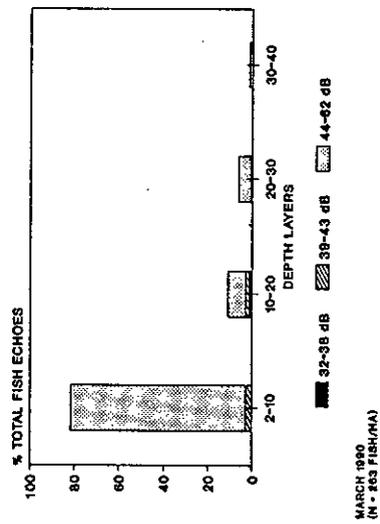
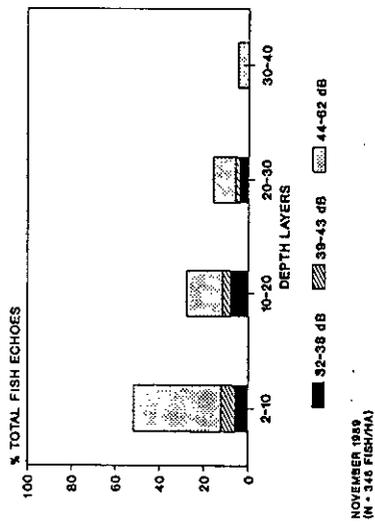
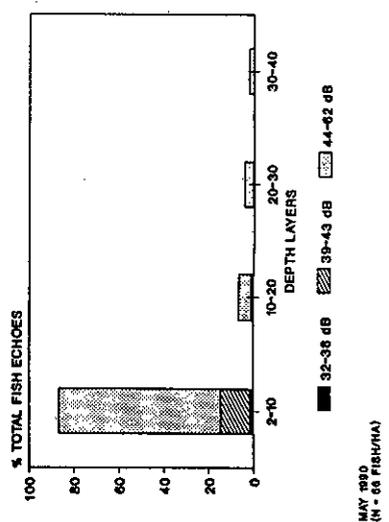
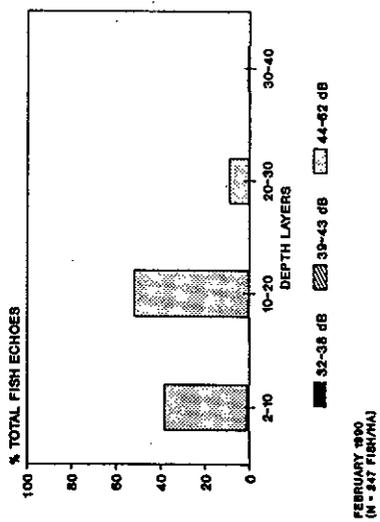
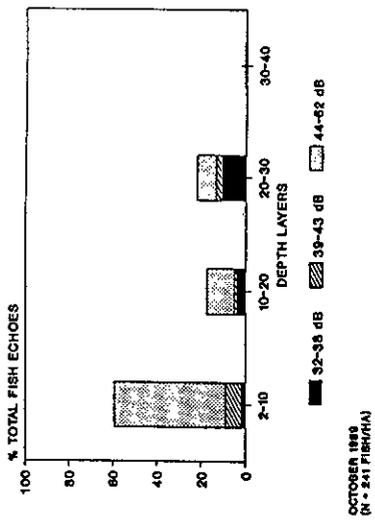


Fig. 5 Windermere fish size distribution in the South Basin.

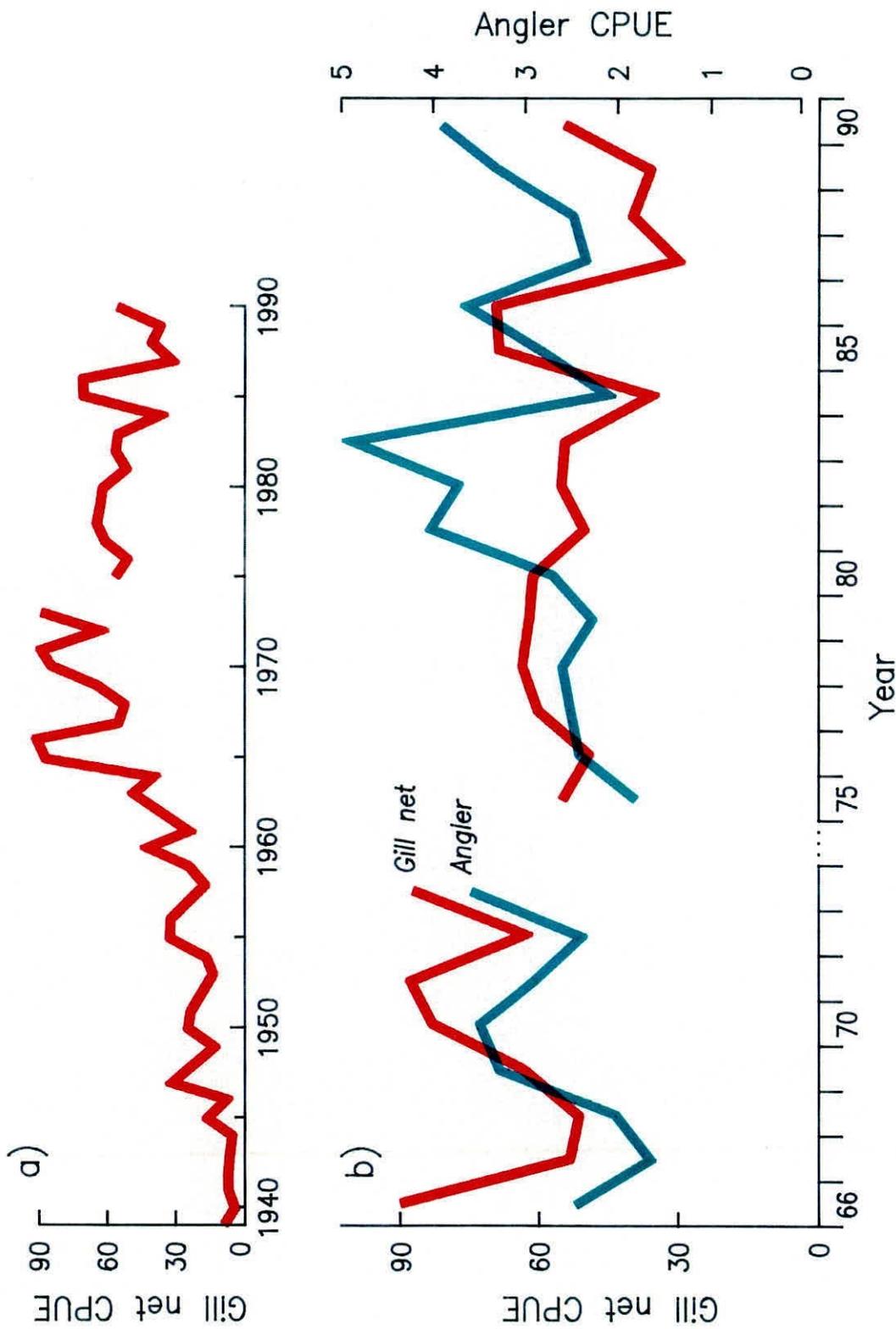


Fig. 6 (a) Gill - net catch per unit effort (CPUE) for charr at Windermere North Basin spawning sites from 1939-1990. CPUE is the mean catch per gill-net day in November at Low Wray Bay (1939 - 1973) and North Thompson Holme (1975-1990) spawning sites. (b) Gill net CPUE (red line) and angler CPUE (green line) from 1966 to 1990. Angler CPUE is the mean catch per boat per hour. The scales for gill-net and angler CPUE have been arranged so that the overall means for each coincide.

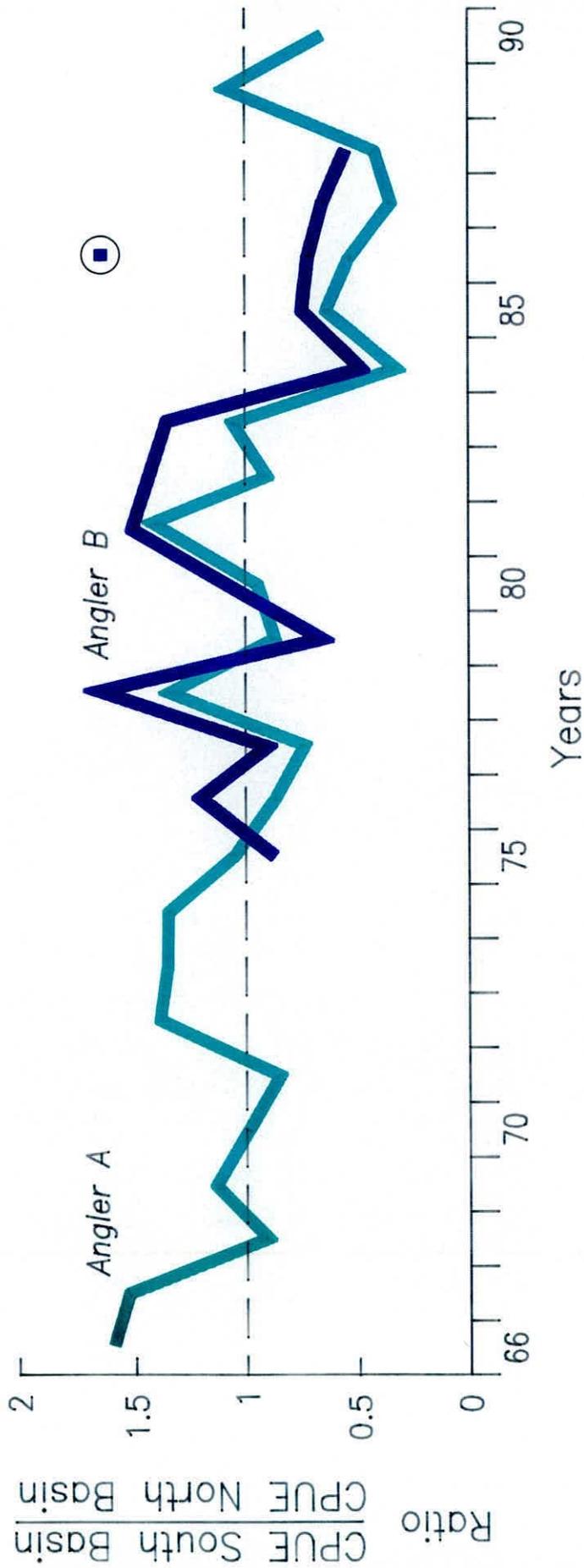


Fig. 7 Ratio of angler CPUE for South Basin for angler A (green line) from 1966-1990 and angler B (blue line) from 1975 to 1988. (Note: the high encircled value for angler B in 1986 was due to the inclusion of one exceptionally high catch in the South Basin; when this was excluded from the analysis the estimated ratio was very similar to adjacent values.)

