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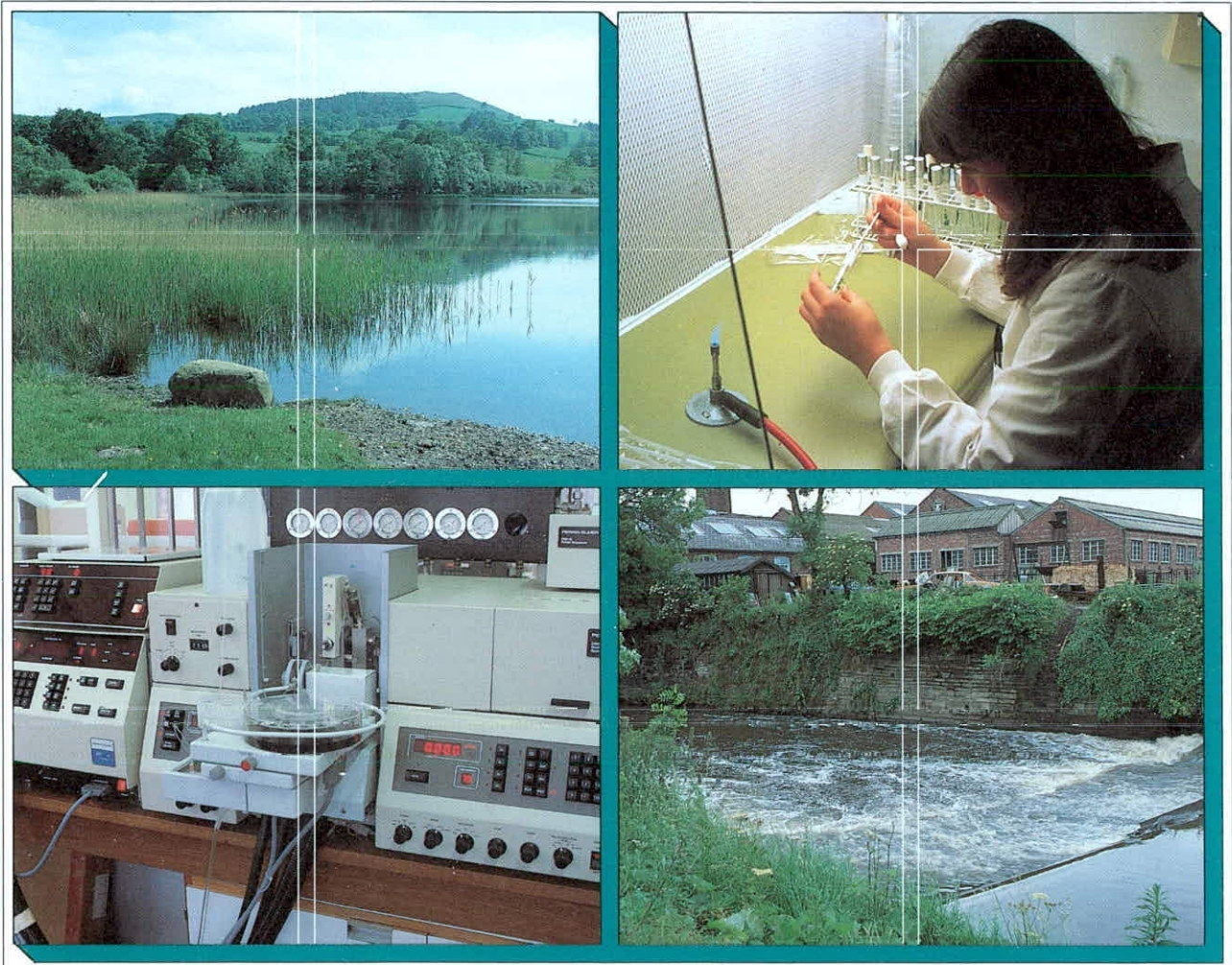
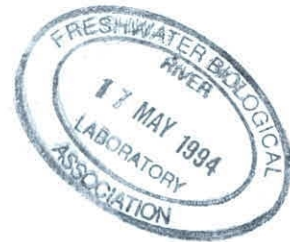
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Ecology of the Schelly, *Coregonus lavaretus*, in Haweswater

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ECOLOGY OF THE SCHELLY, *COREGONUS LAVARETUS*, IN HAWESWATER

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CONTENTS

	Page
Summary	
Chapter 1 Introduction	1
1.1 Background to the present investigation	
1.2 General ecology of schelly	
1.3 Haweswater as a schelly habitat	
1.4 Objectives of the present investigation	
Chapter 2 Population biology and distribution of schelly	7
2.1 Introduction	
2.2 Methods	
2.3 Results	
2.4 Discussion	
Chapter 3 Spawning grounds of schelly	21
3.1 Introduction	
3.2 Methods	
3.3 Results	
3.4 Discussion	
Chapter 4 Long-term records of lake levels and abstraction volumes	25
4.1 Introduction	
4.2 Methods	
4.3 Results	
4.4 Discussion	
Chapter 5 Long-term records of entrapment of schelly and other fish species	32
5.1 Introduction	
5.2 Methods	
5.3 Results	
5.4 Discussion	
Chapter 6 Biology of entrapped schelly and charr	39
6.1 Introduction	
6.2 Methods	
6.3 Results	
6.4 Discussion	
Chapter 7 General discussion	45
Acknowledgements	49
References	50

SUMMARY

1. The ecology of the rare schelly (*Coregonus lavaretus*) in Haweswater was investigated over the period from April 1990 to March 1994, with particular reference to the impact of the water abstraction system.
2. The schelly population was found to be composed of only a few year classes, indicating inconsistent recent recruitment. Quantitative echo sounding indicated that even these fish were present at only low densities, particularly when compared with a more robust schelly population in the nearby Ullswater.
3. Direct observations of the present inshore areas failed to locate any schelly spawning grounds and revealed that much of the habitat in such areas was unsuitable in this context.
4. Inshore areas which did offer physically-suitable spawning habitat are known to be subject to periodic exposure to air. Examination of long-term lake level data confirmed that this sometimes happens during the schelly incubation period of January, February and March. Furthermore, the frequency of such events may have increased in recent years.
5. Fluctuations in lake levels during the summer months were also found to have undoubtedly increased in recent years, with an almost certain adverse effect on the ecology of young schelly.
6. The numbers of entrapped schelly and other fish species were found to have declined since the early 1970s, suggesting that they have also declined in abundance in the lake itself.
7. The population biology of entrapped schelly, like that of those sampled from the lake itself, were found to show a dominance by only a few year classes. This contrasts with the age structure of schelly entrapped during the mid 1960s, which also exhibited better growth rates.

8. Despite the above trends and present low abundance of schelly, comparisons of the numbers entrapped with their densities in the lake observed by echo sounding indicated that entrapment itself is not a significant source of mortality.
9. All of the evidence collected in this project indicates that the schelly population of Haweswater is in state of marked decline. Furthermore, it appears that the present lake level regime is the cause of this situation.
10. Further research and management options relevant to the conservation of this nationally important schelly population are suggested, including the maintainance of entrapment monitoring as an invaluable source of data documenting trends in relative abundance and biological parameters

CHAPTER 1 INTRODUCTION

1.1 Background to the present investigation

The present investigation forms a logical successor to a general assessment of the environmental and biological features of Haweswater and their susceptibility to change which was conducted for North West Water Limited by the Institute of Freshwater Ecology in 1990 (Elliott *et al.*, 1990).

Among other things, the above review noted that Haweswater contains one of the U.K.'s few populations of schelly (*Coregonus lavaretus*), which is one of only four fish species to be protected by the Wildlife and Countryside Act of 1981 where it is listed under the common name of 'whitefish'. However, Elliott *et al.* (1990) also noted the accidental entrapment of schelly by the water abstraction system, although the magnitude and impact of this entrapment on the schelly population was unknown. Despite this potential threat and the significant conservation importance of the Haweswater schelly, it has been the subject of only two primary scientific publications, i.e. Swynnerton & Worthington (1940) and Bagenal (1970), although a very limited amount of preliminary information may be found in the unpublished thesis of Mubamba (1989) which was concerned primarily with the related vendace (*Coregonus albula*). Of these three articles, only Bagenal (1970) provides a substantial source of information relevant to the present study. However, further relevant information is to be found in the first part of a report by the authors to the National Rivers Authority (Winfield *et al.*, 1993a) covering an extensive study of the status of all *Coregonus* populations in England and Wales over the years 1990 to 1993. By agreement with the NRA, this work is referred to where appropriate within the present report, even though it is not yet truly within the public domain. A second part of the above report

(Winfield *et al.*, 1994), which is a review of the scientific literature on *Coregonus* species, is also cited upon occasion although the same restrictions apply to its present availability.

The present investigation has been instigated and designed with the aim of contributing to the conservation of the schelly in Haweswater. In order to appreciate the approach, strengths and limitations of this study, it is useful to be aware of some general aspects of schelly ecology. Given such information, the research priorities for Haweswater become more obvious.

1.2 General ecology of schelly

The scientific name of the schelly is *Coregonus lavaretus* (L.). Together with other members of its genus, known collectively as whitefishes, the schelly is of major importance in commercial fisheries elsewhere in Europe (Luczynski, 1986). The British Isles lay towards the southern limits of the distribution of this genus and offer only a few sites capable of meeting their requirements for relatively cool and oxygen-rich water, although populations are found in England, Scotland and Wales (Maitland & Lyle, 1991). Indeed, Bagenal (1970) concluded that water temperature is a factor of major importance in determining the distribution of the stenothermic, or cold-loving, schelly in the relatively warm U.K.

Coregonus lavaretus is now regarded as a species complex rather than a simple species, although the precise differences which exist between the various U.K. and mainland European populations remain a subject of active research (Bodaly *et al.*, 1991). This biological diversity is reflected in the number of common names used within the U.K. for *Coregonus lavaretus*. In Scotland, where it is found in Lochs Lomond and Eck, it is known as the powan, while in Wales where it occurs

in Llyn Tegid or Bala Lake it is called the gwyniad, and in England, where it is confined to the Cumbrian lakes of Brotherswater (see Winfield *et al.*, 1993b), Ullswater, Haweswater and Red Tarn, it is of course known as the schelly, although this is sometimes written and pronounced as skelly.

The schelly is a silver, streamlined fish, possessing a small but distinct adipose fin between the dorsal fin and the tail (Fig. 1.1), features which separate it at a glance from the other lake fishes of England, Scotland and Wales with the exception of the vendace. A typical maximum age for the schelly is 12 or 13 years, by which time it may have attained a length of up to 35 cm (Bagenal, 1970). Although studies of the diet of schelly have been very restricted, *C. lavaretus* elsewhere begin life feeding on zooplankton such as *Daphnia*, but then progress to feeding on larger invertebrates of the lake bottom (Jacobsen, 1982).

Reproduction occurs during the winter months when many small (between 2 and 3 mm in diameter) eggs are scattered in silt-free inshore areas, which then have a long incubation time before hatching sometime in the following spring (Bagenal, 1970). As schelly eggs are not deposited in the relative safety of redds, as they are in salmonids such as salmon (*Salmo salar*) and trout (*Salmo trutta*) which have similarly long incubation periods, they face a very long period during which they are susceptible to siltation (Resetnikov, 1988; Sterligova *et al.*, 1988), predation by benthivorous fish such as ruffe (*Gymnocephalus cernuus*) (Pokrovskii, 1961) or being exposed by falling lake levels (Salojarvi, 1982). Following hatching in spring, the littoral zone is an important habitat for young *Coregonus lavaretus* through the summer (Naesje *et al.*, 1986). In contrast to coregonids such as the vendace, the littoral zone is also often an important feeding ground for adult *Coregonus lavaretus*, although their use of this habitat may be impaired

by water level fluctuations associated with reservoir management (Heikinheimo-Schmid, 1985). As in many fish species, events during the first year of life are thought to be of critical importance to the dynamics of the population as a whole (Salojarvi, 1982). However, research in this area of schelly, and other lake fish, ecology remains hampered by the difficulty of sampling the young stages (Winfield, 1991).

1.3 Haweswater as a schelly habitat

In the context of European coregonid populations, the original lake of Haweswater (see Fig. 1.2) is likely to have represented a near-ideal *Coregonus lavaretus* habitat. According to Elliot *et al.* (1990), the only other members of the fish community of this relatively high altitude (240 m above sea level), large (present surface area 3.9 km²) and deep (present maximum depth 57 m) lake (general data from Ramsbottom, 1976) are brown trout (*Salmo trutta*), eel (*Anguilla anguilla*), Arctic charr (*Salvelinus alpinus*), perch (*Perca fluviatilis*), minnow (*Phoxinus phoxinus*) and three-spined stickleback (*Gasterosteus aculeatus*). In contrast to many European populations, the schelly in this lake are not threatened by eutrophication, although this situation could change if in-lake fish-farming is introduced (see Elliott *et al.*, 1990). However, it is clear from the above summary that the present use of Haweswater as a reservoir may impact on the schelly population through the following two distinct mechanisms.

Firstly, the numbers of schelly entrapped by the pumped water abstraction may have a significant impact on the population as a whole, particularly as entrapment is associated with spawning fish which suggests that the intake lays near a spawning ground (Bagenal, 1970).

Secondly, the considerable water level fluctuations of Haweswater may interfere with the use by schelly of the littoral zone as a spawning ground, nursery area, or adult feeding location. This second area of concern involves issues of fundamental schelly ecology, including possible interactions with other fish species of the lake.

1.4 Objectives of the present investigation

The overall objective of the present investigation specified in the proposal produced by IFE in March 1991 was to investigate the ecology of the schelly in Haweswater with particular reference to the impact of the water abstraction system. The following specific objectives were also identified.

1. To investigate the fish species and numbers, including seasonal variations, entrapped by the water abstraction system from 1972 to the present.
2. To investigate the biology (size, age, growth, etc.) of schelly entrapped by the water abstraction system over the study period.
3. To investigate the horizontal and vertical distribution of schelly with particular reference to the water abstraction intake and water level fluctuations.
4. To investigate the location and nature of schelly spawning grounds.
5. To investigate the population biology (size, age, growth, etc.) of the schelly over the study

period.

6. To investigate the position of the schelly in the fish community, with particular reference to interactions with the charr.

For reasons which will become apparent, the emphasis of the study has shifted slightly since its inception, but specific objective 1 is reported in Chapter 5, 2 in Chapter 6, 3 in Chapters 2 and 4, 4 in Chapter 3 and 6 in Chapters 2 and 5. Specific objective 5 has only been achieved through the examination of entrapped schelly reported in Chapter 6, although the attempt to achieve this objective and the reasons for its failure are discussed briefly in Chapter 2.

CHAPTER 2 POPULATION BIOLOGY AND DISTRIBUTION OF SCHELLY

2.1 Introduction

The population biology of *Coregonus lavaretus* has been well studied elsewhere in Europe because of the commercial importance of this species in capture fisheries, but comparisons with the unfished schelly population of Haweswater must be performed with this fundamental difference in mind. Assessment of the population biology of the latter is particularly important because this aspect of the ecology of a fish population is arguably the best indicator of its current status.

Although the population biology of *Coregonus lavaretus* is extremely variable (see review by Winfield *et al.*, 1994), there are several aspects common to all populations. As is the case with most species of fish, growth rates are extremely plastic and dependent on environmental conditions, particularly with respect to food resources, as is fecundity which is nevertheless relatively high. Consequently, mean sizes of fish of equivalent ages not only vary between lakes but also between years in the same lake. Typical growth patterns can therefore be defined only in the vaguest of terms. Nevertheless, growth rates are usually quite high and lengths well in excess of 100 mm are commonly attained during the first year of life.

Trends in abundance, which are an extremely important aspect of the population ecology of any fish species, are only detectable with long-term data from either scientific sampling or commercial fisheries. Of course, neither of these data sources exist for the Haweswater schelly, although some information can be gleaned from the long-term entrapment records kept by NWW

and is covered in Chapter 5.

There is thus little background data on which to base a contemporary study of the population ecology of schelly in Haweswater. Bagenal (1970) is the only published such study, although even this was based exclusively on entrapped fish as a source of information. Thus, although entrapment poses a potential threat to the schelly in Haweswater (see Elliott *et al.*, 1990), it does have a positive aspect in the generation of invaluable population data. Some information is also available from the early 1990s in the report of the NRA project described in Chapter 1, although work was hampered by the logistical difficulties of sampling on Haweswater and the apparent present scarcity of schelly (Winfield *et al.*, 1993a). It was concluded from the latter work that the schelly population in Haweswater had suffered from inconsistent recruitment in recent years and thus gave some cause for concern.

The objective of this component of the project was to add to our present knowledge of the population ecology of the schelly in Haweswater through both scientific netting, to provide specimens for detailed examination of condition, growth, diet and other population parameters, and through quantitative echo sounding to assess the current abundance and distribution of the population, particularly with respect to the abstraction point on the east shore of the lake.

2.2 Methods

Gill netting

Previous attempts to sample schelly from Haweswater during the summer months in a research

programme commissioned by the National Rivers Authority (Winfield *et al.*, 1993a) resulted in the capture of very few fish. Consequently, an attempt was planned in the last summer of the present project to collect further specimens for diet and other population analyses by repeating the earlier gill netting for each of the summer months with an increased sampling effort.

On the evening of 24 May 1993, three monofilament survey nets, three multifilament survey nets and three 33 mm single mesh nets were set in water of depth 50 m just to the north of the echo-sounding transect described below. The nets, which had a total surface area of 511 m², were lifted on the morning of the following day and the catch returned to the laboratory for examination.

However, even with this amount of sampling effort, the catch was so low (see results) that an adequate sample size could not be obtained and so the planned further sampling was aborted. Nevertheless, the small number of schelly captured were still aged by examination of their opercular bones.

Echo sounding

Fieldwork

Echo sounding was carried out using a Simrad EY 200P portable echo sounder with a 200 kHz single beam transducer of beam angle 7 ° (Simrad Subsea A/S, Horten, Norway). Throughout the surveys, gain and attenuation settings were maintained at 3 and -15 dB respectively, pulse duration was set at 1.0 ms, and a 40 log R TVG employed. In addition to the real-time production of an echogram through a colour printer, data were also recorded to analogue audio

tape using a Nakamichi 550 Versatile Cassette System. The system was deployed from a 3.2 m dinghy powered by a 2 horse power petrol outboard engine and moving at a speed of between 1.5 and 1.9 m s⁻¹, depending on wind conditions. The transducer was positioned approximately 0.5 m below the surface of the water.

The above system was first deployed on an extensive series of 15 transects around Haweswater during daylight on 19 May 1992 (Fig. 2.1, Table 2.1). For comparative purposes, a series of 8 similar transects was made during daylight on Ullswater, which also contains schelly, on 27 May and 1 June 1992 (Fig. 2.2). During these extensive surveys, the ratios of coverage (length of surveys : square root of research area) were 7:1 for Haweswater, which is comparable to those of other studies (Jurvelius, 1991), but only 2:1 for Ullswater. A series of transects repeated at one location at intervals of c. 30 minutes over dusk was also made at Ullswater (see again Fig. 2.2) on 1 June 1992, an approach which was subsequently repeated on Haweswater at approximately monthly intervals (Table 2.1) between October 1992 and September 1993. Between October 1992 and May 1993 inclusive, two series of transects were made (hereafter the standard and tower transects, the latter starting at the abstraction tower of the east shore, see again Fig. 2.1), while from June 1993 to September 1993 only the standard transect was made. In addition, in June 1993 the transects were continued throughout the night and subsequent dawn (Table 2.1).

Immediately before or between the early transects of each surveying session, vertical profiles of temperature (°C) and dissolved oxygen (mg l⁻¹) were taken in deep water at a point along the transect using a YSI Model 58 dissolved oxygen and temperature meter (Yellow Springs Instrument Co., Inc., USA). However, as dissolved oxygen levels were always far higher than

required by Schelly, these data are not considered further in this report (although the temperature data were used in the development of a Haweswater-Windermere regression used in Chapter 5).

Data analysis

Data on the audio tapes were processed using version 4.02 of the hardware and software Hydro Acoustic Data Acquisition System or HADAS (Lindem Data Acquisition Systems, University of Oslo, Norway). Using this system, analogue signals from the audio tape were digitised and transferred to an IBM-compatible PC where they were further processed to examine patterns of spatial distribution, abundance and target strength, the latter by the indirect statistical algorithm of Craig & Forbes (1969). Prior to such data processing, the system was calibrated using a sphere of target strength -39.2 dB.

Following exploratory data analysis and the advice of the producers of HADAS, default software settings were used for all parameters with the exceptions of the following. In both lakes, the bottom level was set at 4000 mV, the bottom recognition to 15 samples, the bottom backstep to 0 m to allow the recognition of fish echoes close to the bottom, and the single fish recognition to 14 samples.

For the present purposes, analysis was restricted to those sections of the transects where the water depth exceeded 5 m. In both Haweswater and Ullswater, the water column of each transect was divided into a top stratum of from 2 m below the transducer to 5 m, and then 5 m deep strata down to the lake bottom. The scarcity of fish in Haweswater resulted in many estimates of abundance and target strength being made using smaller than ideal sample sizes of echoes.

However, the problem of the estimation of target strength and hence size was largely reduced by considering data only in three size categories of small medium and large as described in detail below.

Estimates of target strengths produced by HADAS were converted to fish lengths using a rearrangement of the relationship recommended for physoclists by Foote (1987) of

$$TS = (20 \log L) - 67.4$$

where TS is target strength in dB and L is fish length in cm. Targets were then pooled into three length classes of small (4 to 10 cm), medium (10 to 25 cm) and large (greater than 25 cm) fish.

2.3 Results

Gill netting

The catch of fish in May was very small and consisted of only two schelly, measuring 268 (male, age 4 years) and 271 (female, age 3 years) mm in length and weighing 248 and 256 g respectively. Although the gut contents of both fish were preserved for future examination, this has not been carried out because the planned diet study was terminated.

Echo sounding

Example echograms from the extensive surveys of Haweswater and Ullswater are shown in Fig.

2.3 and Fig. 2.4, respectively. In Haweswater (Fig. 2.3), fish were noticeably scarce in all parts of the lake, but particularly so in the southerly 'new' lake areas. More fish traces were evident in Ullswater (Fig. 2.4), both near the surface and at greater depths around the 40 to 50 m stratum. Given the lack of simultaneous netting during this project, the likely identities of the different size classes of fish (i.e. small, medium and large as defined in the methods section) are considered in the discussion, although it is pertinent to note here that on the basis of the earlier netting of Winfield *et al.* (1993a) and the size distributions of entrapped fish reported in Chapter 6, almost all of the large fish are likely to be schelly. Whatever species were recorded, it must be remembered that traces on such echograms are biased towards deeper individuals due to the effect of the sonic beam widening with depth and thus insonifying more water. This effect is removed by the software analysis of HADAS, through which the following figures were produced.

Fig. 2.5 shows that during the extensive survey of Haweswater, the densities of small (4 to 10 cm) fish reached up to 10176 individuals ha^{-1} , although it is likely that in some areas of the lake these estimates were complicated by false small fish echoes arising from the steep sides and possibly tree debris from the flooding of this lake. With the exceptions of only three transects, the density of medium (10 to 25 cm) fish remained below 60 individuals ha^{-1} throughout the lake, while large (greater than 25 cm) fish were only recorded in the areas occupied by the original lake, and then again always at a density of below 60 individuals ha^{-1} .

The above values may be compared with those of Fig. 2.6 which shows equivalent data for Ullswater. Here, inspection of the echograms had shown that false echoes were relatively scarce and so the peak density of small fish of 3401 individuals ha^{-1} is likely to be real. Medium fish were present at densities in excess of 100 individuals ha^{-1} on most transects, while large fish peaked at

88 individuals ha^{-1} , thus both medium and large fish were generally more abundant than in Haweswater. Changes in fish density over dusk in Ullswater are shown in Fig. 2.7 and show little or no increase for all three size classes.

The results of the more extensive dusk surveys made across the standard transect in Haweswater are presented in Figs. 2.8 to 2.12, although given that only the large class can be reliably identified as schelly (see discussion) only data for these fish are presented. In the autumn and early winter (Fig. 2.8), there was little change in densities over dusk. Surveys in the late winter (Fig. 2.9) were more restricted due to poor weather conditions, but again there was no marked increase in density. The same pattern continued in the spring and early summer (Fig. 2.10) to the extent that in May no large fish were recorded after sunset. Results of the echo sounding during June, which was continued through the night, is reported in Fig. 2.11 and again shows no great increase in density during the night for small, medium or large fish. Note that the apparent great increase in the density of large fish at 02.00 hours was probably an artefact, as explained below. Finally, in the later summer (Fig. 2.12), densities of large fish again showed no consistent trend over dusk.

Across the tower transect, a similar pattern of consistency over dusk for large fish was found in the autumn and early winter (Fig. 2.13). Trends in the late winter showed a consistent increase over dusk, but the magnitude of the change was very small (Fig. 2.14). During the February transects, it was noticeable from the echograms (see example in Fig. 2.15) that the distribution of large fish was not uniform but strongly concentrated at a depth of 20 to 30 m near the abstraction tower of the east shore. There was no corresponding concentration at equivalent depths on the west shore. In the spring (Fig. 2.16), there was no obvious change over dusk in the

density of large fish across the tower transect.

Seasonal changes in the densities of small, medium and large fish across the standard transect is summarised in Fig. 2.17. Given the absence of any consistent trend in fish density over dusk, both figures are constructed using the peak densities observed each month with the exceptions of very high outlier values for large fish recorded at 0.200 hours in June and 21.00 hours in July. Detailed inspection of the vertical distributions of fish in these two transects revealed that the high densities were caused by single fish echoes in the uppermost depth stratum (2 to 5 m), the effects of which were greatly exaggerated by the analysis of HADAS which compensated for the very narrow beam width in this part of the water column. Small fish reached their greatest densities of up to 16166 individuals ha^{-1} during the early spring, although a second peak of 10130 individuals ha^{-1} was recorded in September. Medium fish peaked in the summer at 540 individuals ha^{-1} , while large fish showed less variation with an annual peak of 122 individuals ha^{-1} in November. Overall, small, medium and large fish were typically present at densities of several thousand, less than 200, and less than 100 individuals ha^{-1} , respectively. Note that the density of large fish during the spawning season (see again Fig. 2.17) was not noticeably higher than at other times.

Corresponding information for the less extensive tower transects is shown in Fig. 2.18. Densities and seasonal trends of small, medium and large fish were similar to those reported above for the standard transect. Again, no marked increase in density was observed at spawning time, although the local concentration of fish near the abstraction tower itself was noted above.

2.4 Discussion

By any standards, the attempts to sample schelly from Haweswater in this and our previous study (Winfield *et al.*, 1993a) have been unsuccessful. Undoubtedly, this lake presents considerable practical problems to fish fieldwork, ranging from its considerable depth to its unpredictable and often hazardous weather conditions, which contributed to the problems of this study. The results of the echo sounding discussed below suggest that the present scarcity of schelly in Haweswater was also a contributory factor.

The abandonment of the netting programme after the initial capture of just two schelly in May 1993 was made in order to allow more productive concentration on other parts of the project, including the study of entrapped fish which provided similar information as considered in Chapter 6. Little can be deduced on the basis of the capture of just two fish, other than to note that they too came from the same age groups (3 and 4 years old) that dominated the entrapped fish, and that they showed good individual condition and growth.

As expected, the echo-sounding study produced far more information. Indeed, as with other areas of remote sensing with which this technique may reasonably be classed, the problems were not of insufficient data, but of too much and of the need for 'ground truthing'. In the present context, the latter problem means identifying which species are being recorded as echoes. Fortunately, analysis of the size distributions of entrapped fish (see Chapter 6) indicates that almost all of the large (greater than 25 cm) fish of the echo-sounding analysis of Haweswater are likely to be schelly. Unfortunately, the situation is less clear with the two smaller size classes of echoes, although the small (4 to 10 cm) class is likely to contain only underyearling schelly along with

young charr, perch and perhaps trout. The medium (10 to 25 cm) class potentially contains both the majority of the charr together with immature schelly beyond their first year of life, although again the entrapment data suggest that the latter group of fish is presently rare in Haweswater. In Ullswater, all of the large deepwater echoes are likely to be schelly given their dominance in this part of the lake, although the smaller size classes may also contain numbers of perch (Winfield *et al.*, 1993a). Given this complexity, the following discussion concentrates on the large fish which may reasonably be taken to be schelly in both lakes and which form the most important component of the population in the context of its future survival, given that it holds all mature individuals.

Coregonus lavaretus shows very variable distribution patterns and as adults may be found very near to the bottom in inshore and offshore areas, or even in the upper parts of the open water column (see Winfield *et al.*, 1994). However, not all lakes contain fish in all three habitats and it is known that adults avoid foraging in littoral inshore zones damaged by marked lake level fluctuations (Heikinheimo-Schmid, 1985) or in open water areas when charr are present, presumably due to the effects of competition for zooplankton (Pomeroy, 1991). Both of these factors, i.e. water level fluctuations and the presence of charr, occur in Haweswater and thus it was not surprising that our earlier study (Winfield *et al.*, 1993a) found schelly only in deepwater areas at all times of the year sampled with the exception of the spawning season. In contrast, identical sampling techniques found adult schelly inhabiting the inshore of Ullswater throughout the year. Consequently, when comparing the results of echo sounding from these two lakes, it must be remembered that while all of the schelly population of Haweswater was likely to have been surveyed, in Ullswater a significant component was probably in very shallow (i.e. less than 4 m) inshore areas and thus missed.

Echograms from extensive surveys of Haweswater and Ullswater were visibly different even before quantitative analysis, with numbers of small fish being present at great depth in the latter but absent from the former. From their size and the time of year, these fish were probably dominated by schelly of approximately 1 year of age. Further analysis confirmed this difference between the lakes and, furthermore, a significant number of the apparent small fish echoes recorded from Haweswater were probably false echoes caused by the steep sides and debris of certain areas of this lake. While such complications can be avoided during the analysis of echo-sounding data for truly pelagic fish (e.g. Elliott & Baroudy, 1992) by excluding echoes near the bottom and sides, this is obviously inappropriate when studying a potentially bottom-dwelling species such as schelly. Both medium and large fish were also relatively more abundant in Ullswater, even though as noted above the technique is likely to have sampled only a part of the schelly population. Given the relative infancy of quantitative echo sounding on *Coregonus lavaretus* populations, it is impossible to put the observed absolute densities of schelly into a broader context, although it may be noted that the observed adult densities for Haweswater were the lowest recorded for any of the large-lake populations of England and Wales by Winfield *et al.* (1993a).

The stability over dusk of the schelly density estimates in both Ullswater and Haweswater, and through the June night in the latter lake, was remarkable given the considerable increases observed in studies of other fish species such as charr (e.g. Elliott & Baroudy, 1992) and vendace (Jurvelius *et al.*, 1988). However, under some conditions it is to be expected that schelly will become less amenable to echo sounding after dusk as they migrate into shallow inshore areas which cannot be adequately searched by standard echo-sounding equipment. When this fact and logistical aspects are considered, daytime echo-sounding transects seem most appropriate for the purposes of

monitoring the schelly populations.

The use of peak monthly densities, taken from series of repeated transects run over dusk, to construct a summary of seasonal changes in schelly density in Haweswater is thus justified. Even so, it is difficult to interpret changes in small fish densities because they are so strongly influenced by the abundance of underyearling schelly which probably become detectable by the system used towards the end of their first summer. However, it is safe to conclude that the numbers of such fish were consistently low when compared with observations made by Winfield *et al.* (1993a). The densities of medium and large fish, the latter undoubtedly dominated by mature schelly, showed relatively little seasonal variation. Most noticeable was the lack of any marked increase in abundance across either the standard or abstraction tower transects during the spawning season of January, February and March, even though the majority of entrapped schelly are taken during this period (see Chapter 5). However, peak densities were observed in November for both transects which may indicate a pre-spawning concentration of fish in this general area of the lake, although the evidence for this is far from convincing.

It is clear, however, that dense aggregations of mature schelly do occur in the immediate vicinity of the abstraction point on the east shore of Haweswater during February, rather than across the width of this part of the lake. It is equally noticeable that no similar aggregations form at similar depths on the opposite shore. Whether this is pure coincidence or reflects some feature of the lake bottom favoured by both schelly and abstraction point architects is unclear. The facts that entrapped fish are not taken over a very short period (see Chapter 5) and are not strongly dominated by males (see Chapter 6), both features which would be expected to arise from an actively spawning aggregation, do suggest that the abstraction point lies in an assembly area rather

than on a spawning ground itself. This admittedly tenuous conclusion is also supported by the fact that at least some of the Haweswater schelly migrate into the very margins of Haweswater to spawn, where they are well away from the abstraction point itself (Winfield *et al.*, 1993a).

CHAPTER 3 SPAWNING GROUNDS OF SCHELLY

3.1 Introduction

The findings of Chapter 2, and particularly those presented later in Chapter 6, suggest that the schelly population of Haweswater has suffered from inconsistent recruitment in recent years, resulting in a present scarce population dominated by only two or three year classes. This is in marked contrast to the current status of the other two *Coregonus lavaretus* populations of large lakes in England and Wales (i.e. Ullswater and Llyn Tegid), which are both abundant and show consistent recent recruitment (Winfield *et al.*, 1993a).

The reason for poor recruitment in Haweswater is thus likely to lie within the lake itself, rather than be attributable to unfavourable climatic conditions which would be expected to have also affected populations of the other lakes. Moreover, the reproduction of coregonids is known to be particularly susceptible to local changes to their spawning grounds. Recruitment of *Coregonus lavaretus* populations may be adversely affected by siltation associated with eutrophication (e.g. Wilkonska & Zuromska, 1982; Sterligova *et al.*, 1988), by predation on incubating eggs by recently-introduced populations of ruffe (*Gymnocephalus cernuus*) (see Winfield, 1992), or by being exposed by falling lake levels (Salojarvi, 1982), all of which may reduce egg survival. This factor has also been observed to be reduced in the related *Coregonus clupeaformis* by sedimentation caused by changes in lake levels manipulated for hydro-electric purposes (Fudge & Bodaly, 1984). In the absence of eutrophication (Elliott *et al.*, 1990) and ruffe introduction (Winfield *et al.*, 1993a), only changes in lake levels may have adversely affected egg survival on the spawning grounds of schelly in Haweswater.

Successful *Coregonus lavaretus* recruitment requires access to suitable spawning grounds, which are typically clean gravel areas in relatively shallow (i.e. less than 10 m deep) areas of the lake (Winfield *et al.*, 1994). Such areas undoubtedly existed in the original Haweswater prior to the construction of the dam, but no studies have been made of the new inshore areas in this context. Consequently, the ambitious aims of this part of the project were to examine the apparent suitability for schelly reproduction of selected inshore areas and, by carrying out the investigation during the known schelly incubation period of early March, to locate one or more actual spawning grounds.

3.2 Methods

Potential spawning grounds were searched by a combination of direct observation by SCUBA divers equipped with an underwater still camera and by remote sensing using a video camera.

SCUBA divers were used to search and collect sediment samples from three areas on the east and south shores of Haweswater (Fig. 3.1) during three days in early March 1992 when schelly eggs were in the early stages of incubation and thus at their most abundant. In addition, underwater still photographs were taken of the substrate at each site. Given the low water temperatures, such diving was restricted to approximately one hour on each day. Observations and samples could not be taken near to the abstraction point due to diver safety considerations.

At the same time as the diving, observations were made using a Super-mini Underwater TV Camera Model FM-1000 (Aquascan International Limited, Newport, U.K.) recording to a National Panasonic NV-180 portable VHS video recorder.

3.3 Results

Observations by divers, still photography and video camera showed that several inshore areas of Haweswater contain areas of clean gravels and stands of *Isoetes lacustris* and *Callitriche* sp. during the period of schelly egg incubation. The inshore area relatively near to the abstraction tower, however, contained only very limited areas of exposed gravel and was largely composed of a bottom strewn with rocks and boulders (Fig. 3.2). More physically-suitable potential spawning habitats were found in the two southerly arms of the lake (Fig. 3.3 and Fig. 3.4). However, despite the investment of considerable sampling effort, no eggs were found either *in situ* or in sediment samples examined in the laboratory

3.4 Discussion

The ambitious aim of definitively identifying schelly spawning grounds by locating incubating eggs was not achieved, even though the site on the east shore of the lake was previously frequented by spawning schelly (Winfield *et al.*, 1993a). Searching for small (2 to 3 mm diameter) coregonid eggs *in situ* by diving or any other means is extremely difficult, although considerable effort was deployed. The implication is that either the wrong areas were searched, which was apparently not the case given the earlier netting captures, or that eggs were present at very low densities or even absent. Even though eggs were not recovered, study of the literature suggests that the present spawning grounds of schelly in Haweswater are likely to occur within the 'new' inshore regions of the lake. If the schelly have retained their original spawning sites, their present great depth, which is in excess of 30 m when the lake is full, is three times greater than the deepest of those typically used elsewhere (see Winfield *et al.*, 1994).

While nothing is known of the inshore areas of the original lake, it is very apparent from the observations of the divers of the present study that the area investigated on the east shore offers a poor spawning habitat for schelly because areas dominated by large rocks or boulders are not frequently used by this species. The spawning that does appear to occur here, as evidenced by net captures of spawning adults, is likely to be restricted to the small available areas of gravel at depths of less than 5 m. The degree of incubation success in such areas is unknown.

The two 'new' inshore areas of the southern lake surveyed by the divers offered more physically-suitable spawning habitats in the form of areas of clean gravel or macrophytes, both of which form suitable incubation substrata for schelly. However, both areas also contained amounts of terrestrial grasses which testify to their periodic exposure to air. The important issue of water level fluctuations with respect to use by schelly of the inshore zone for reproduction is considered in detail in Chapter 4.

In summary, the present survey by divers failed to find any ideal schelly spawning areas in the present Haweswater.

CHAPTER 4 LONG-TERM RECORDS OF LAKE LEVELS AND ABSTRACTION VOLUMES

4.1 Introduction

The results of Chapter 2, together with those of Chapter 6 presented later, indicate that schelly recruitment in Haweswater has been poor throughout much of the early 1990s and at least the late 1980s. Furthermore, as explained in the introduction to Chapter 3, this is probably due to changes specific to the lake itself, which may include a deterioration in the habitats of incubating eggs, early life stages, or even adults. The inshore areas of the lake are likely to be important to all three of these life stages because elsewhere they constitute spawning grounds (see Winfield *et al.*, 1994), nursery areas for young (see Naesje *et al.*, 1986) and an important feeding area for adults (Heikinheimo-Schmid, 1985).

Clearly, the inshore areas of Haweswater were changed fundamentally when the new lake was formed in the 1940s, during which the lake surface was raised by almost 30 m. Nevertheless, the schelly population apparently adapted to the new conditions extremely successfully because during the 1960s it continued to show consistent, if variable, recruitment (Bagenal, 1970). If there has indeed been a subsequent decline in schelly recruitment, and also in their abundance as suggested by Chapter 5, its underlying reasons may be discovered in records of lake levels over the period from the 1960s to the present. Consequently, the primary aim of this part of the project was to analyse lake level data relating to this period in the context of the requirements of schelly eggs, young and adults. In addition, less extensive data on the amounts of water abstracted from Haweswater were also examined, in part to compensate the entrapment data of

Chapter 5 to allow for changing abstraction volumes.

4.2 Methods

Lake levels

Long-term records of the Haweswater daily lake level covering the periods from 1 January 1961 to 1 July 1984 and from 1 August 1989 to 31 December 1992 were obtained from NWW. These data, supplied as computer files, were manipulated into a form in which they could be analysed with respect to schelly ecology by IFE using PC-based software.

Abstraction volumes

More restricted records of the daily flows of water abstracted from Haweswater, as measured at Watchgate Water Treatment Works inlet meters, were obtained from NWW for three periods during the 1970s, 1980s and 1990s. Specifically, these were from 6 February 1973 to 30 December 1975, from 1 July 1983 to 31 May 1987, and from 1 August 1989 to 31 December 1992. As for lake level data, this information was manipulated into a form in which it could be analysed by PC-based software at IFE. While these data are briefly described in the results section of the present chapter, their primary use was to correct the entrapment data of Chapter 5 to allow for variations in sampling 'effort', i.e. the volume of water effectively fished.

4.3 Results

Lake levels

Gross trends in the daily lake level of Haweswater from the early 1960s to the early 1990s are shown in Fig. 4.1. Even though data are unavailable for the latter half of the 1980s, it is clear that the drawdown of this reservoir has become more marked since the mid 1960s. While the lake was never less than 7 m below full during this earlier period, since the 1970s it has usually dropped to more than 10 m below full, with values in excess of 15 m occurring upon occasion.

As noted in Chapter 1, such drawdowns may adversely affect schelly populations through interference with the use of the littoral zone as a spawning ground, or as a nursery area and adult feeding location. Influences in the context of spawning will occur during January, February and March (Bagenal, 1970), while effects on nursery and feeding considerations are more likely during the period of June to October (Naesje *et al.*, 1986). Consequently, long-term changes in lake levels during these two periods have been investigated separately.

During January, February and March, drawdown was only limited in the 1960s (Fig. 4.2) and the lake level fell to more than 3 m below full in only 1963 and 1964. This level was frequently exceeded during the 1970s (Fig. 4.3), with 1974 and 1976 beginning with the lake at least 10 m below full. While this low level was maintained in 1976, the lake rose quickly during the early period of the schelly spawning and incubation period in 1974. Lake levels were again uniformly high during the early 1980s, although they were considerably lower in 1984. Data are unavailable for the remainder of this decade. The situation so far in the 1990s (Fig. 4.5) resembles that of the

1970s.

Over the entire dataset, drawdown during June, July, August, September and October was usually more extensive than that reported above for the early part of each year. Although during the 1960s (Fig. 4.6) the lake still rarely fell to more than 5 m below full, there was much greater variation in the 1970s (Fig. 4.7) including years such as 1973 and 1976 when the level quickly dropped to 10 m below full and eventually dropped a further 5 m. The more limited datasets of the 1980s (Fig. 4.8) and early 1990s (Fig. 4.9) show a continuation of the heavy drawdown pattern of the 1970s.

The above long-term trends in lake levels are summarised in Fig. 4.10 and Fig. 4.11. Fig. 4.10 shows changes in the mean, maximum, minimum and range of daily water level during January, February and March. Regression analyses revealed no significant trends in any of these parameters, although the data suggest an increase in range. Further analysis if and when data from the latter half of the 1980s become available would be worthwhile. More marked trends are clearly evident for equivalent parameters for June, July, August, September and October (Fig. 4.11), with significant downwards trends in mean ($r = 0.602$, $p < 0.001$), minimum ($r = 0.727$, $p < 0.001$) and range ($r = 0.726$, $p < 0.001$) of lake levels.

Abstraction volumes

With the notable exceptions of certain late summer periods when abstraction was reduced, the daily volume of water abstracted from Haweswater was remarkably uniform with the three time

periods for which data are available in the 1970s, 1980s and 1990s (Fig. 4.12). Between 1973 and 1975, the mean abstraction was approximately 300 MI day⁻¹, increasing to the order of 325 MI day⁻¹ between 1983 and 1987, and to almost 400 MI day⁻¹ between 1989 and 1992. These increases are also shown in Fig. (4.13) in terms of the total amount of water abstracted during January, February and March, when most schelly are entrapped (see Chapter 5).

4.4 Discussion

As is to be expected, and indeed as is inevitable, the present operation of Haweswater as a reservoir has resulted in considerable fluctuations in its water level. Moreover, it is clear from the present analysis that the magnitude of these fluctuations has increased in recent decades. While lake levels typically fell to 5 m below full in the 1960s, when the schelly population recruited consistently (Bagenal, 1970), in the 1970s, 1980s and early 1990s, by which time recruitment had become very inconsistent as shown in Chapters 2 and 6, falls in the lake level to 10 m below full were frequent and drops to 15 m below full were recorded. It is pertinent to note that a 7 m fluctuation in the water level of Lake Kemijarvi in Finland has been considered to be damaging to a *Coregonus lavaretus* population and as a result the lake is stocked with fingerlings each year (Heikinheimo-Schmid & Huusko, 1990), at a considerable cost to the reservoir operators.

As noted in the introduction to this chapter, lake level fluctuations may impact on the survival of incubating eggs in the early part of the year, or on the feeding conditions of the young and adults during the summer months. While larger adults may be able to forage alternatively on macroinvertebrates of the deepwater sediments, younger and smaller *Coregonus lavaretus* are excluded from such areas by the threat of predation (Hessen *et al.*, 1986). Consequently, the

inshore zone and its macroinvertebrate fauna are of paramount importance for underyearling schelly.

With respect to the requirements of incubating schelly eggs, the trend in water fluctuations during January, February and March over the last three decades is similar to that of the overall fluctuations. In the 1960s, levels changed little during this critical period of the year and so egg incubation was likely to have been very successful. However, several years during the 1970s, such as 1974 as an extreme case, involved level changes in excess of 5 m which are likely to have caused egg mortality by the obvious agency of exposure, or even by the less obvious agency of changing patterns of sedimentation due to an increasing lake level (see Fudge & Bodaly, 1984). From an analytical viewpoint, it is frustrating that level data from the late 1980s are presently unavailable because such information could be investigated with respect to the relative year-class strengths of schelly from this period onwards derived from the examination of entrapped fish (see Chapter 6). Such additional information would also add to the assessment of the statistical significance of apparent changes during this part of the year. In the meantime, the avoidance of abrupt changes to the lake level during the first three months of the year is strongly recommended.

Drawdown during the summer has been a feature of the management of Haweswater throughout the duration of the present dataset, but again it has become more marked in recent years with respect to the mean, minimum and range of lake levels at this time of year. Under such conditions it is extremely unlikely that the inshore areas of the lake will develop significant macroinvertebrate populations typically consumed by young or adult schelly, such as *Asellus* which are important in the diets of such fish in Ullswater (Winfield *et al.*, 1993a). Consequently, it is not surprising that adult schelly do not frequent the Haweswater inshore zone outside the

spawning season, but instead occur in the deep areas where they feed on chironomid larvae of the bottom sediments (Winfield *et al.*, *op. cit.*). As noted earlier, young schelly do not enjoy the option of such a switch in foraging behaviour. For such fish, the more likely result of a drawdown inshore zone is individual poor growth and perhaps death, which for the population results in poor recruitment.

In summary, there are strong indications that the present lake level regime of Haweswater results in unsuitable habitat conditions for the schelly. While improving this situation for the summer period may be difficult given other operating requirements, a more sympathetic management of lake levels during the early part of the year is highly desirable and may be relatively easy to achieve with little cost to other aspects of the lake's utilisation.

CHAPTER 5 LONG-TERM RECORDS OF ENTRAPMENT OF SCHELLY AND OTHER FISH SPECIES

5.1 Introduction

It was noted in the introduction to Chapter 2 that trends in fish population abundance are only detectable with long-term data from either scientific sampling or commercial fisheries, but neither of these data sources exist for the Haweswater schelly. However, in the absence of such data it is often possible to use less appropriate but available sources of information. Entrapment data are one such source of invaluable long-term records which, if interpreted with additional information and with caution, can be extremely useful and have indeed been used in the investigation of conservation aspects of another *Coregonus lavaretus* population in the U.K. (Maitland & East, 1989).

The aim of this part of the project was to analyse entrapment records for Haweswater kept by NWW from the early 1970s to the present. Although such data are inevitably biased for a variety of reasons, often including changes in observer identity and performance, they offer a unique avenue for the exploration of parts of the population ecology of schelly and other fish species in Haweswater over the last two decades. Equally importantly, they also allow an assessment of the likely direct impact of entrapment on the schelly population. The latter factor may be particularly important for the schelly of Haweswater because, in contrast to the usual situation with entrapped populations, the study of Bagenal (1970) revealed that entrapment is clearly linked to spawning activities, which greatly increases its potential to affect the population as a whole.

5.2 Methods

Fish entrapped by the abstraction system at Haweswater are transported by aquaduct to the Garnett Bridge filtration plant at Watchgate Water Treatment Works near Kendal, where they are retained by meshes and removed. Near-daily records of these fish have been kept by NWW since 1 April 1972 to the present. The original notebooks containing this information were obtained, photocopied, and their data tabulated and entered onto a PC-based computer database covering the period from 1 April 1972 to 31 March 1994 (although records continued to be maintained by NWW at the time of writing).

The above data were subsequently analysed for all fish species to investigate long-term trends in the numbers entrapped, including a correction for varying 'sampling effort' using the abstraction data of Chapter 4, and to investigate the seasonal pattern of entrapment.

For schelly, an analysis was also made of the daily pattern of entrapment during the peak months of January, February and March. Although neither NWW nor IFE hold any long-term water temperature data for Haweswater, daily temperatures for the above period from 1973 to 1994 were reconstructed using a regression linking Haweswater surface water temperature to that of Windermere. The regression was made using intermittent data collected at Haweswater during the present study and the IFE long-term Windermere 'back bay' records and took the form

$$H = 0.951W - 1.008$$

where H is the water temperature ($^{\circ}$ C) of Haweswater and W is that of Windermere ($r^2 = 0.963$).

In addition, near-daily temperature records for the period from 1989 to 1992 were obtained from a fish farm operated by Lakeland Smolt Limited which draws water from Haweswater. Although these are not considered further in the present report because of their as yet relatively short duration, regression with the intermittent data collected from the lake surface showed a very close relationship (Farm temperature = 1.002 [Haweswater temperature] + 0.189, $r^2 = 0.999$) and so they may be of use in future investigations of the ecology of schelly or the limnology of Haweswater.

5.3 Results

During the years from 1973 to 1993 inclusive, i.e. all of the years for which complete data are available, totals of 4242 schelly, 16616 charr, 711 eel, 465 perch, and 276 trout were entrapped (Fig. 5.1). However, during this period the annual entrapment has declined for both schelly and charr (see again Fig. 5.1), the two most abundant species. While typically several hundred schelly and over 1000 charr were entrapped during the 1970s, these figures have now decreased to less than 100 and several hundred, respectively.

Patterns have also emerged with respect to the seasonality of entrapment over this period. Schelly and charr were both entrapped largely during the winter (Fig. 5.2), with over 80% of schelly being taken during January, February and March. Monthly entrapment of eel and perch was less variable although it tended to be higher in the autumn, while that of trout showed even less variation (Fig. 5.3).

The following results concentrate on the peak entrapment period for schelly of January, February

and March which, as suggested above and confirmed in Fig. 5.4, typically accounted for over 80% of annual schelly entrapment, together with approximately 50% of annual charr entrapment. Like the annual entrapment totals, the numbers of schelly and charr taken during this part of the year have declined markedly since the early 1970s.

One possible reason why entrapment has fallen is that the amount of water abstracted, and hence the 'sampling effort', has decreased over the observed period. However, as reported in Chapter 4 this is not the case and abstraction volumes have actually increased. Consequently, allowing for this change in 'sampling effort' and expressing the entrapment data of schelly and charr in terms of catch-per-unit-effort (CPUE) still shows a marked decrease between the early 1970s and the early 1990s (Fig. 5.5). The similarity of the schelly and charr declines in entrapment is reflected in a significant positive relationship (Fig. 5.6) in the numbers of these two species entrapped during January, February and March of each year ($r = 0.825$, $p < 0.01$).

Finally, it became apparent during the above analyses that there had been a shift in the daily pattern of schelly entrapment within January, February and March of each year. This is shown in Fig. 5.7 which also incorporates data from 1965, 1966 and 1967 published by Bagenal (1970). In the 1960s and early 1970s, most schelly were entrapped during the first 30 days of the year, but during the 1970s this shifted such that by the early 1980s most fish were taken from day 50 onwards. During the period of the present project, the distribution of daily entrapment has again shifted to return to the pattern of the 1960s. These changes are seen more clearly in terms of the day of the year on which schelly entrapment was first recorded (Fig. 5.8), although it is clear that this parameter bears no significant relationship with the reconstructed water temperature of these days (see again Fig. 5.8, $r = 0.258$, $p > 0.10$).

5.4 Discussion

The aims of this part of the project were twofold, i.e. to investigate trends in the entrapment of schelly and other fish species over approximately the last 20 years, and to determine the effect on the schelly population of this source of mortality. The latter aspect will be discussed first.

In the early 1970s, several hundred schelly were entrapped each year, although the then population size of the lake was unknown. In the early 1990s, this figure had dropped to consistently less than 100 individuals each year which, from the echo-sounding surveys of Chapter 2, represents the fish from only a few hectares. Even though these are spawning adults (see Chapter 6), it is the authors' opinion that this is not a significant direct source of mortality for the schelly of Haweswater. In addition to having no significant negative effect on the schelly population, it can be argued that entrapment has a positive aspect in the form of the generation of invaluable population data as considered below and in Chapter 6.

Entrapment obviously produces a biased sample of the Haweswater fish community and so is of little use for the assessment of community composition other than indicating which species are present in the lake, although the absence of a species from the entrapped catch does not necessarily mean that it is also absent from the lake. Assuming that changes in the personnel making the entrapment observations have had no significant effect on the validity of the data, the value of the Haweswater entrapment data lies in its documentation of trends in species abundance since the early 1970s. In this context, it is alarming that most of the entrapped species have been taken in smaller numbers over the last decade, suggesting that they are present in smaller numbers in the lake itself. For the eel, which has not been entrapped since 1990, this may in part reflect

reduced recruitment to the lake because it is difficult to accept that the construction of the dam will have had no adverse influence on the arrival of elvers. It is also pertinent to note that while gill nets are extremely inefficient at catching eels, this species does leave a distinctive slime mark on such nets but such marks were never observed at Haweswater during the extensive netting of Winfield *et al.* (1993a) carried out in the early 1990s. Numbers of perch and trout have fluctuated rather than declined steadily, enjoying a resurgence in the mid to late 1980s before falling to very low levels during the present study. Consequently, little biological information is available for these species (see Chapter 6). As shown for schelly and charr, and which also holds for the other fish species, the long-term trend in 'entrapment-per-unit-effort' is also downwards which further suggests that real declines are occurring in the fish populations of Haweswater.

Part of the differences between the observed species-specific patterns of entrapment originates from differences in spatial distributions within the lake, which leads to a bias towards the deepwater schelly and charr over the more inshore perch and eel when the present entrapment data are compared with the deepwater survey data presented in Winfield *et al.* (1993a). Moreover, the observed monthly patterns of entrapment of eel and perch, which both increase during the autumn, probably reflect the seaward and deepwater migrations, respectively, which these species are known to undertake (e.g. see Winfield *et al.*, 1993c). The trough of charr entrapment observed during the summer may reflect a movement of this species up into the open water to forage on zooplankton at this time of year, as suggested by its diet composition reported in Winfield *et al.* (1993a), while the concentration of schelly entrapment into January, February and March is clearly linked with a spawning migration, as has already been discussed in Chapter 2.

The concentration of schelly entrapment into the first quarter of the year means that future monitoring of the entrapment of this species could be maintained at extremely low cost in terms of effort, although if at all possible it is recommended that records continue to be kept and specimens collected (see Chapter 6) all year round. The latter activity will gradually build a unique database through which aspects of the interactions within the fish community could be addressed. For the moment, it is relevant to note that there is a positive relationship between the entrapments of schelly and charr within each year, which would not be expected if their numbers were determined on a continuous and long-term basis by interspecific competition as has been implied elsewhere (e.g. Pomeroy, 1991). In contrast, in Haweswater it appears that the abundance of schelly and charr is primarily affected by some unknown and independent aspect of the environment.

Finally, some comment must be made on the undoubted but inexplicable shift in the daily pattern of schelly entrapment since the mid 1960s when data were first collected by Bagenal (1970). As with most long-term datasets, the addition of further data will be invaluable and for this reason alone it would be worthwhile continuing data collection given its high ease and low cost. No relationship could be found with water temperature, nor with aspects of the lake level not presented in this report. In the absence of long-term changes in day length, which clearly have not occurred over the last approximately 30 years, it is possible that changes in the mean individual sizes of spawning schelly have been involved in the production of the observed shifts. However, in the absence of long-term biological data, such as that presented for the recent short-term in Chapter 6, this hypothesis cannot be investigated further.

CHAPTER 6 BIOLOGY OF ENTRAPPED SCHELLY AND CHARR

6.1 Introduction

As recorded in Chapter 2, the present project was largely unsuccessful in the direct scientific sampling of the schelly population of Haweswater. This problem, which was also shared by the earlier fieldwork of Winfield *et al.* (1993a), was due in part to logistical difficulties of sampling fish on Haweswater, but also to the present low abundance of schelly in this lake.

Consequently, it was decided in the early stages of the present project to exploit entrapped schelly as a source of population data, even though such fish undoubtedly represent a biased sample of the total population. Furthermore, the same biases, whatever they may be, will have also acted on the fish examined by Bagenal (1970) which was based exclusively on schelly entrapped during the mid 1960s. Thus, by carrying out some analyses designed after those of Bagenal (1970), the possibility also arose of making a direct comparison of the population biology of schelly entrapped during the 1990s and 1960s.

The aim of the present part of the project was thus simply to describe the population biology of schelly entrapped during the period of the present study, i.e. 1991 to 1994, and then to compare it with that of fish entrapped during the mid 1960s by reference to Bagenal (1970). More limited information on entrapped charr is also presented, as is an analysis of the length frequency distributions of these two species designed to aid the interpretation of the echo-sounding data of Chapter 2.

6.2 Methods

With the co-operation of NWW, a domestic freezer was installed at the Garnett Bridge filtration plant on 1 November 1991 in anticipation of an expected entrapment of schelly and other fish species during the following months. Upon each near-daily inspection of the filters, all fish not in a state of decay (which was rare given the prevailing low water temperatures) were placed in a dated plastic bag and frozen to await collection by IFE staff. The start of the collection of entrapped fish was delayed to early 1992 by engineering works at Garnett Bridge which resulted in the plant being taken off-line for a considerable period in late 1991 and the early days of 1992, but this was the only major disruption which occurred between the beginning of collection and 31 March 1994 when processing was stopped for the purposes of the present project (although collection was still maintained by NWW at the time of writing).

Entrapped fish were subsequently returned to the laboratory where they were identified, measured, weighed, and, in the case of schelly and charr, sexed, and reproductive state assessed. Opercular bones were also removed from all schelly for subsequent ageing. In addition, and with the investment of negligible further effort, otoliths and scales were removed from all charr to allow future ageing although this has not been possible within the present project.

6.3 Results

During the study period, 154 schelly were collected between 21 February 1992 and 4 February 1994, while 472 charr were taken between 1 November 1991 and 28 March 1994. Two perch, one trout and one stickleback were also collected but are not considered further here.

The length frequency distributions of all entrapped schelly and charr are shown in Fig. 6.1 and show relatively little overlap, with the mean length of schelly (274 mm, Standard Error 2 mm) being significantly greater than that of charr (193 mm, SE 2 mm) (t test assuming unequal variances, $t = 29.978$, $df = 437$, $p < 0.001$). Nevertheless, the mean schelly length was itself obviously smaller than that of schelly entrapped during the 1960s and reported by Bagenal (1970) as shown in Fig. 6.2. This figure also shows that schelly less than 100 mm in length were entrapped during the 1960s, but in the 1990s the only fish as small as this were charr (see again Fig. 6.1). Finally with respect to length frequency distributions, Fig. 6.3 shows the entrapped schelly and charr of the present study assigned to size classes matching the small (4 to 10 cm), medium (10 to 25 cm) and large (greater than 25 cm) fish categories of the echo-sounding analysis of Chapter 2. If entrapped individuals constitute a fair reflection of the individual size distributions of the schelly and charr populations of Haweswater, medium fish are almost exclusively charr while large fish are almost exclusively schelly.

The age distributions of schelly entrapped during January, February and March of 1992, 1993 and 1994 were very restricted and dominated by fish of ages 3, 4 and 5 (Fig. 6.4), which themselves largely originated from 1989 and 1990. This contrasts markedly with a more equitable age structure reported for schelly entrapped during the 1960s by Bagenal (1970) as is shown in Fig. 6.5. Growth has also changed over this period, with schelly now growing more slowly and to a smaller ultimate size (Fig. 6.6, fitted von Bertalanffy growth parameters L_{∞} , K and t_0 of 339 mm, 0.245 and -2.921, respectively, for the present study compared with 410 mm, 0.740 and -0.375 reported for the 1960s).

For all schelly pooled, weight (W) and length (L) were related such that

$$\ln W = -9.264 + 2.652 \ln L$$

where W is body weight (in g) and L is length (in mm) ($r = 0.923$, $p < 0.001$).

A total of 48 ripe female schelly was collected during the study period, with all but two of them being entrapped during the months of January, February and March.

6.4 Discussion

The implications of the findings of this chapter for the interpretation of the echo-sounding surveys of Chapter 2, i.e. that adult schelly and charr could be reliably distinguished on the basis of body size and hence target strength, were discussed in that chapter and so will not be considered further here.

Of more biological interest is the observation that the entrapped schelly of the 1990s were of a smaller mean length and lower size range than were those collected during the 1960s by Bagenal (1970). Furthermore, while schelly less than 100 mm in length were entrapped during the earlier period, the length of the smallest individual taken during the present project was 225 mm. Moreover, this is likely to have reflected a real change in the schelly population rather than being an artifact of changing entrapment procedures (e.g. mesh size at the filters) because charr as small as 61 mm were entrapped during the present project. It is clear from a comparison of the age frequency distributions of schelly entrapped during these two periods that the smaller mean size

of individuals in the 1990s arises from the fact that they are also on average considerably younger. Furthermore, the reason that the current schelly population is composed of younger individuals appears to be poor recruitment in the late 1980s. As noted in Chapter 4, a high priority of future research should be to obtain the presently unavailable lake level data for the mid to late 1980s and examine them to determine if they contain any distinctive features which may be responsible for the failed year classes of that period. At present, the schelly population of Haweswater is dominated by just two year classes which can be observed passing along the entrapped population. It is also notable that the numbers of 8 year old fish which formed a secondary peak in the age frequency distributions of the 1992 sampling of Winfield *et al.* (1993a) and in the 1992 entrapment sample, were absent from the age frequency distribution of the entrapped fish of 1994. There is no sign yet of the arrival of another good year-class of schelly in Haweswater.

Finally, a comparison of growth rates and individual conditions may be made between the 1960s and the present, although it must be borne in mind that the pooling of data in Bagenal (1970) means that only relatively crude growth curves may be compared. Nevertheless, it is clear that growth in the 1990s is much poorer than that recorded for fish from the 1960s. In contrast, the length-weight analysis of the present study shows that individual schelly of a given length are now much heavier than they were in the 1960s. This good current condition of individuals was also expressed in terms of a relatively high fecundity when compared with those of other *Coregonus lavaretus* populations in England and Wales (Winfield *et al.*, 1993a), but on first inspection it appears to contradict the observation that schelly are now growing more slowly. One possible explanation for this apparent conflict is that under current environmental conditions the schelly of Haweswater are growing very slowly as juveniles, which leads to either small post-juvenile sizes or even death. Such small lengths achieved as young fish will tend to follow through the rest

of each individual's life, even if feeding conditions improve as it becomes an adult and begins to feed under different environmental conditions. Under such circumstances, the adult schelly would show a good individual condition and high fecundity, but may still be relatively small for its age and thus the population as a whole would exhibit a relatively shallow growth curve. Of course, much of this explanation is speculative and it is put forward only as a suggestion. One way in which it could be further examined would be by the extensive back-calculation of schelly lengths-at-ages from measurements of otoliths already collected from entrapped fish. A similar analysis of reconstructed charr growth would also be extremely worthwhile and would make a valuable contribution to our understanding of the interactions between the major fish populations of Haweswater and their environment.

CHAPTER 7 GENERAL DISCUSSION

The findings of the various components of this project have already been discussed within their specific chapters, with cross-referencing where appropriate. The aim of the present chapter is not to rework this ground, but to emphasise some of its major findings and to indicate areas of deserving or essential future action. Such activities include both management options and research in the context of the dual role of Haweswater as a habitat to a nationally-rare fish species and as an important reservoir.

The conservation importance of the Haweswater schelly population was stressed at the beginning of this report. Furthermore, during the project's lifetime this importance has increased given the new threats posed to other *Coregonus lavaretus* populations in the U.K. by very recent species introductions (see Winfield, 1992). Present legislation and practices relevant to Haweswater, together with the absence of pike (*Esox lucius*) reduce the likelihood of such unwanted species introductions to this lake, although NWW is still encouraged to avoid any steps which may foster live-baiting which brings with it an increased chance of species introductions. It is also notable that Haweswater remains as one of only two U.K. water bodies to contain both *Coregonus lavaretus* and charr, the other being Loch Eck in Scotland (Maitland & Lyle, 1991).

Nevertheless, the major finding of the present study is that the Haweswater schelly population is in a very poor condition, displaying a very low abundance and an inconsistent recruitment over recent years. A major source of evidence for this conclusion was the entrapment records and catches made available by NWW, a point which will be returned to below. This observation both confirms and amplifies the conclusion drawn from a more extensive study of *Coregonus*

populations in the U.K. (Winfield *et al.*, 1993a). Indeed, the present scarcity of schelly in Haweswater is such that the collection of specimens for laboratory examination proved to be impossible, despite the deployment of sampling efforts far greater than those used successfully elsewhere. As an inevitable consequence, this also precluded the examination of potential interspecific interactions between the schelly and other members of the fish community, particularly the charr. Indeed, one interpretation of the long-term entrapment data is that the population trends of these two species are not determined by their biological interactions, but by some common feature of the environment.

Given that entrapment itself is of insufficient magnitude to constitute a significant source of schelly mortality, together with the observations that neither eutrophication (Elliott *et al.*, 1990) nor species introductions (Winfield *et al.*, 1993a) have occurred in Haweswater in recent years, the known fluctuations in lake level are left as a potential agent of the observed schelly decline. Furthermore, changes in the level regimes which have occurred over the last few decades are likely to have had significant adverse effects on schelly recruitment as considered at length earlier in this report.

Several avenues of future management practices and research may be offered to address this alarming situation. From the point of view of the conservation of the schelly population, the optimum management of Haweswater would undoubtedly be to discontinue its use as a reservoir and thus stop the unnatural fluctuations in water level. However, this is clearly not a realistic option and is not put forward as a practical proposition. A decrease in the level fluctuations during the later summer would be of help to the recruitment of young schelly, although again it is appreciated that this would present considerable problems in the operation of the lake as a

reservoir. However, more sympathetic management of water levels during the crucial incubation period of January, February and March is a more attainable practice and is strongly recommended as detailed earlier in this report.

Some comment must be made on the option of restocking Haweswater with schelly, although this is clearly a policy of last resort and will in any case be ultimately a fruitless exercise if the environment of the lake remains hostile to the survival of a schelly population. Captive breeding of schelly is certainly possible (see Winfield *et al.*, 1993a), although it brings with it concerns over unintended and unknown effects on the genetic integrity of the target population. This is particularly relevant to issues of schelly conservation given the unique and pristine nature of the U.K. populations when compared with their counterparts on the European mainland, where stocking and transfers are commonplace. Moreover, the Haweswater population is itself particularly important in this context because studies of D.N.A. variation now in progress have indicated that it is the most diverse of any of the U.K. populations so far studied (S. E. Hartley, University of Stirling, *personal communication*). In the context of population variability, it is also worth noting that the two small lakes of Blea Water and Small Water which lie within the Haweswater catchment have never been surveyed to determine if they hold schelly populations. While such unrecorded presence may seem unlikely, confirmations of the existence of schelly in Brotherswater and Red Tarn in the Ullswater catchment have only been made in recent years (see Winfield *et al.*, 1993a).

Three major areas of future research may also be identified, each of varying complexity and cost in terms of required resources. Firstly, it would be extremely rewarding to complete the analysis of changes in the lake levels of Haweswater when data from the late 1980s become available.

When coupled with the present data from entrapped fish, this would allow study of the level regime in years which are now known to have resulted in poor schelly recruitment. Secondly, considerably more biological insight into the present status of schelly and charr could be gained by the detailed examination of opercular bones and otoliths already collected from entrapped fish during the present project. With appropriate techniques, such examinations would allow the reconstruction of the growth of adults and young of both species over the last decade. Thirdly, and above all, it is strongly recommended that the monitoring and collection of entrapped fish is continued. Although such data are not ideal, they form an invaluable documentation of the population biology of schelly in Haweswater. The cost of such data collection and documentation is negligible, even though actual analysis may require considerably more resources.

This investigation has shown that the conservation of the schelly in Haweswater gives considerable cause for concern. However, in contrast to the situation with other European populations, the cause is not yet lost and with appropriate future action, one can remain optimistic about the survival of this valuable population.

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Transects	Date	Sunset	Start	Finish
Standard & Extensive	19/5/92	20.48	14.00	17.12
Standard & Tower	29/10/92	16.53	16.15	17.45
Standard & Tower	16/11/92	16.12	14.30	17.00
Standard & Tower	8/12/92	15.53	14.30	17.00
Standard	27/1/93	15.57	15.15	
Standard & Tower	10/2/93	17.12	16.30	18.00
Standard & Tower	26/3/93	18.26	17.00	19.30
Standard & Tower	26/4/93	20.12	18.30	21.30
Standard & Tower	24/5/93	20.56	21.30	23.00
Standard	22/6/93	21.21	21.00	05.30 (23/6/93)
Standard	28/7/93	20.50	20.30	23.00
Standard	25/8/93	19.56	20.15	21.15
Standard	27/9/93	18.52	18.30	20.30

Table 2.1. Dates of echo sounding with the approximate times of sunset and the start and finish of transects. Note that on 27/1/93 only one transect was made due to dangerous weather conditions.

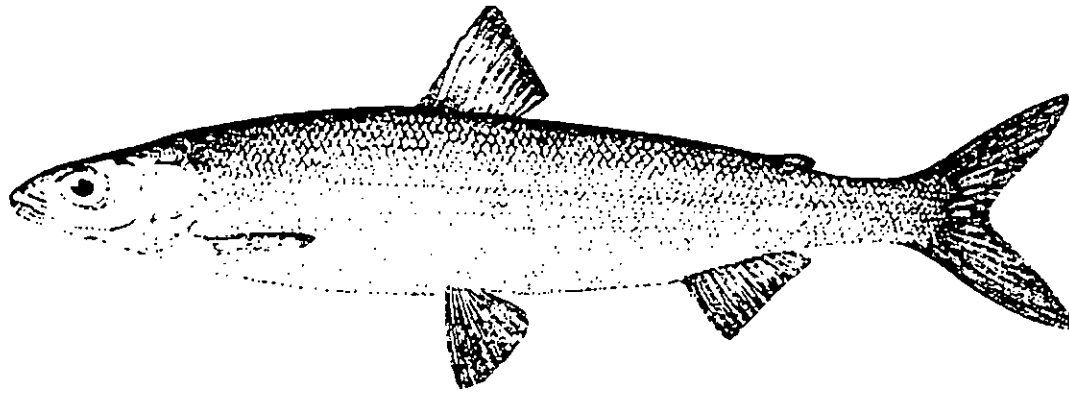


Fig. 1.1 An adult schelly, *Coregonus lavaretus*, measuring approximately 25 cm in length. Redrawn with permission from Maitland (1972).

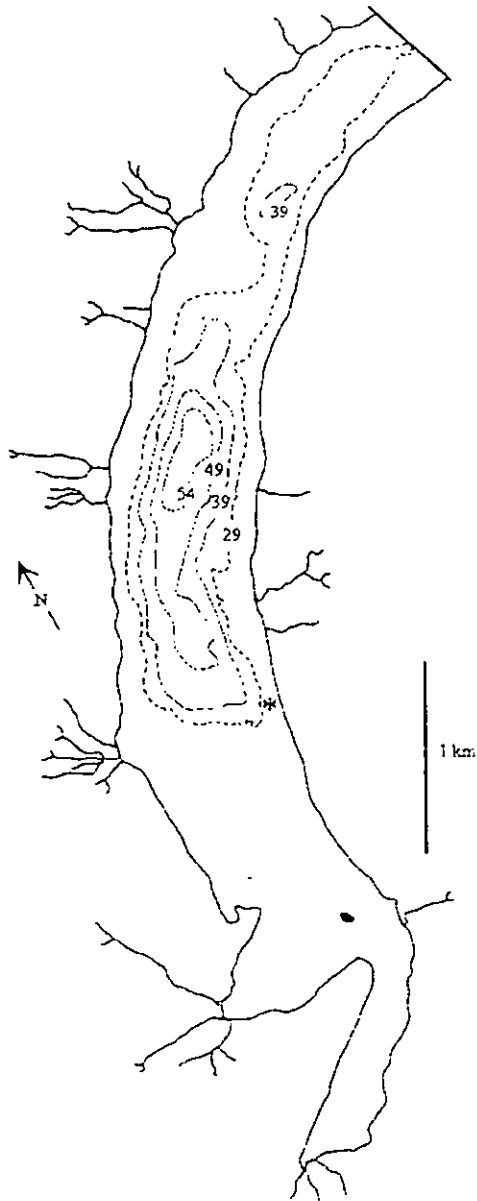


Fig. 1.2 Haweswater showing depth contours (in metres) and the approximate position of the abstraction point (asterisk). The 29 m depth contour follows the outline of the original lake prior to the construction of the dam at the northern end, which was completed in 1941. Redrawn with permission from Ramsbottom (1976).

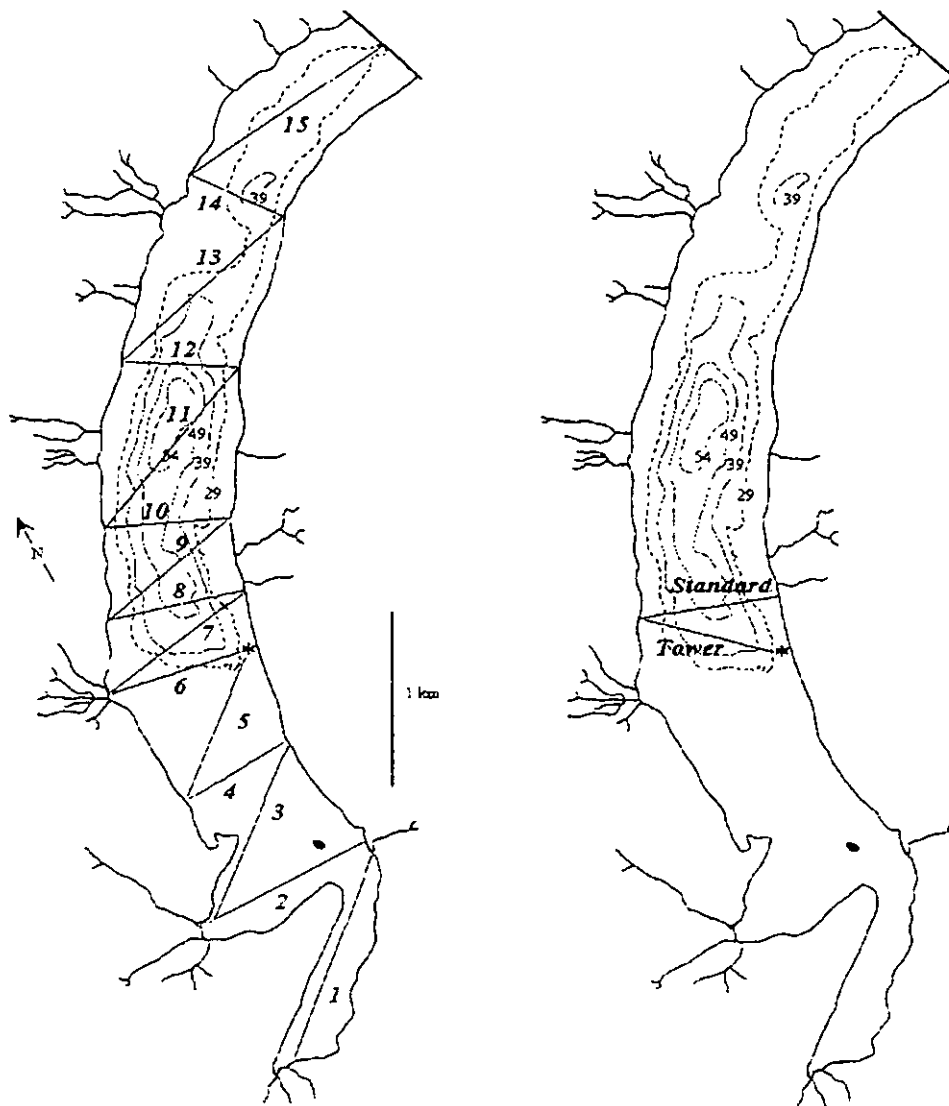


Fig. 2.1 Transects used during the extensive (left) and intensive (right) echo sounding on Haweswater. Transect numbers (left) or names (right) are given in bold italics. Depth contours are given in metres while the approximate position of the abstraction point is shown by an asterisk. Redrawn with permission from Ramsbottom (1976).

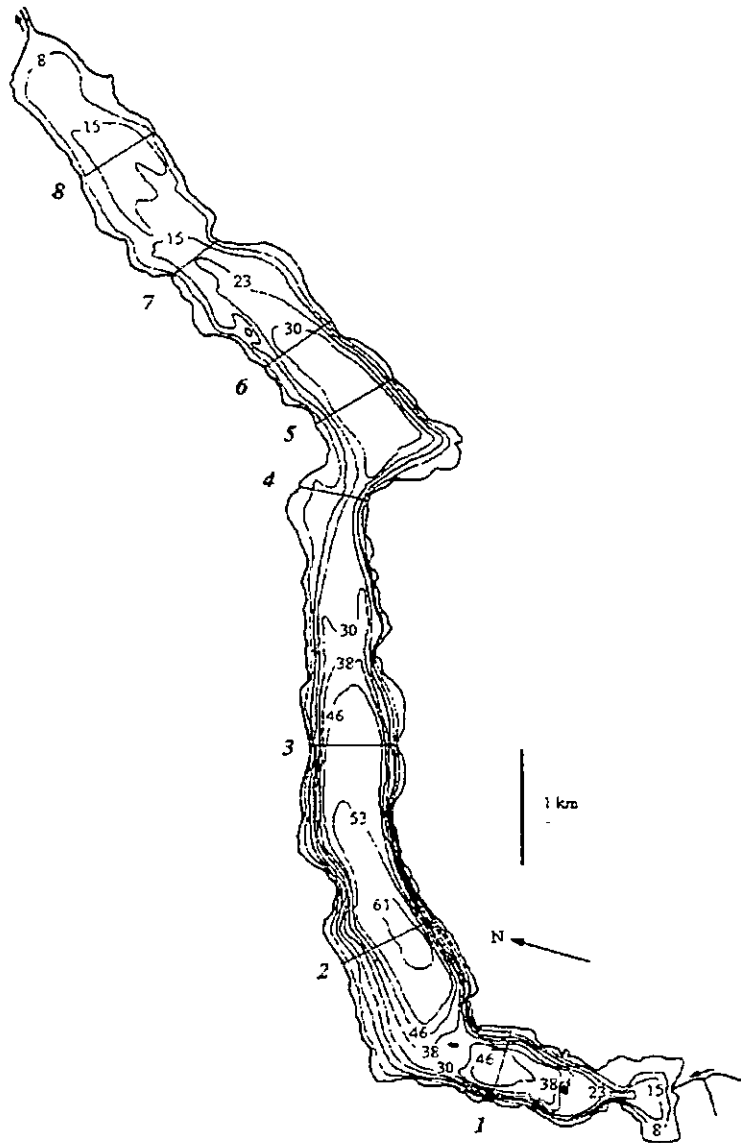


Fig. 2.2 Transects used during the extensive echo sounding on Ullswater. Transect numbers are given in bold italics and contours are given in metres. For transect 5, surveys were also repeated at intervals over dusk. Redrawn with permission from Ramsbottom (1976).

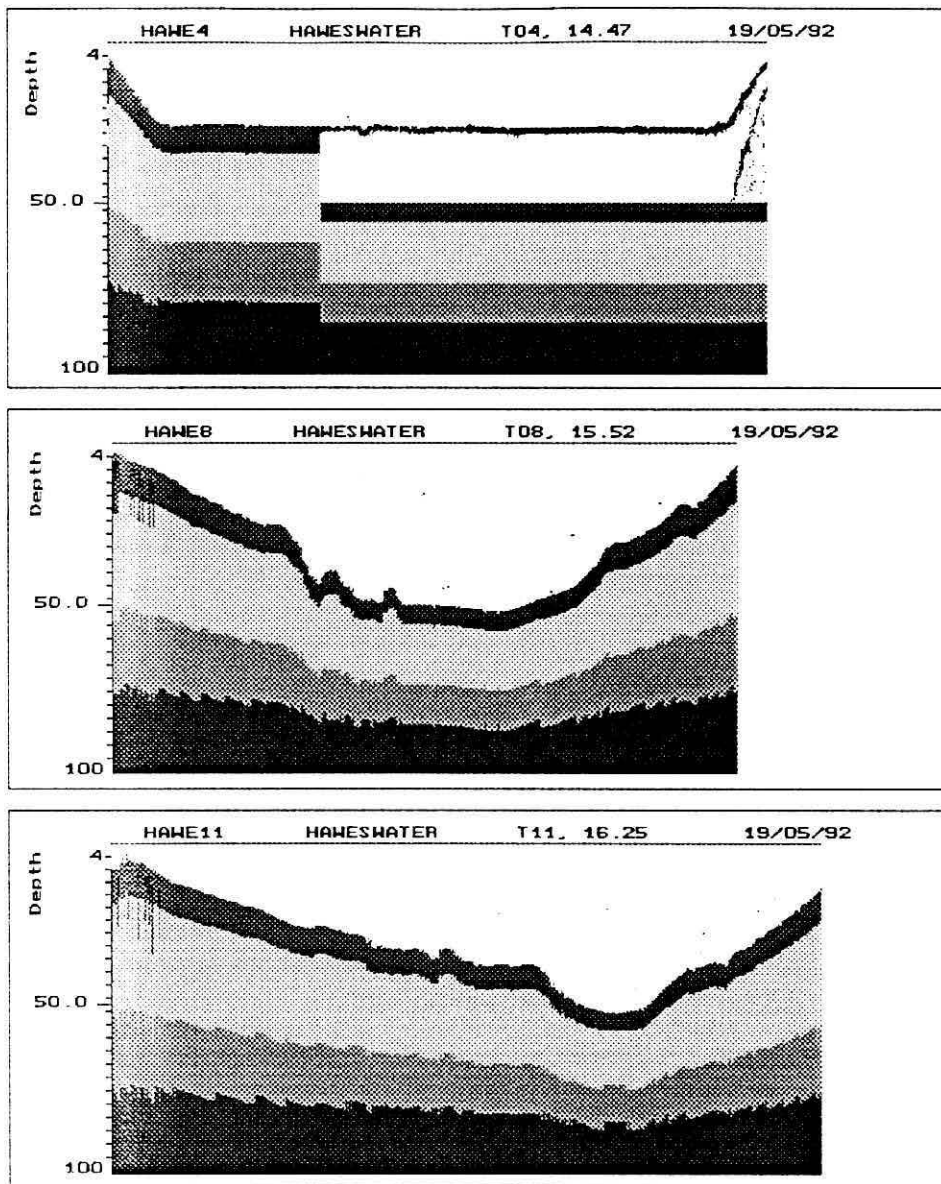


Fig. 2.3 Echograms of three transects made on Haweswater during May 1992. The upper echogram is from the 'new' southern part of the lake (Transect 4 of Fig. 2.1), the middle echogram is from the standard transect considered in depth elsewhere in this report (Transect 8 of Fig. 2.1), and the lower echogram is from a transect passing over the deepest part of the 'old' lake (Transect 11 of Fig. 2.1). Note that the analytical software experienced difficulty in detecting the bottom of the upper transect.

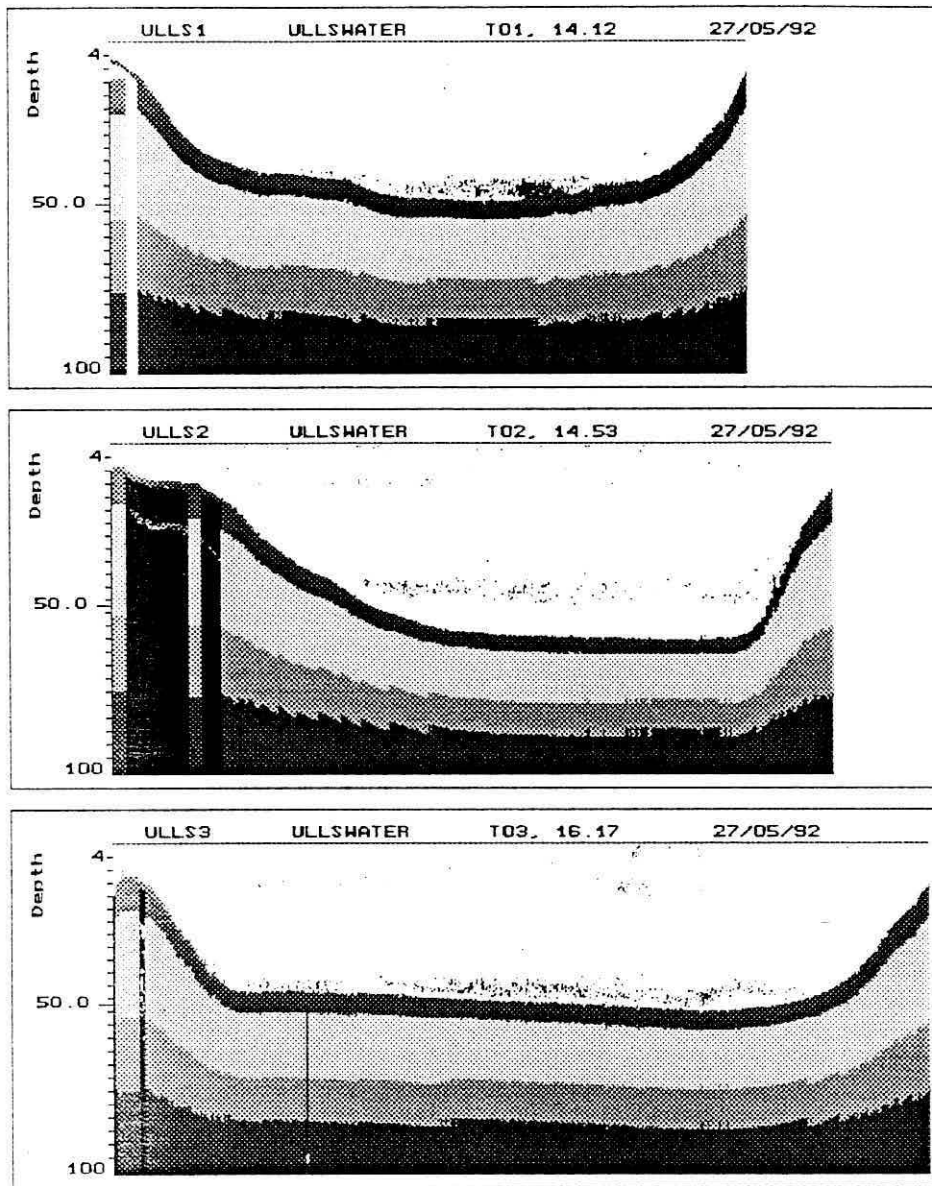


Fig. 2.4 Echograms of three transects made on Ullswater during May 1992. The upper echogram is from Transect 1 of Fig. 2.2, the middle echogram is from Transect 2, and the lower echogram is from Transect 3.

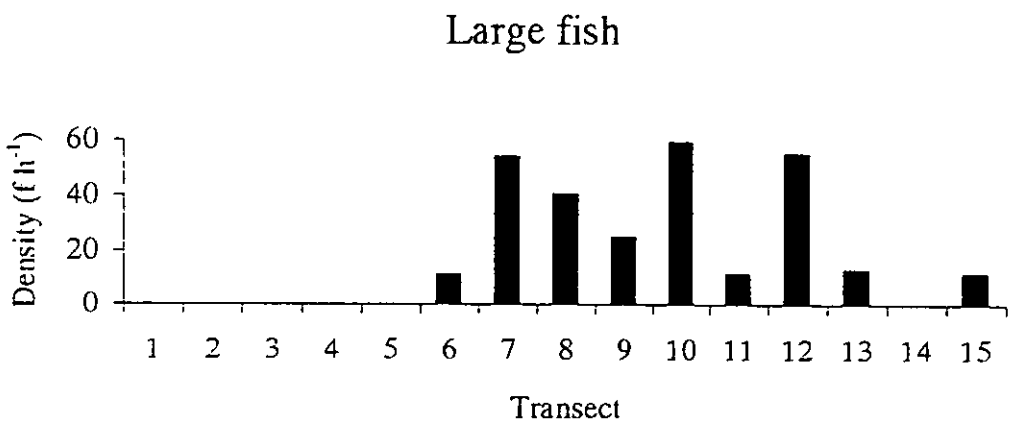
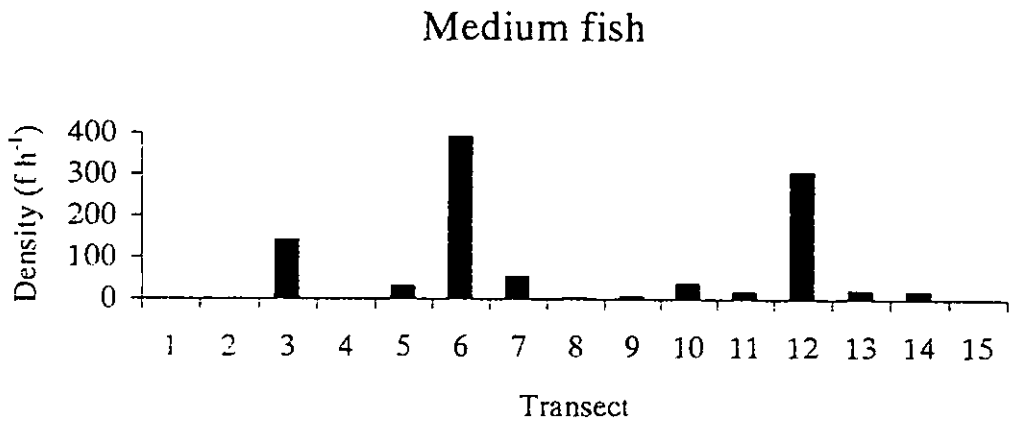
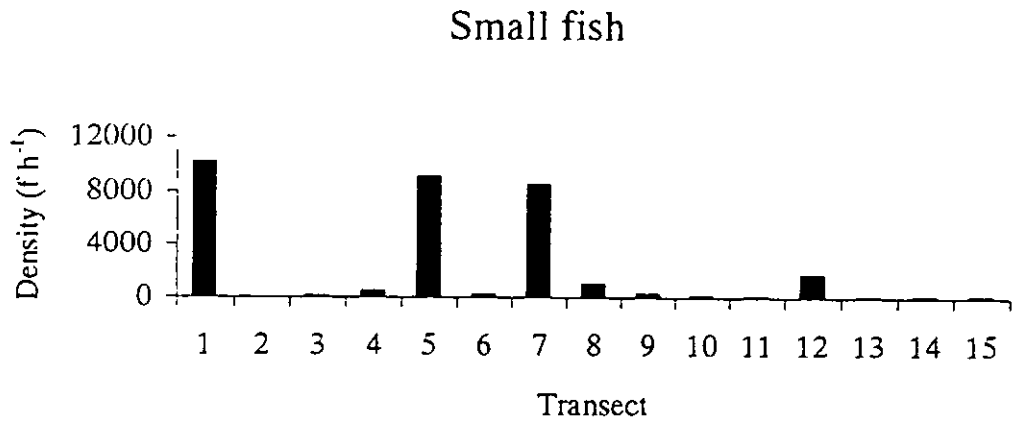


Fig. 2.5 The densities of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across extensive transects around Haweswater during May 1992.

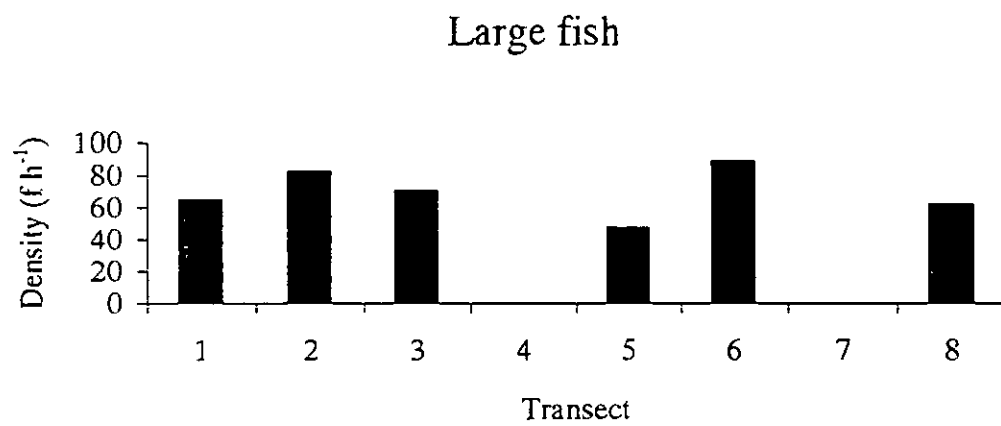
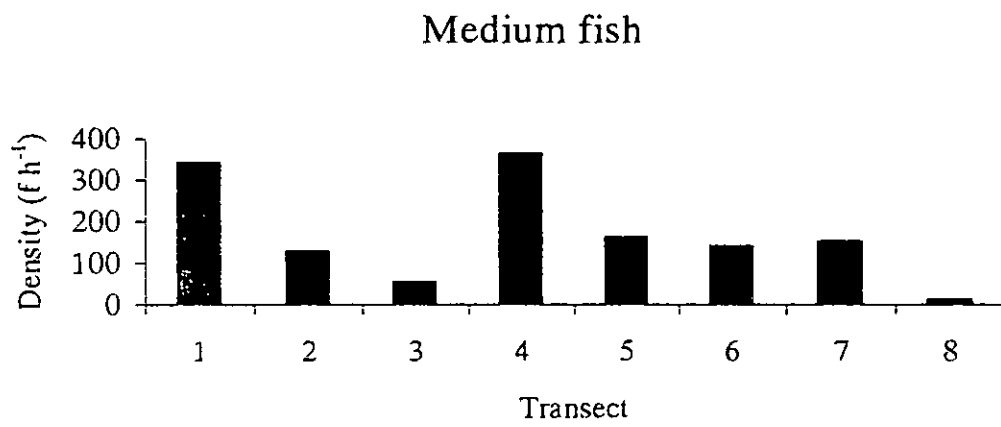
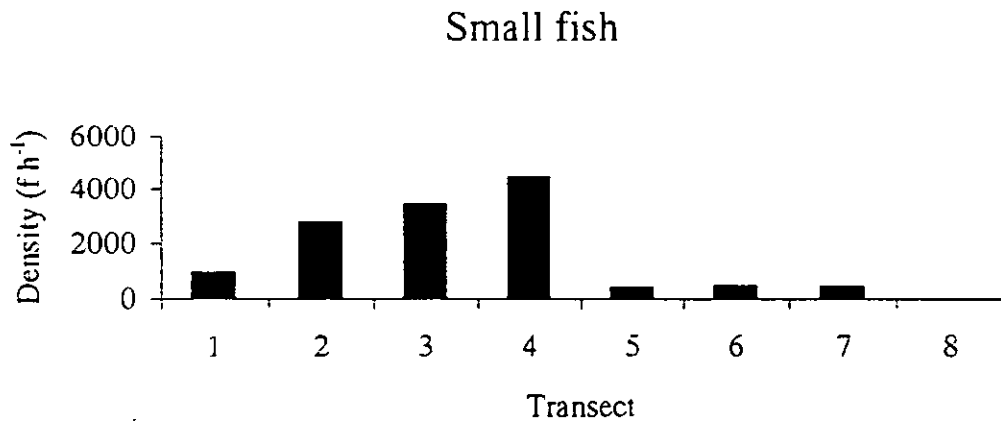


Fig. 2.6 The densities of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across extensive transects around Ullswater during May and June 1992.

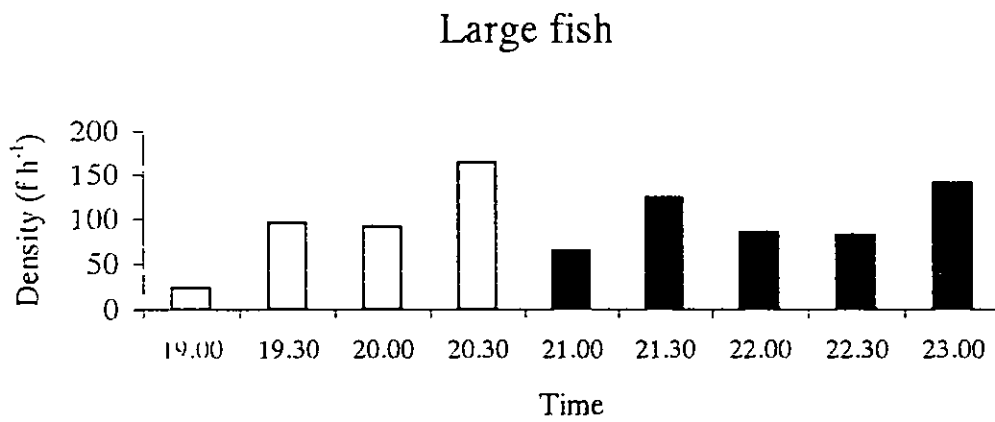
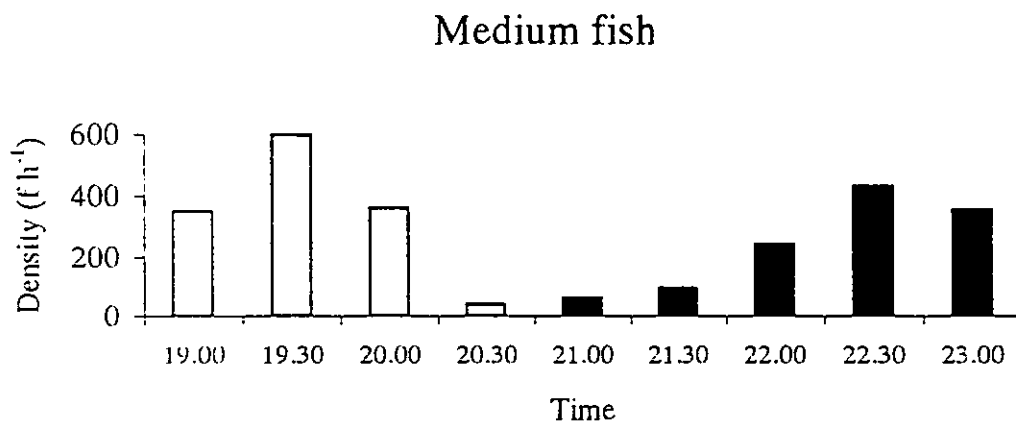
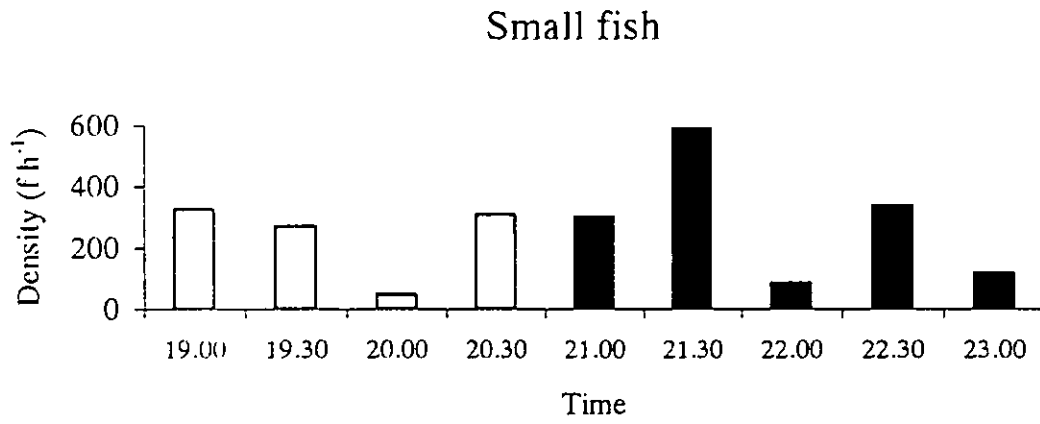


Fig. 2.7 Changes over dusk in the densities of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across a transect in Ullswater during June 1992. Open and closed bars identify transects made before and after sunset, respectively.

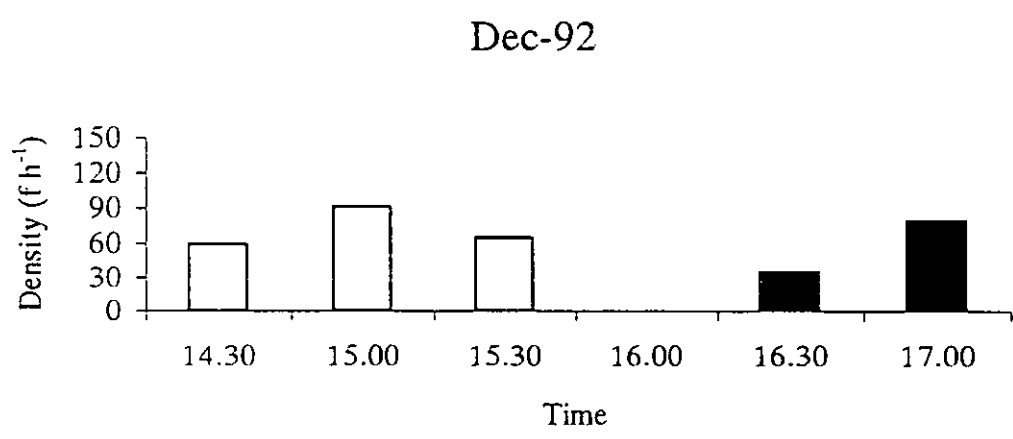
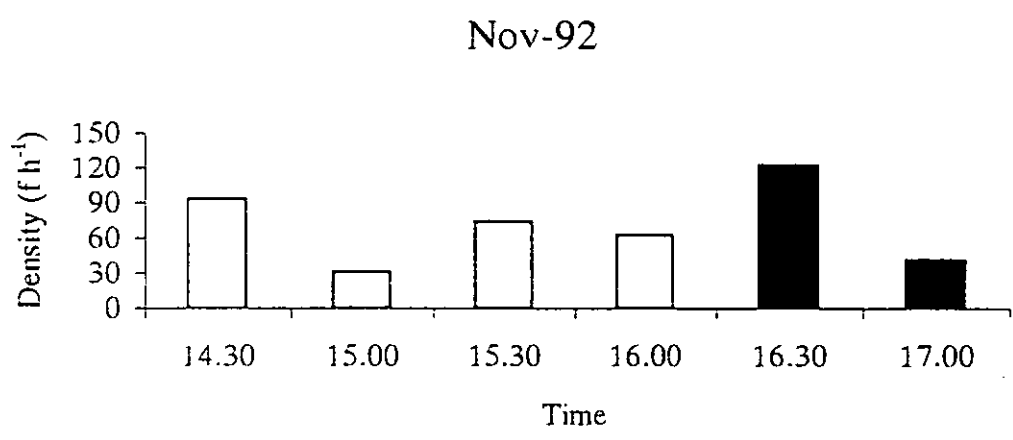
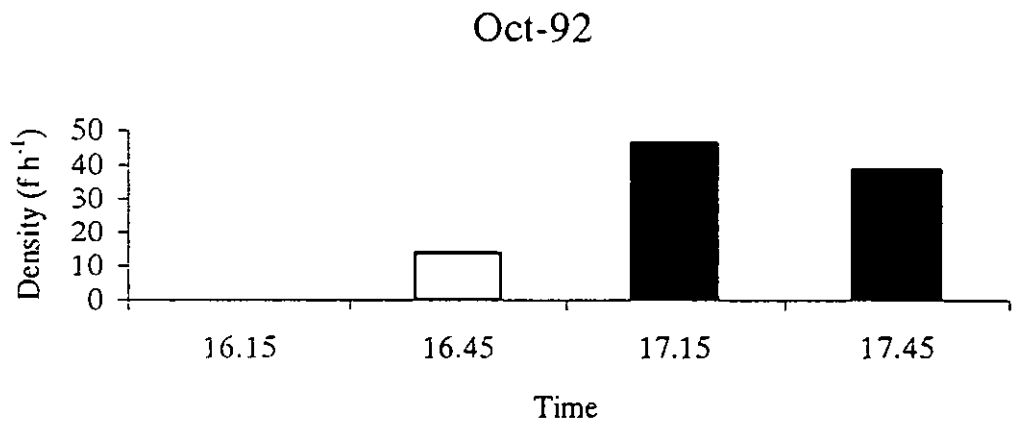


Fig. 2.8 Changes over dusk in the density of large (> 25 cm) fish echoes across the standard transect in Haweswater during October, November and December 1992. Open and closed bars identify transects made before and after sunset, respectively.

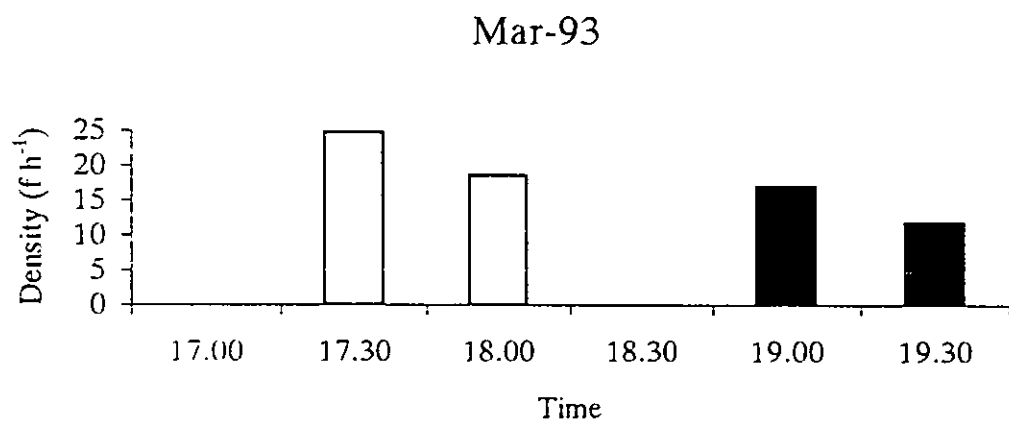
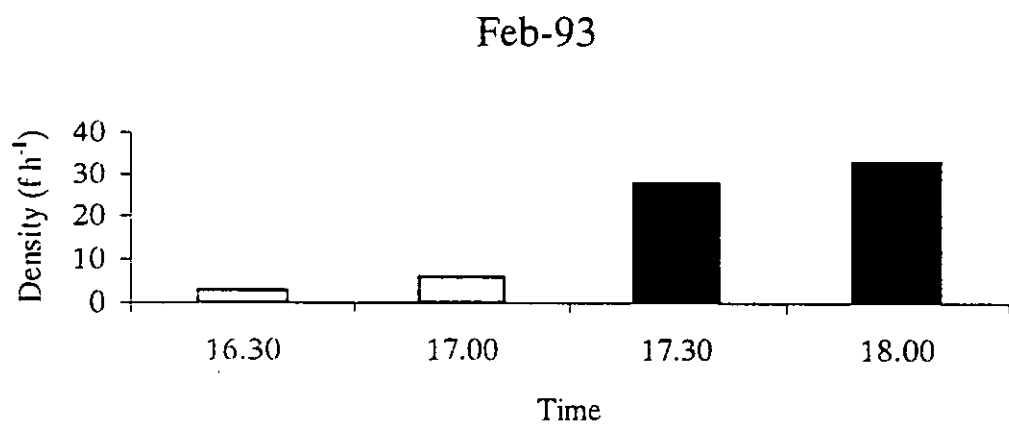
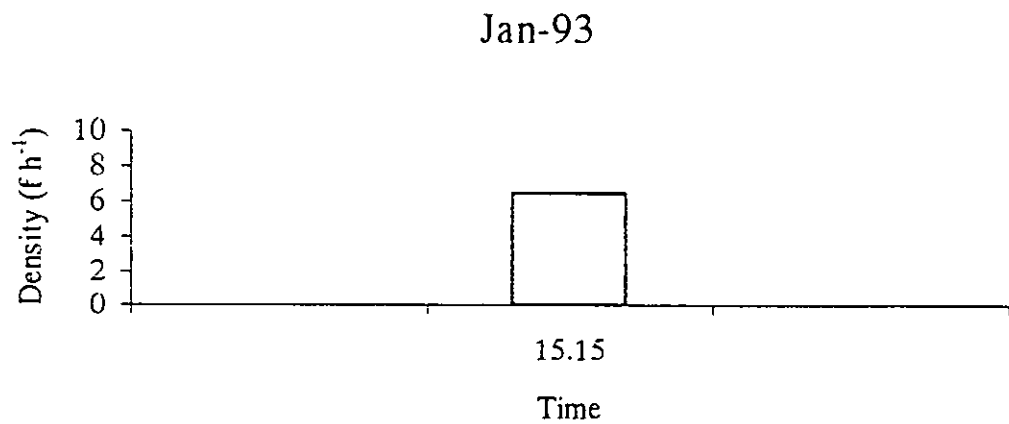


Fig. 2.9 Changes over dusk in the density of large (> 25 cm) fish echoes across the standard transect in Haweswater during January, February and March 1993. Open and closed bars identify transects made before and after sunset, respectively. During January, only one transect was possible due to dangerous weather conditions.

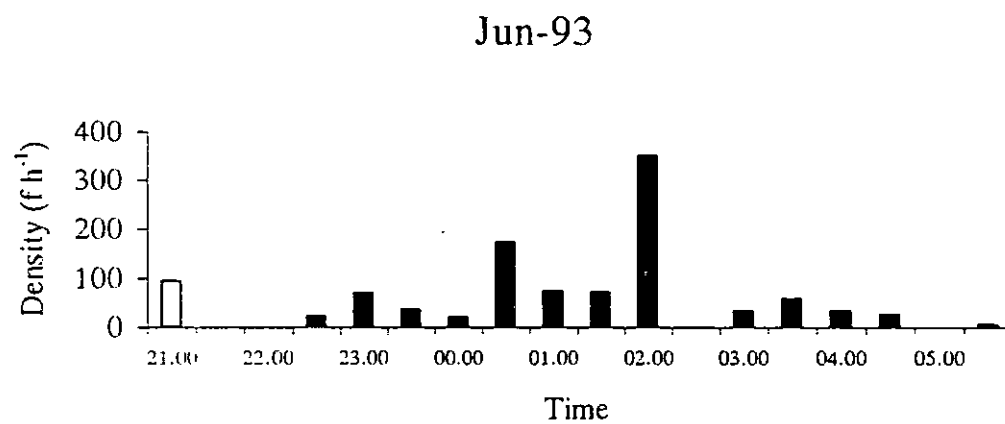
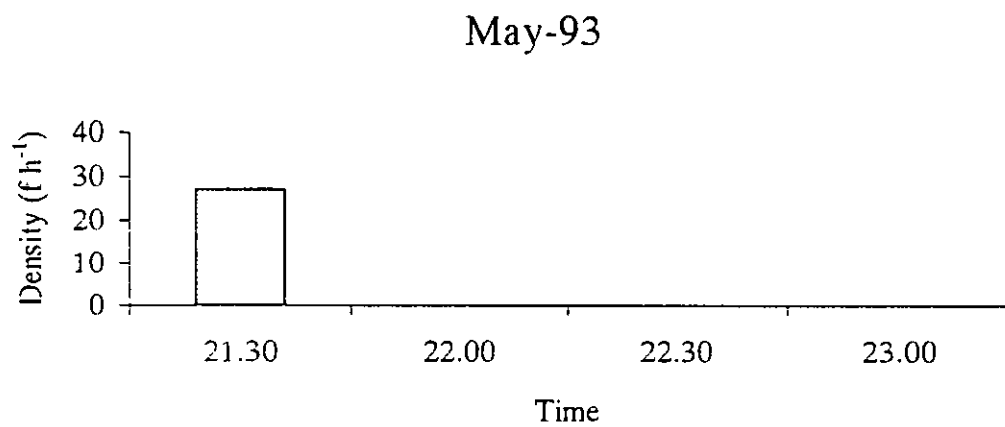
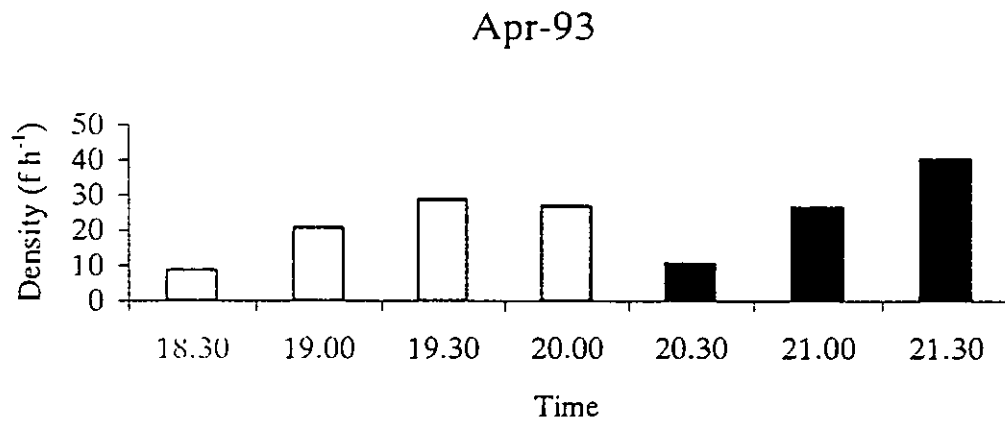


Fig. 2.10 Changes over dusk in the density of large (> 25 cm) fish echoes across the standard transect in Haweswater during April, May and June 1993. Open and closed bars identify transects made before and after sunset, respectively. During June, transects were repeated through the night, with open bars indicating transects made before sunset and after the following sunrise.

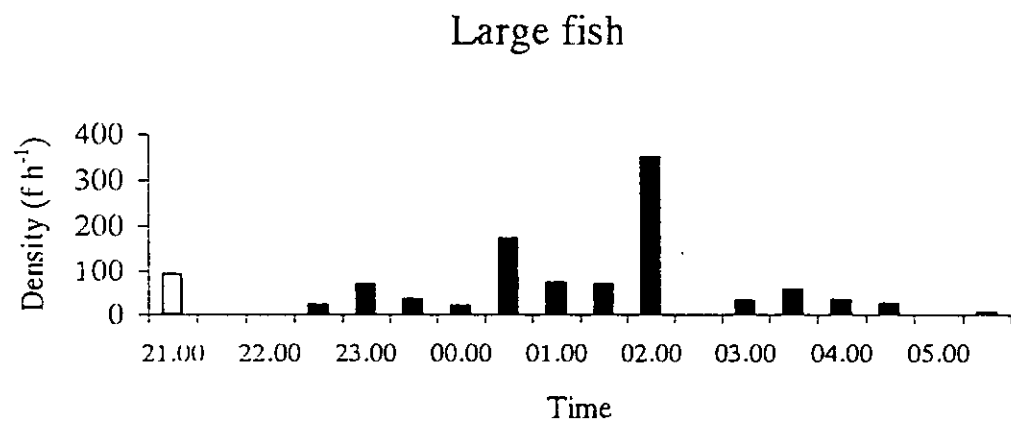
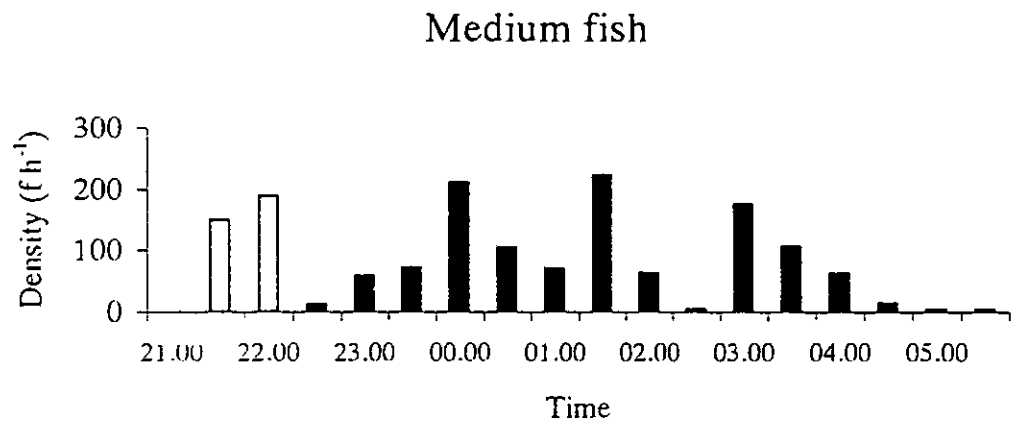
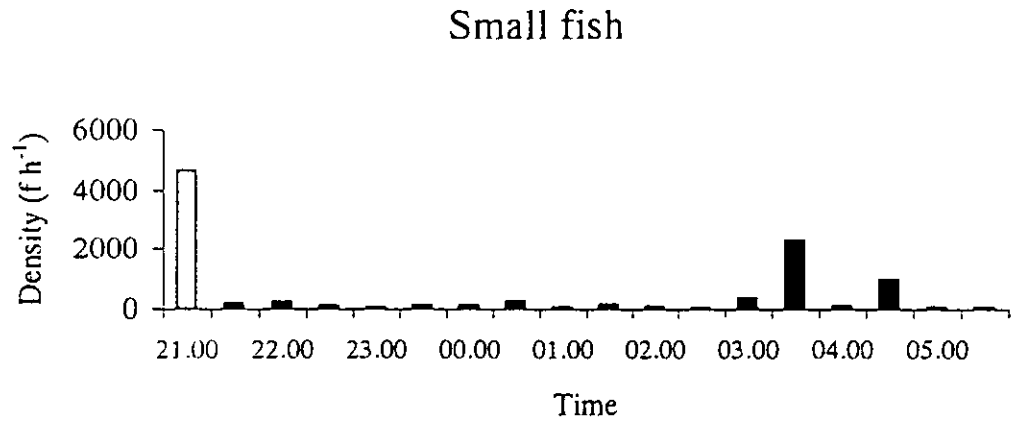


Fig. 2.11 Changes over dusk, night and dawn in the densities of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across the standard transect in Haweswater during June 1993. Open bars indicate transects made before sunset or after sunrise of the following day, while closed bars identify transects made between sunset and sunrise.

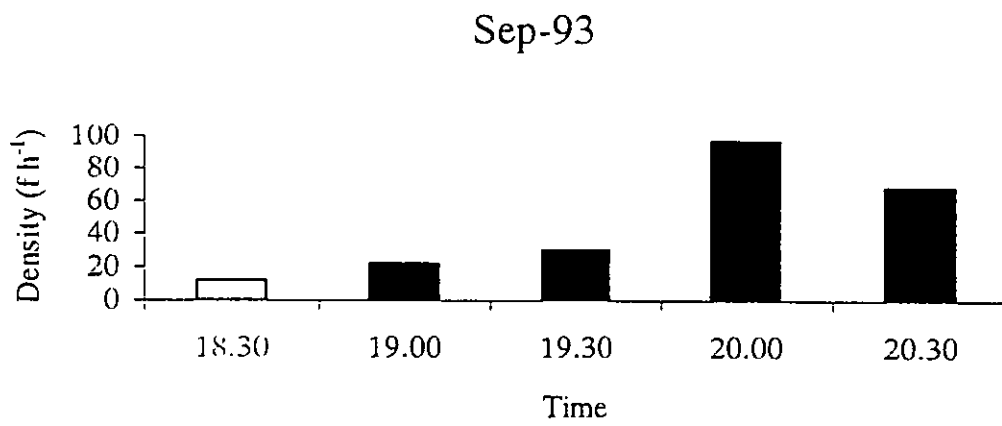
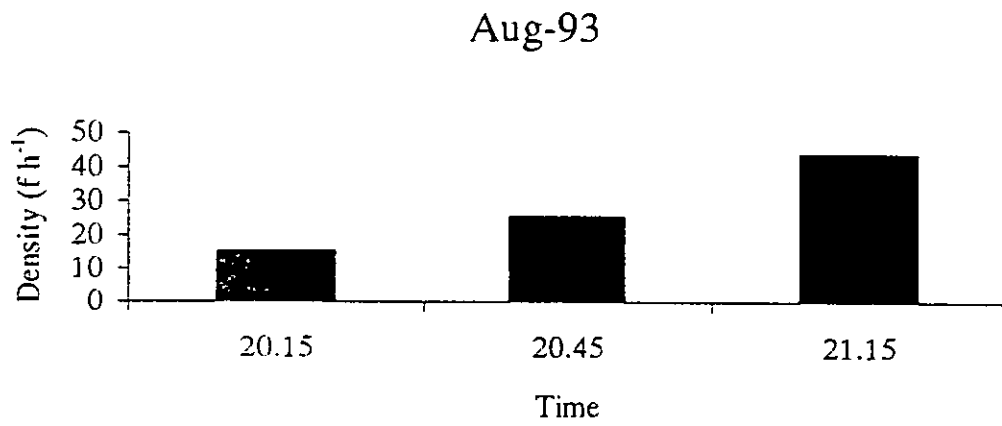
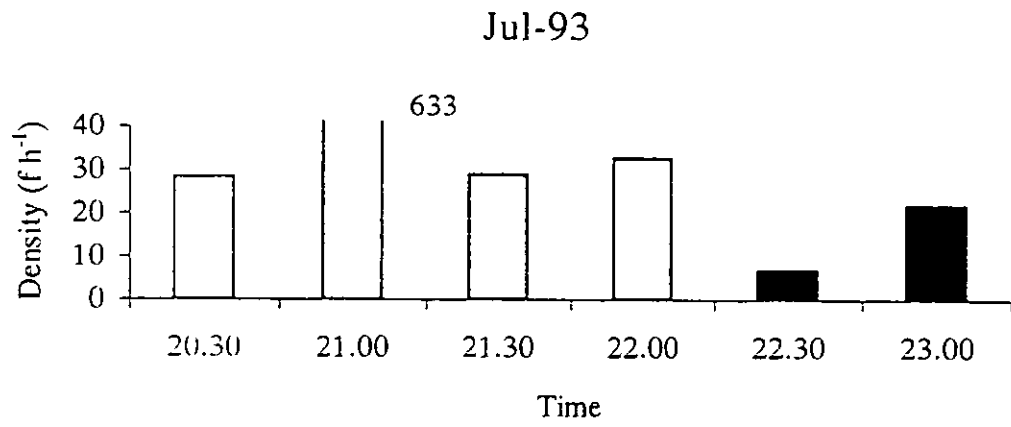


Fig. 2.12 Changes over dusk in the density of large (> 25 cm) fish echoes across the standard transect in Haweswater during July, August and September 1993. Open and closed bars identify transects made before and after sunset, respectively.

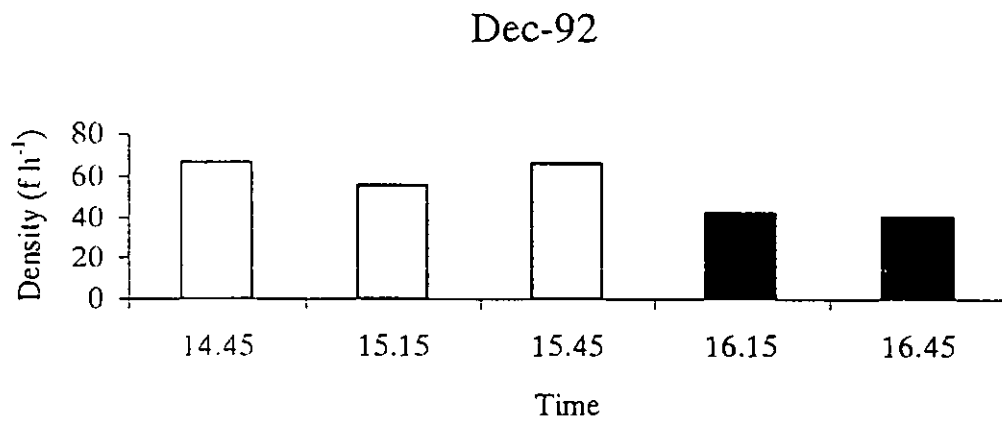
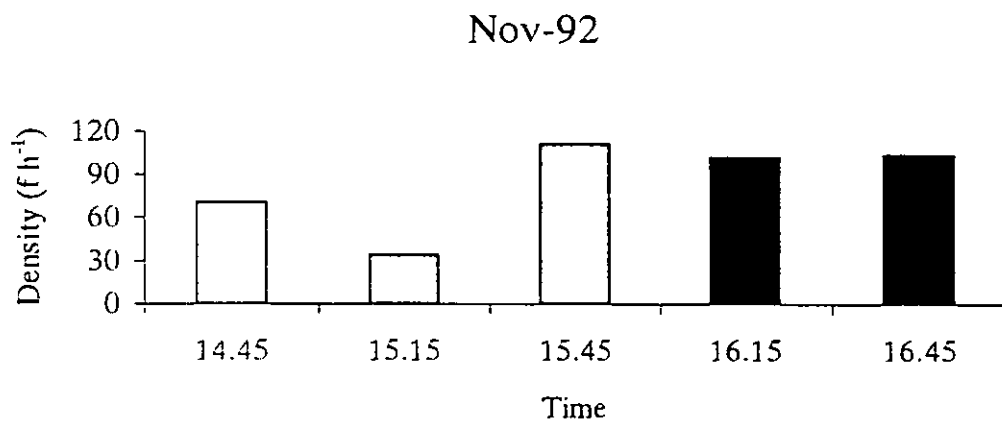
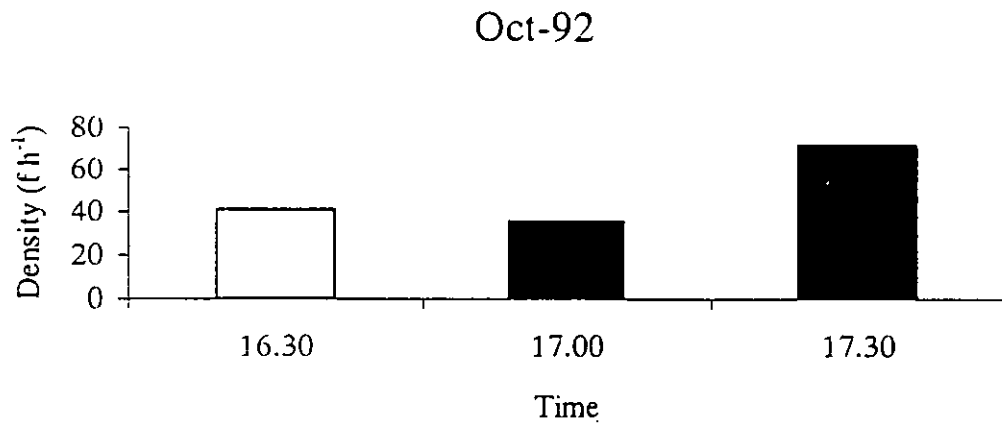


Fig. 2.13 Changes over dusk in the density of large (> 25 cm) fish echoes across the tower transect in Haweswater during October, November and December 1992. Open and closed bars identify transects made before and after sunset, respectively.

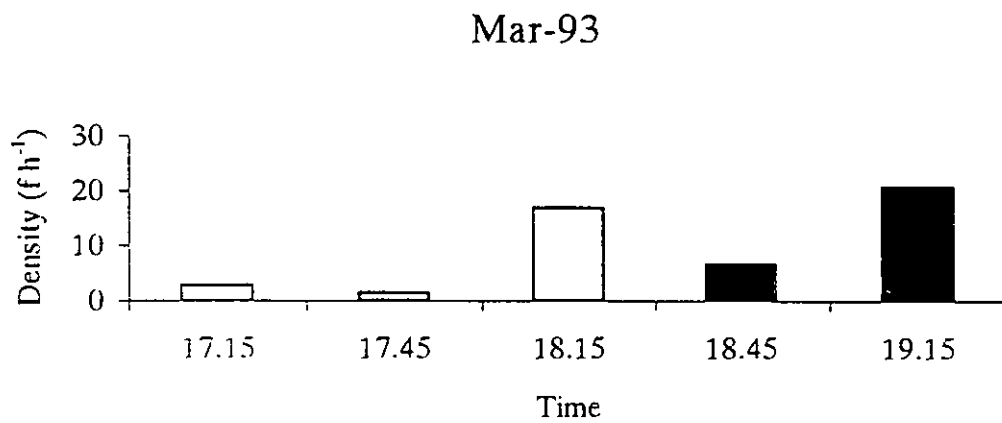
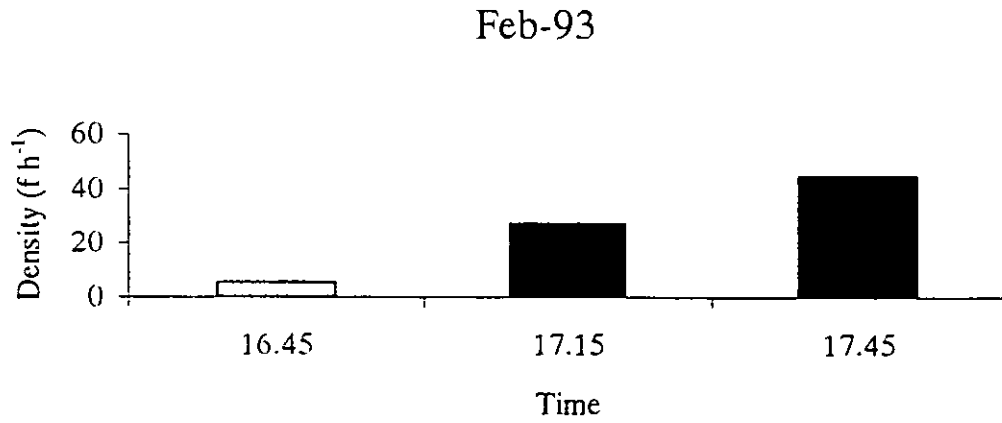


Fig. 2.14 Changes over dusk in the density of large (> 25 cm) fish echoes across the tower transect in Haweswater during February and March 1993. Open and closed bars identify transects made before and after sunset, respectively. No transect could be made during January due to dangerous weather conditions.

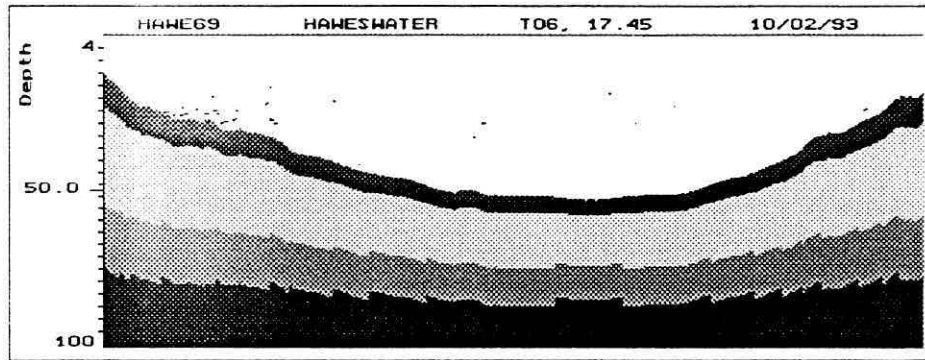


Fig. 2.15 Echogram from the tower transect across Haweswater beginning near the abstraction point of the east shore (left side of echogram) at 17.45 hours on 10 February 1993.

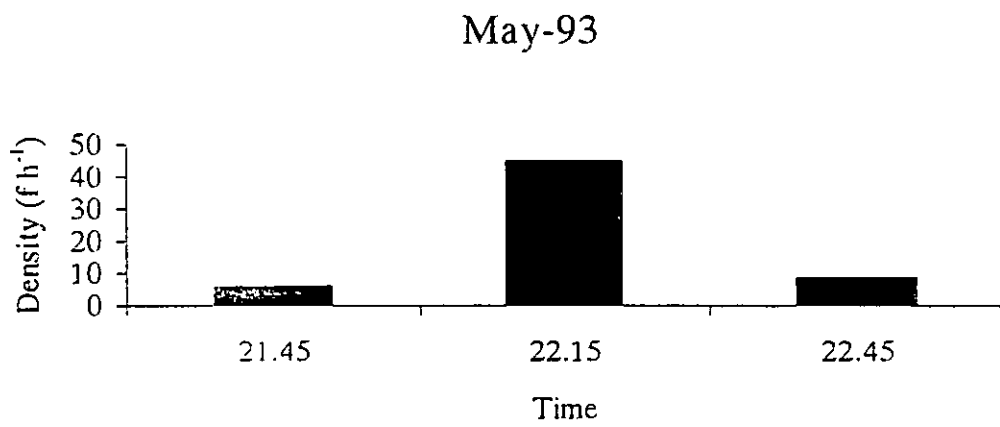
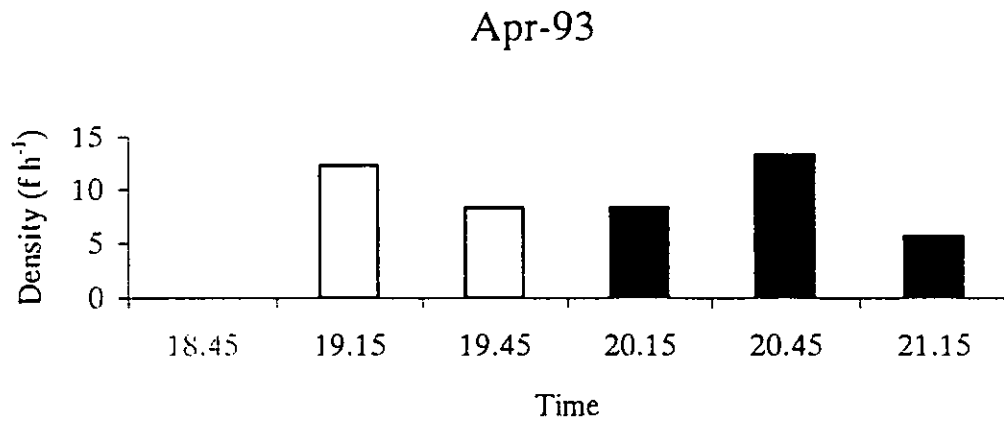


Fig. 2.16 Changes over dusk in the density of large (> 25 cm) fish echoes across the tower transect in Haweswater during April and May 1993. Open and closed bars identify transects made before and after sunset, respectively.

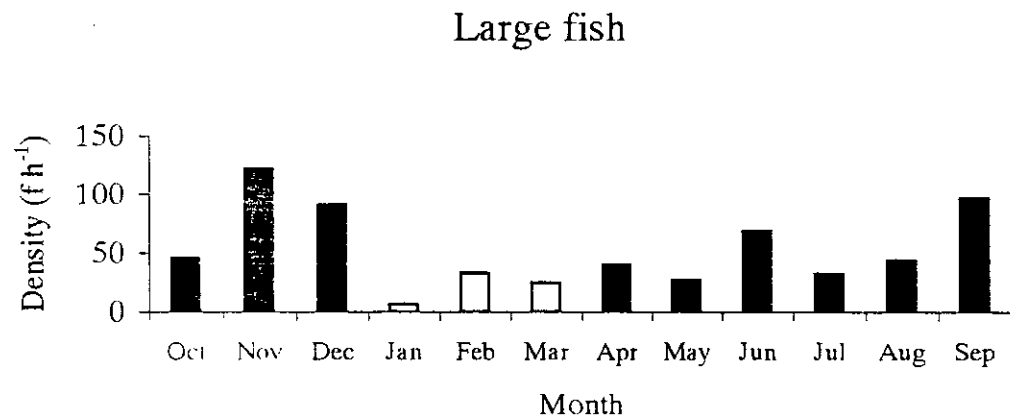
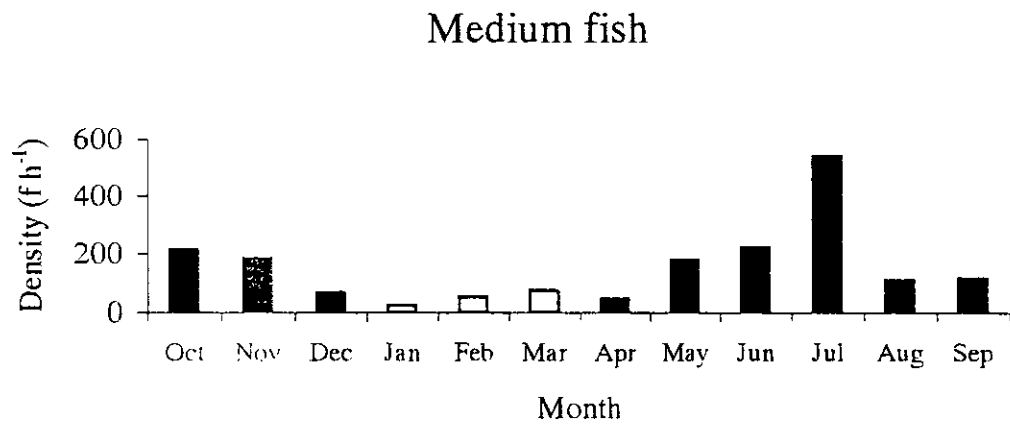
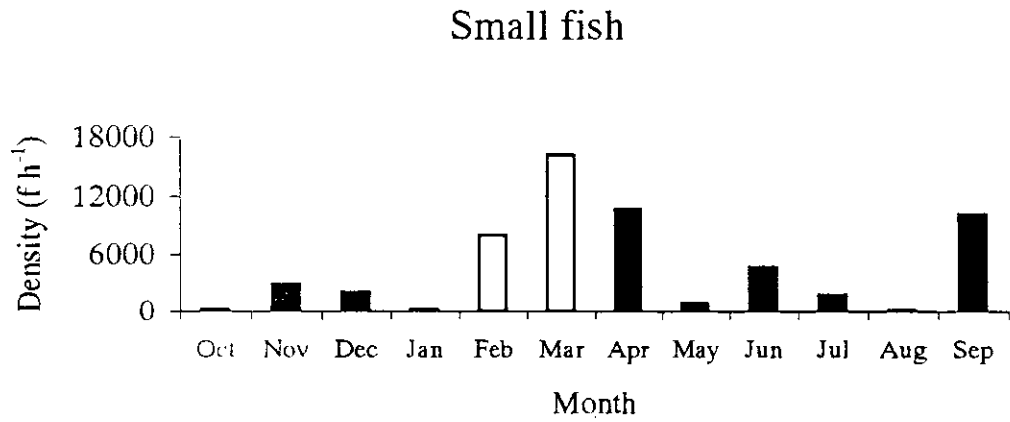


Fig. 2.17 Maximum monthly peak densities (excluding outlier values of large fish in June and July as explained in text) of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across the standard transect in Haweswater between October 1992 and September 1993. The major entrapment period is indicated by open bars.

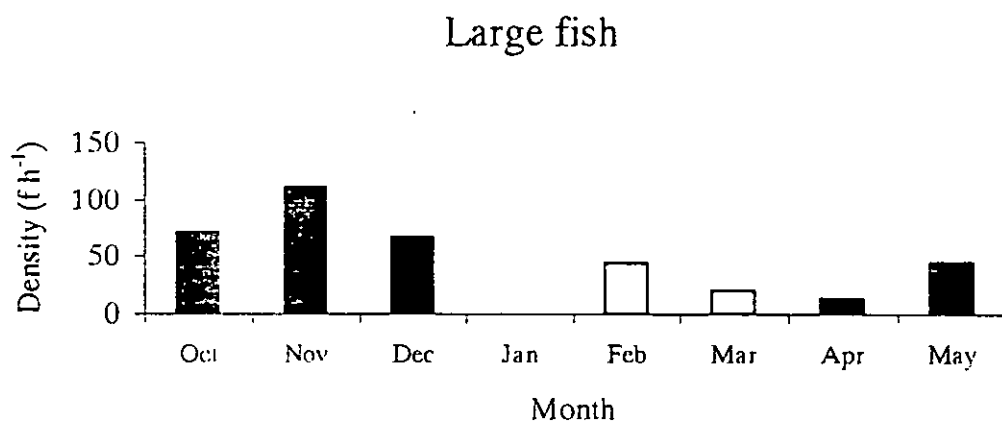
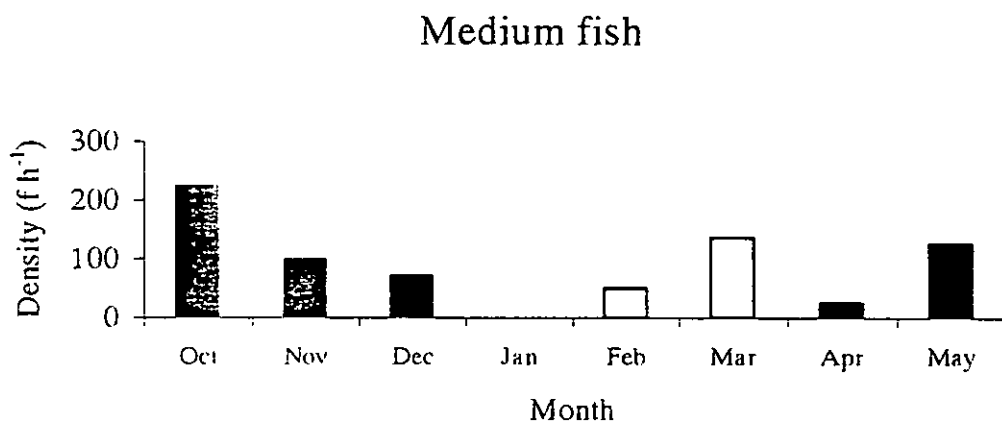
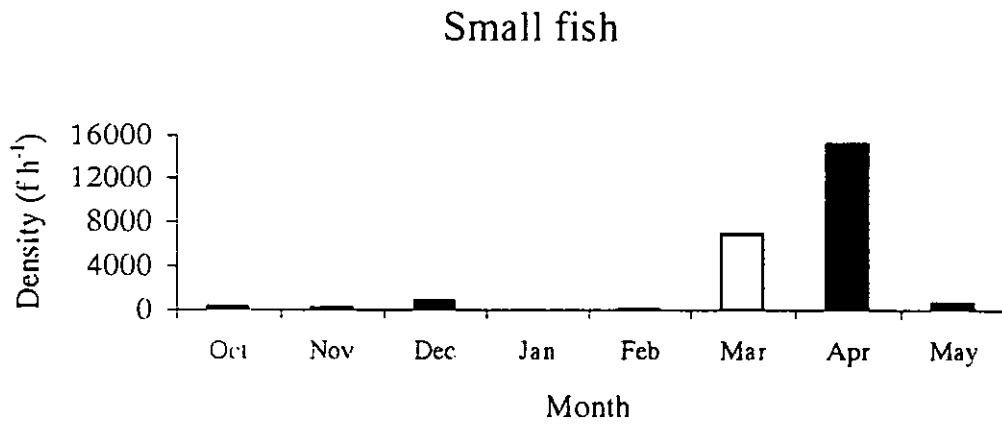


Fig. 2.18 Maximum monthly peak densities of small (4 to 10 cm), medium (10 to 25 cm) and large (> 25 cm) fish echoes across the tower transect in Haweswater between October 1992 and May 1993. The major entrainment period is indicated by open bars.

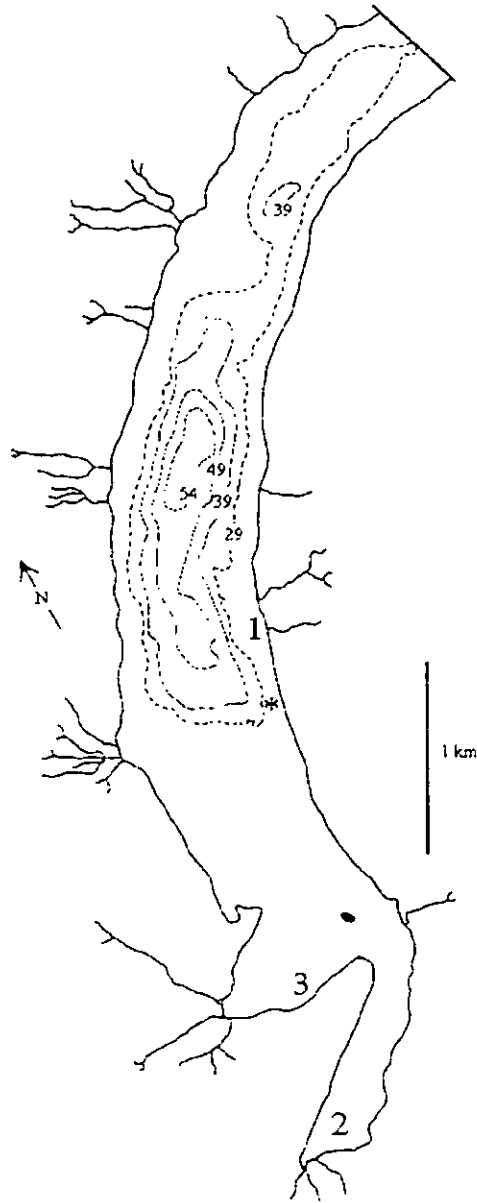


Fig. 3.1 Locations of sites (1, 2 and 3) assessed by divers with still cameras in terms of their suitability as schelly spawning grounds. Depth contours are given in metres while the approximate position of the abstraction point is shown by an asterisk. Redrawn with permission from Ramsbottom (1976).

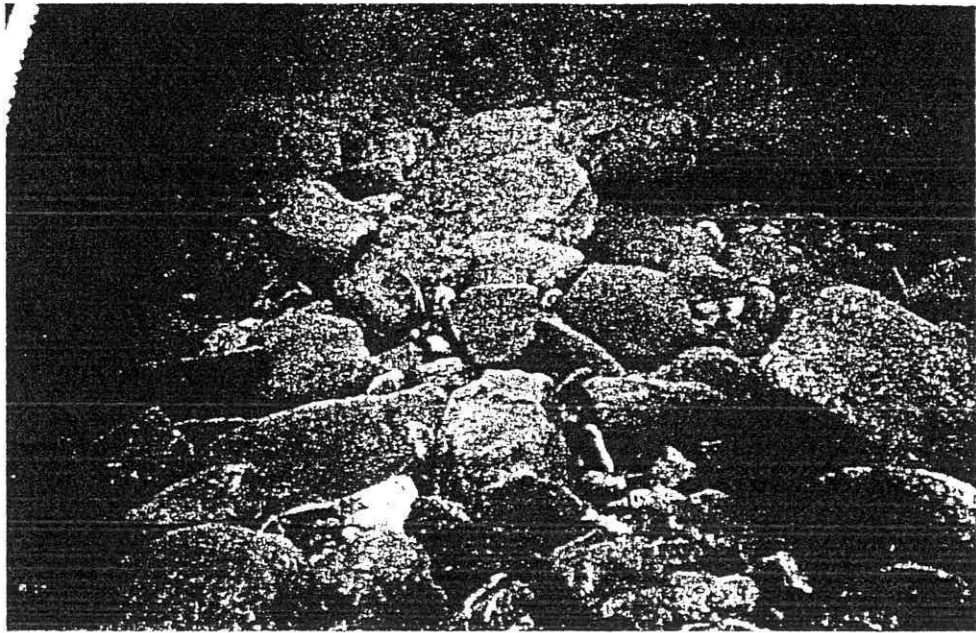


Fig. 3.2 Underwater still photograph of the bottom of Haweswater at Site 1 of Fig. 3.1.



Fig. 3.3 Underwater still photograph of the bottom of Haweswater at Site 2 of Fig. 3.1.



Fig. 3.4 Underwater still photograph of the bottom of Haweswater at Site 3 of Fig. 3.1.

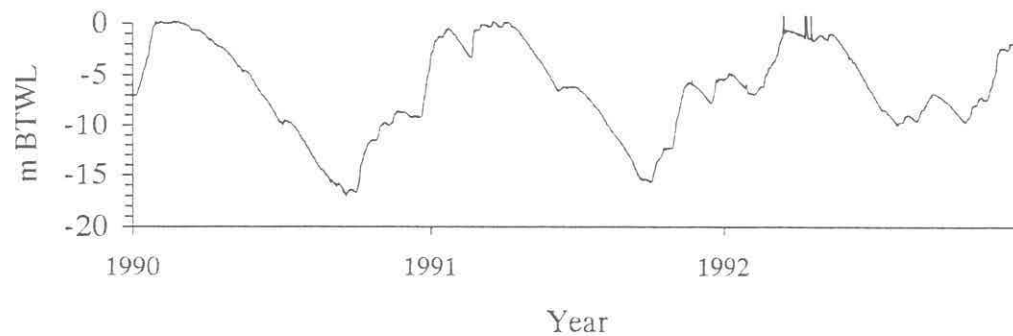
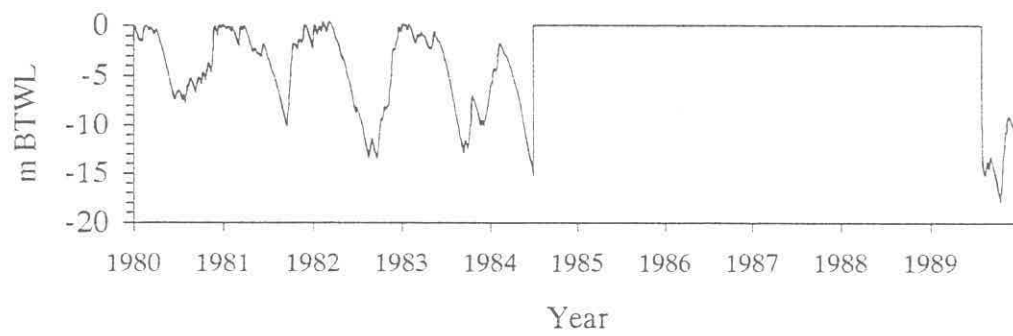
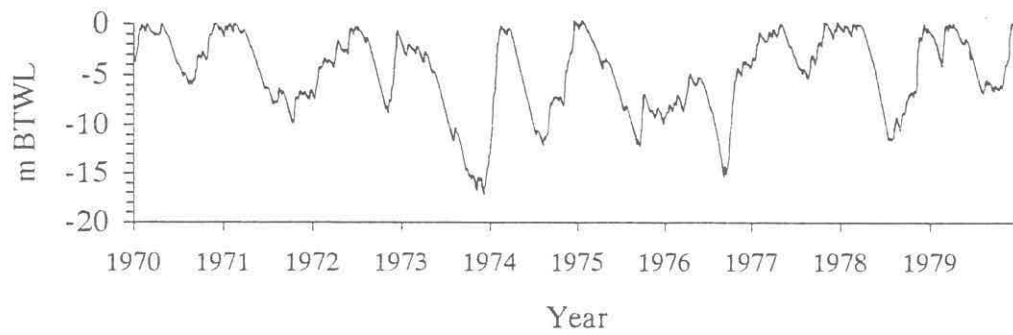
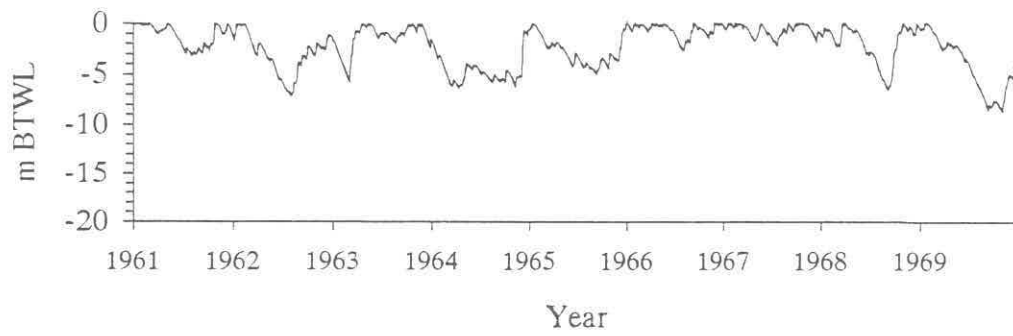


Fig. 4.1 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) from 1961 to 1992. Note that data for mid 1984 to mid 1989 are unavailable.

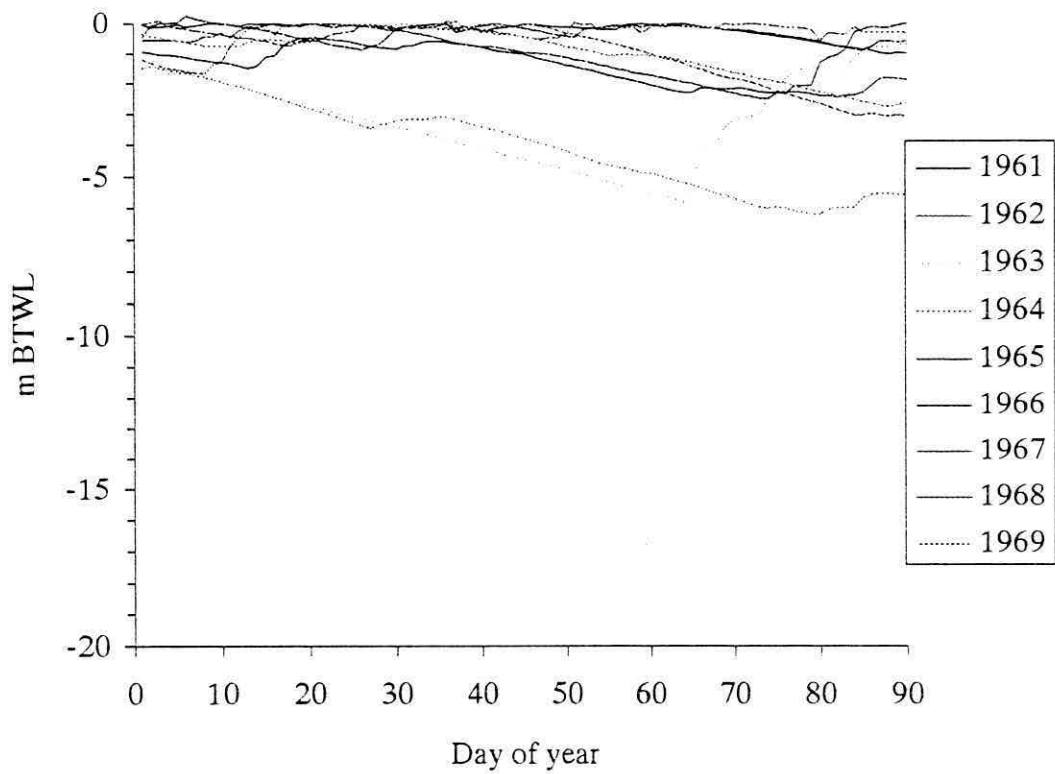


Fig. 4.2 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for January, February and March (covering the first 90 days of the year) from 1961 to 1969.

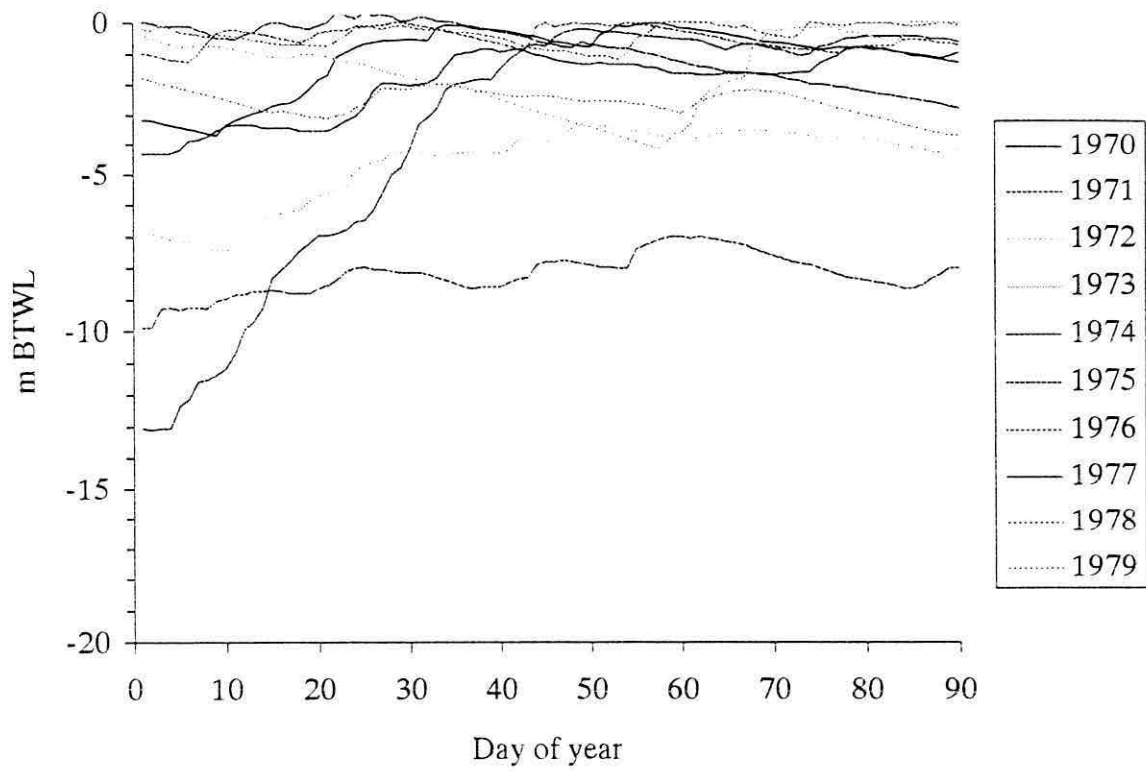


Fig. 4.3 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for January, February and March (covering the first 90 days of the year) from 1970 to 1979.

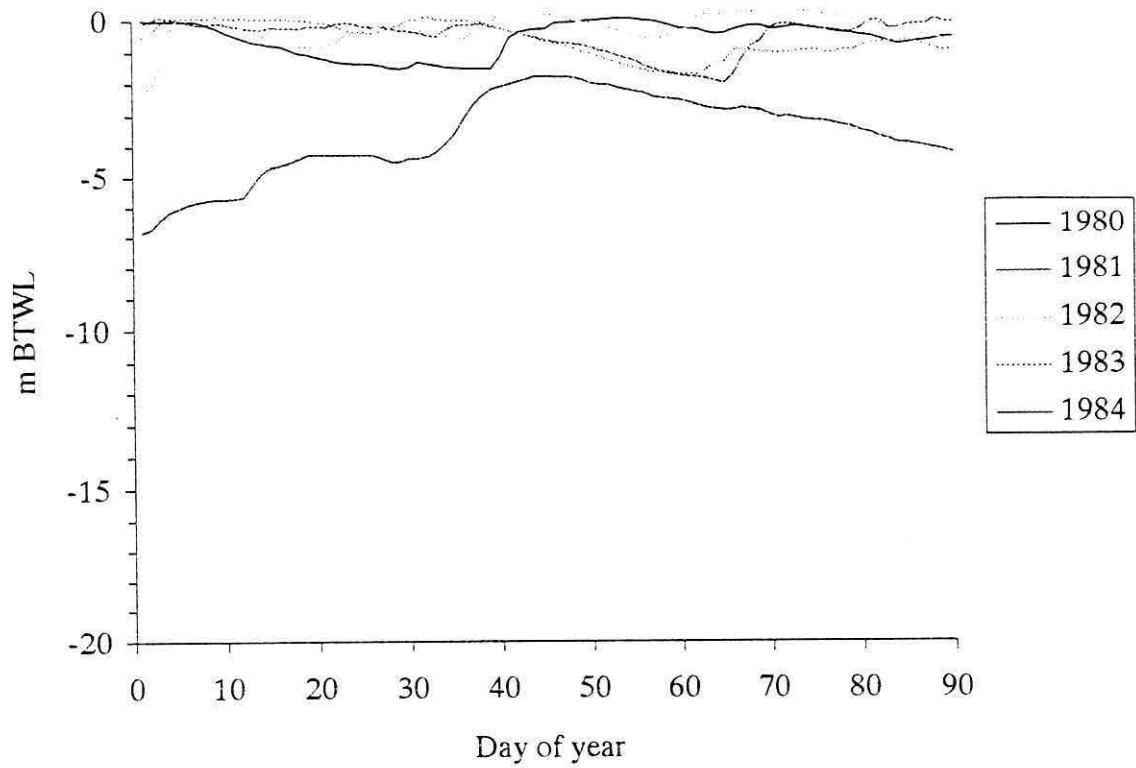


Fig. 4.4 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for January, February and March (covering the first 90 days of the year) from 1980 to 1984. Data for the remainder of the 1980s are unavailable.

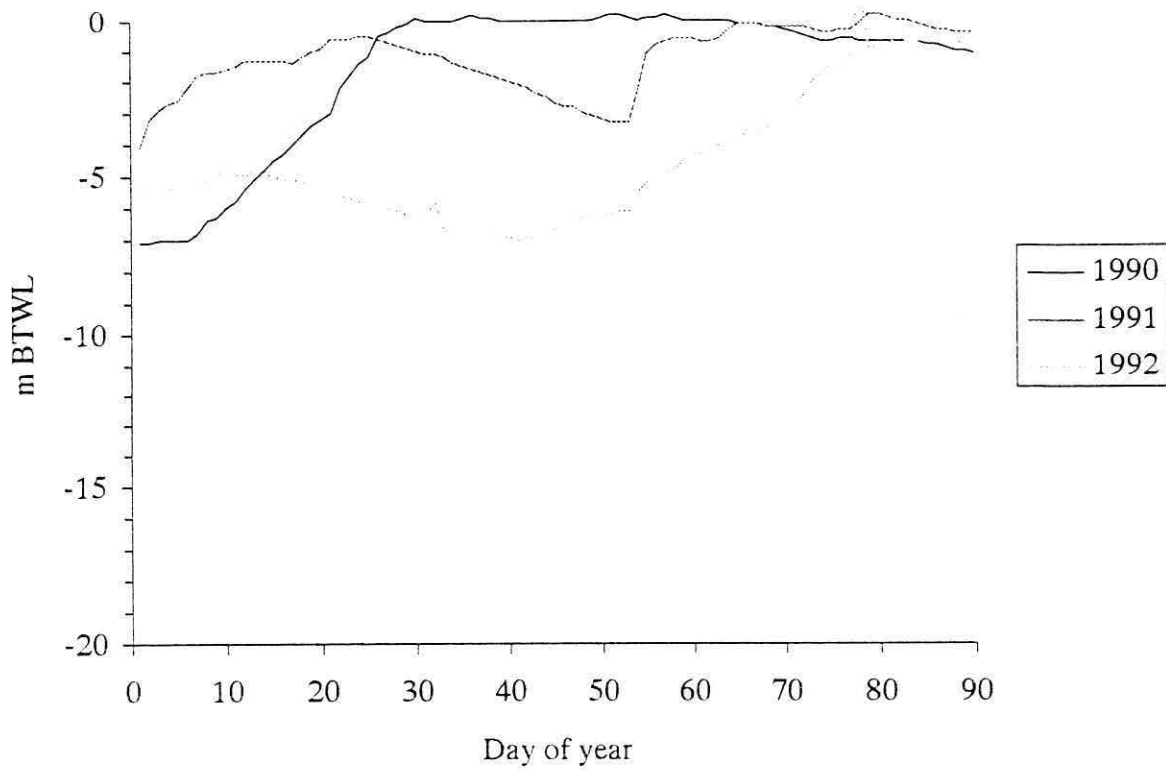


Fig. 4.5 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for January, February and March (covering the first 90 days of the year) from 1990 to 1992. Data for 1993 and 1994 are unavailable.

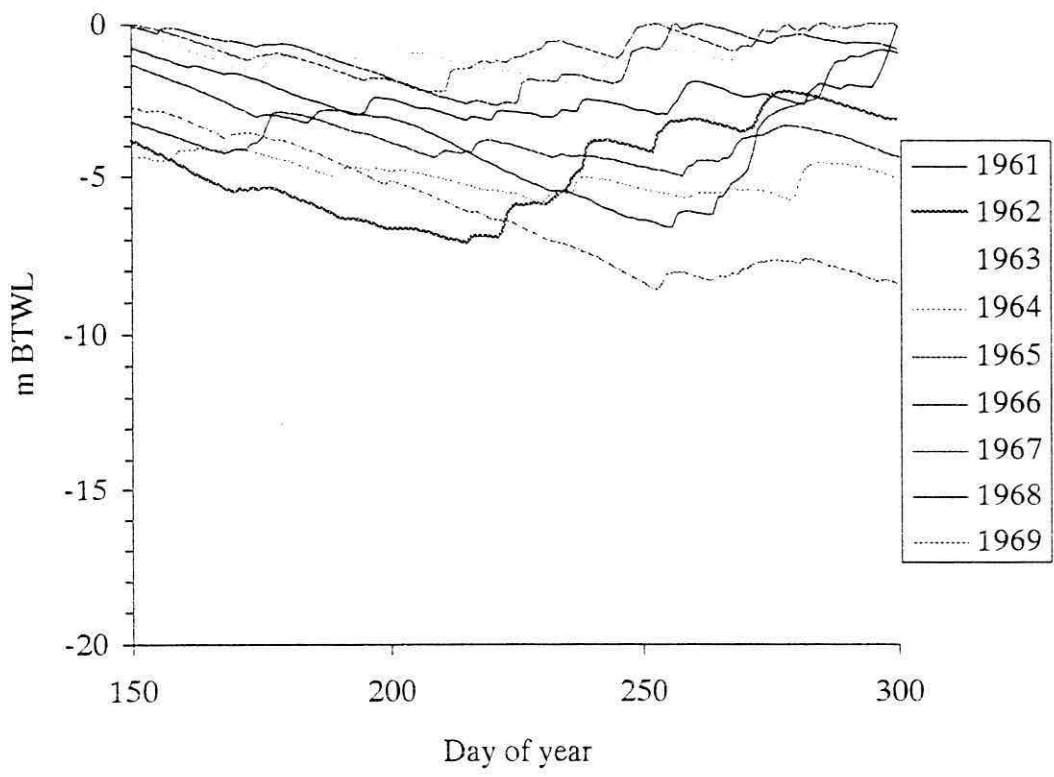


Fig. 4.6 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for June, July, August, September and October (covering days 150 to 300 of the year) from 1961 to 1969.

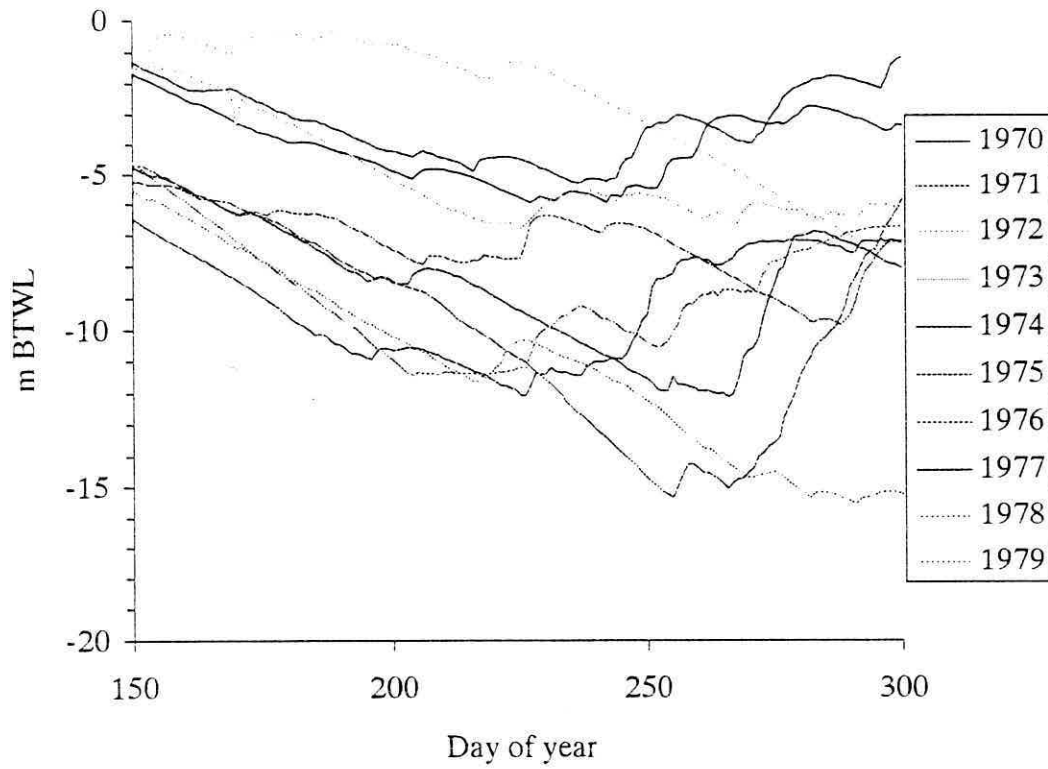


Fig. 4.7 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for June, July, August, September and October (covering days 150 to 300 of the year) from 1970 to 1979.

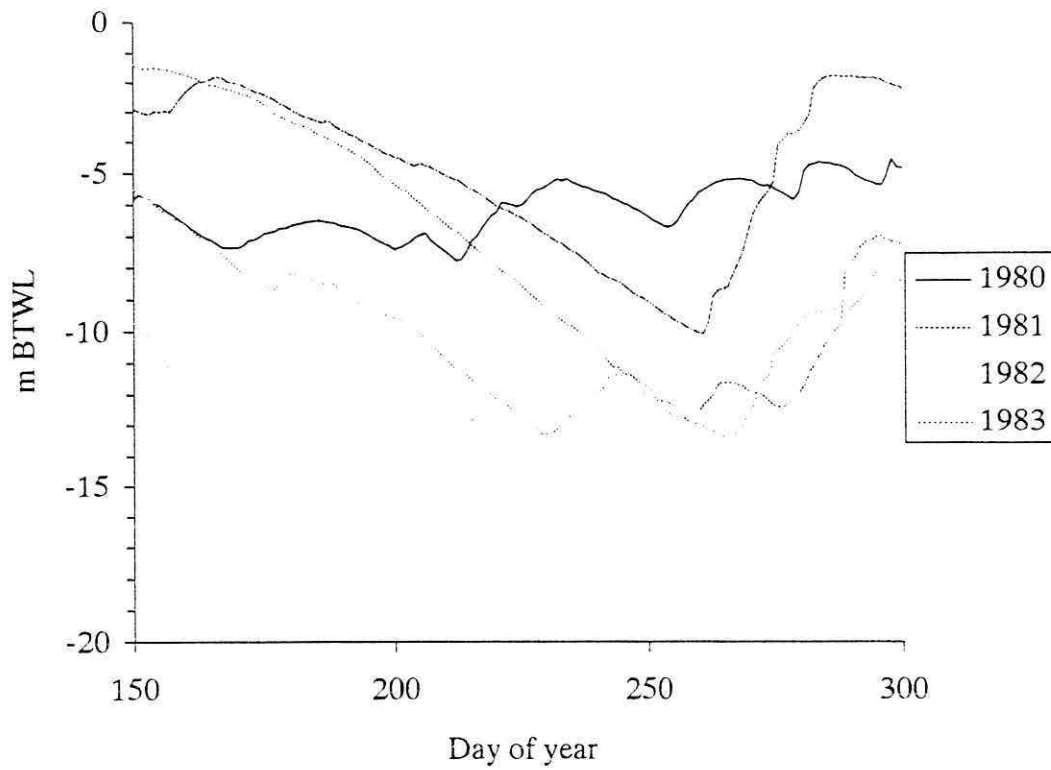


Fig. 4.8 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for June, July, August, September and October (covering days 150 to 300 of the year) from 1980 to 1983. Data for the remainder of the 1980s are unavailable.

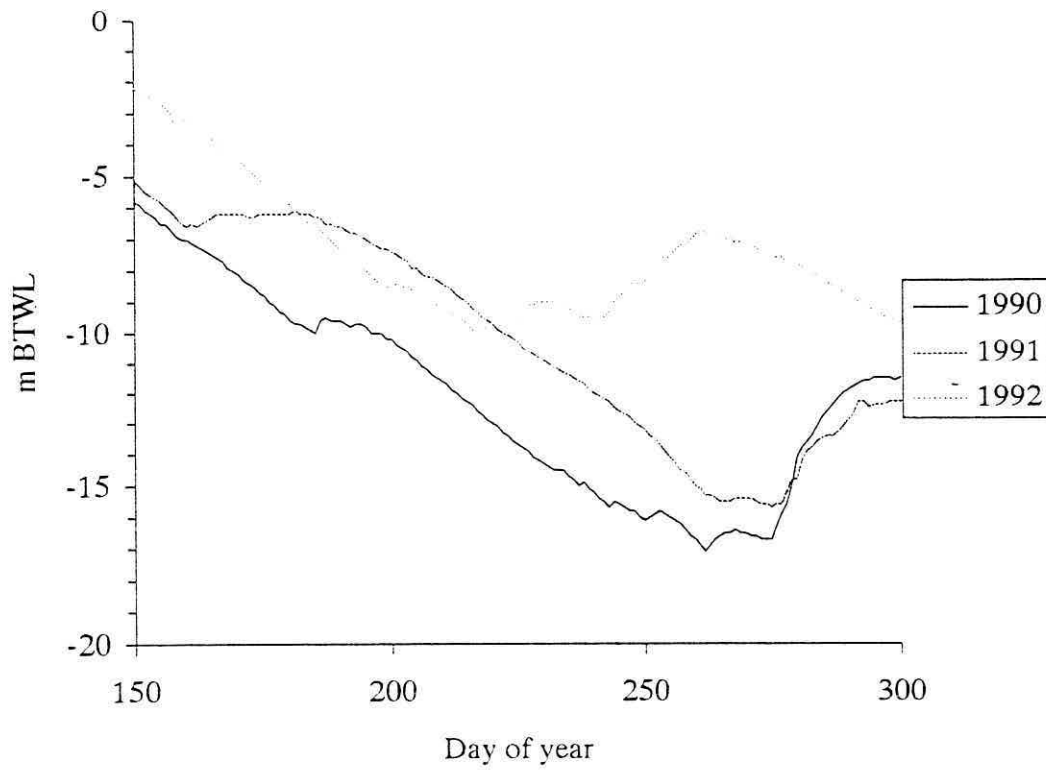


Fig. 4.9 Daily levels of Haweswater from NWW records expressed as metres Below Top Water Level (BTWL) for June, July, August, September and October (covering days 150 to 300 of the year) from 1990 to 1992. Data for 1993 and 1994 are unavailable.

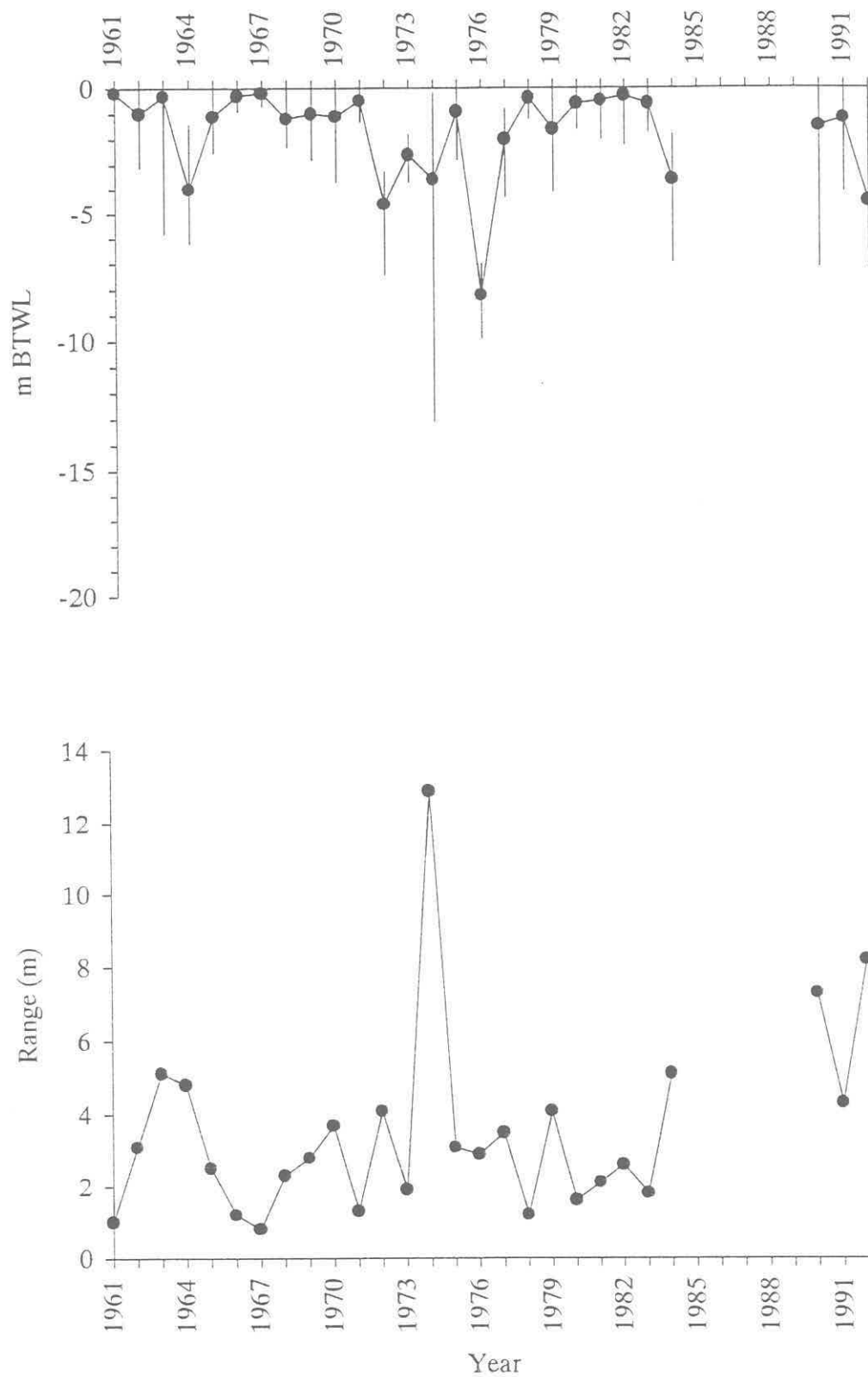


Fig. 4.10 Long-term trends in daily levels of Haweswater during January, February and March from 1961 to 1992 expressed as means with maximum and minimum (upper figure) and range (lower figure). None of the trends were found to be significant at the 5% level by regression analysis.

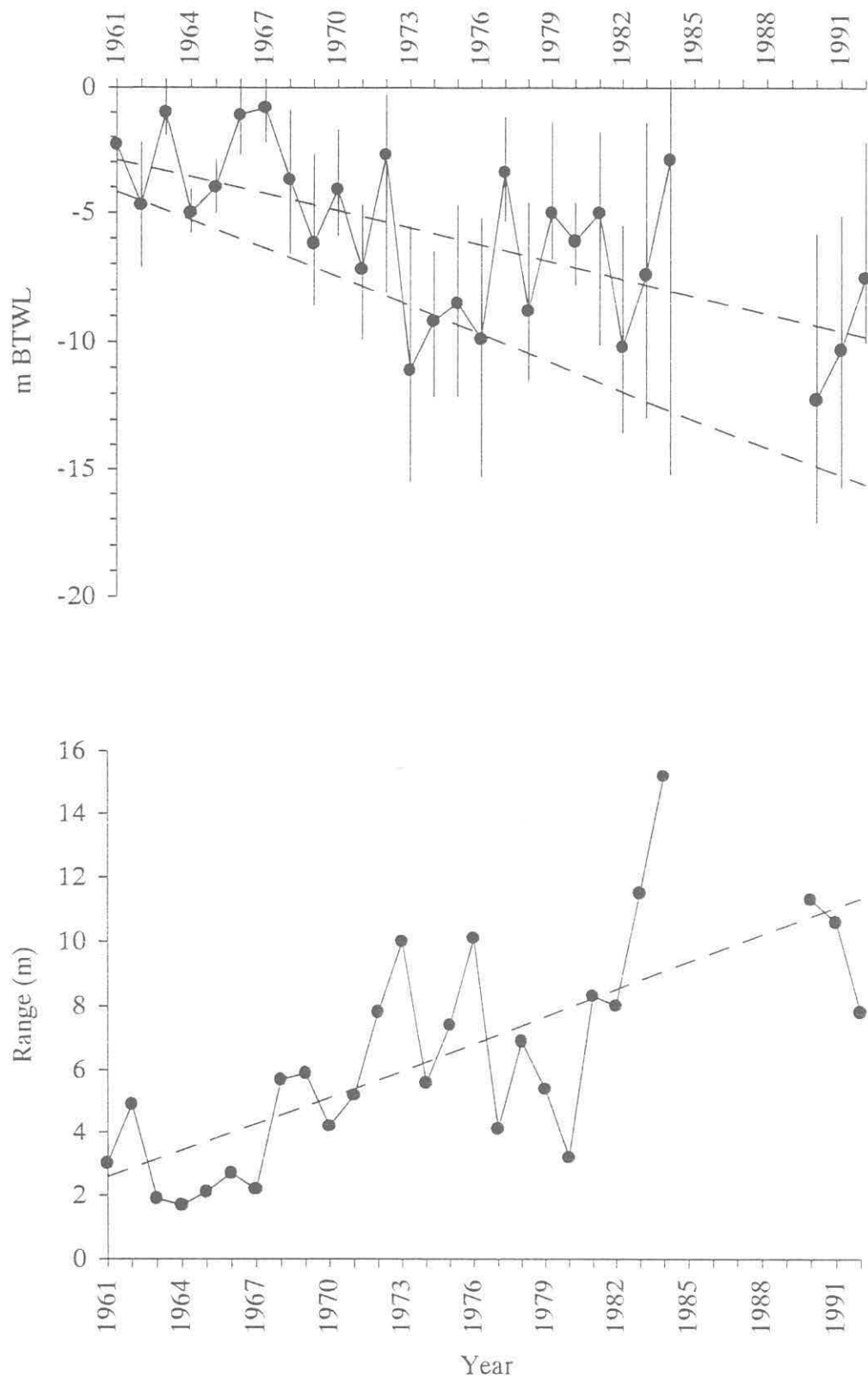


Fig. 4.11 Long-term trends in daily levels of Haweswater during June, July, August, September and October from 1961 to 1992 expressed as means with maximum and minimum (upper figure) and range (lower figure). Trends found to be significant at the 5% level by regression analysis are shown as broken lines.

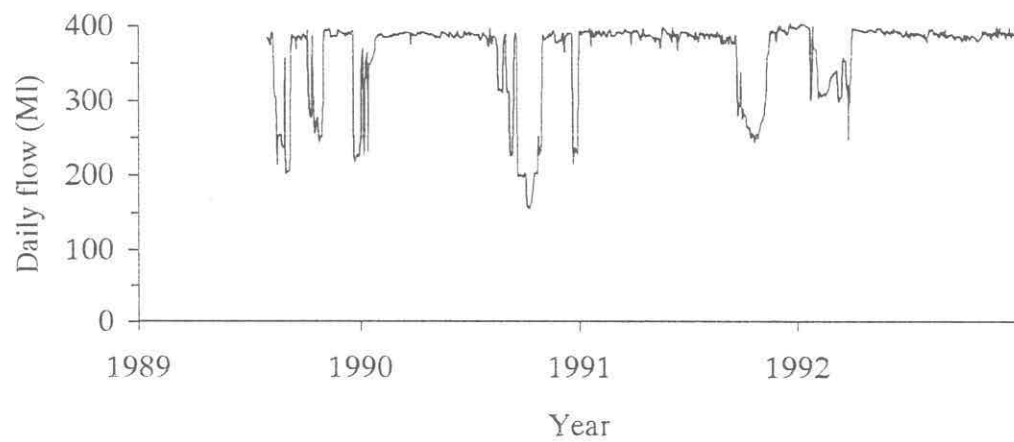
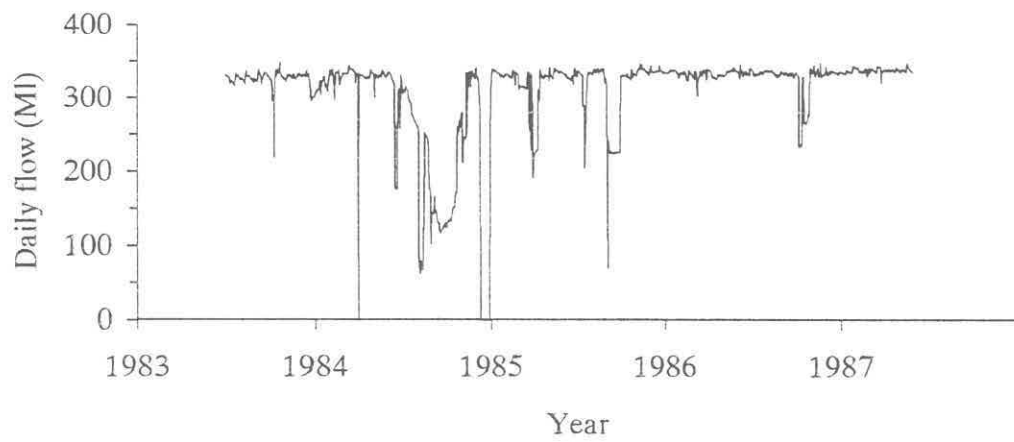
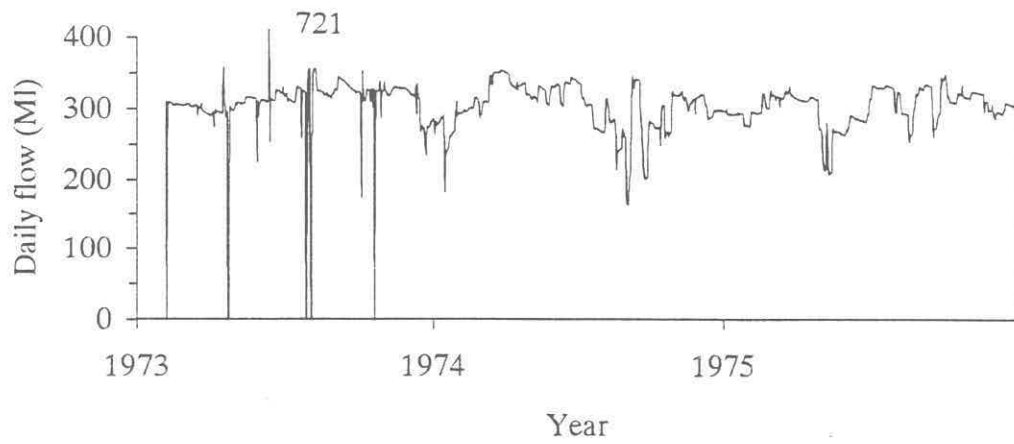


Fig. 4.12 Daily flows of water abstracted from Haweswater, as measured at Watchgate Water Treatment Works inlet meters, for three periods for which records are available from NWW.

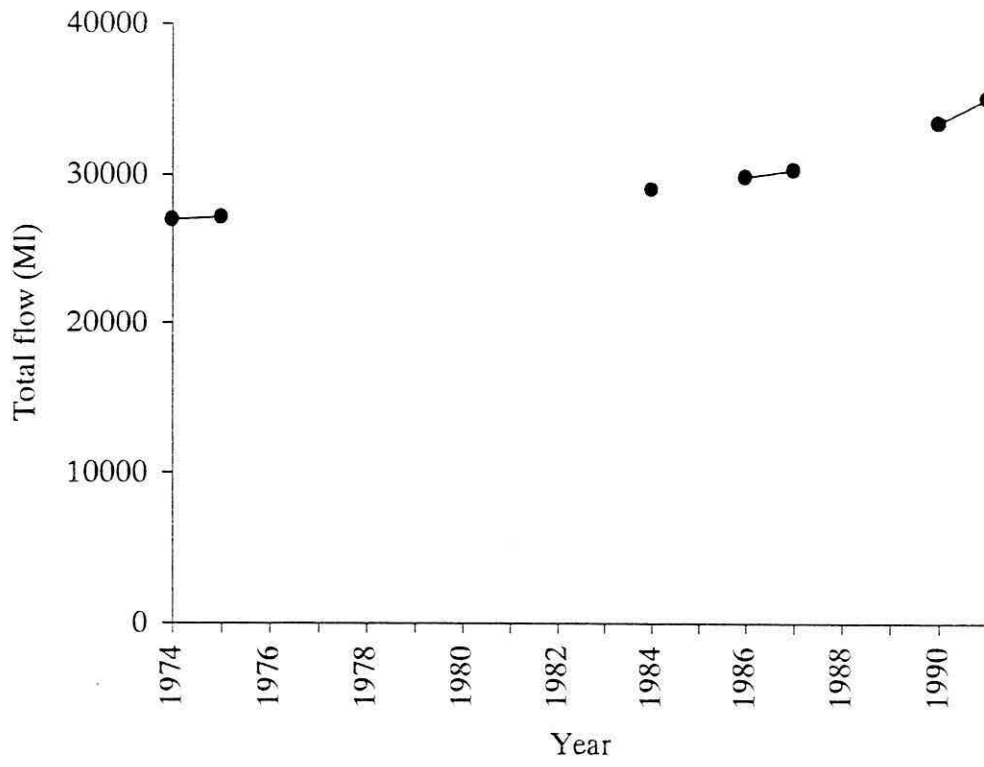


Fig. 4.13 Long-term trend in the total volume of water abstracted from Haweswater during January, February and March between 1974 and 1991. Note that only intermittent data are available from NWW.

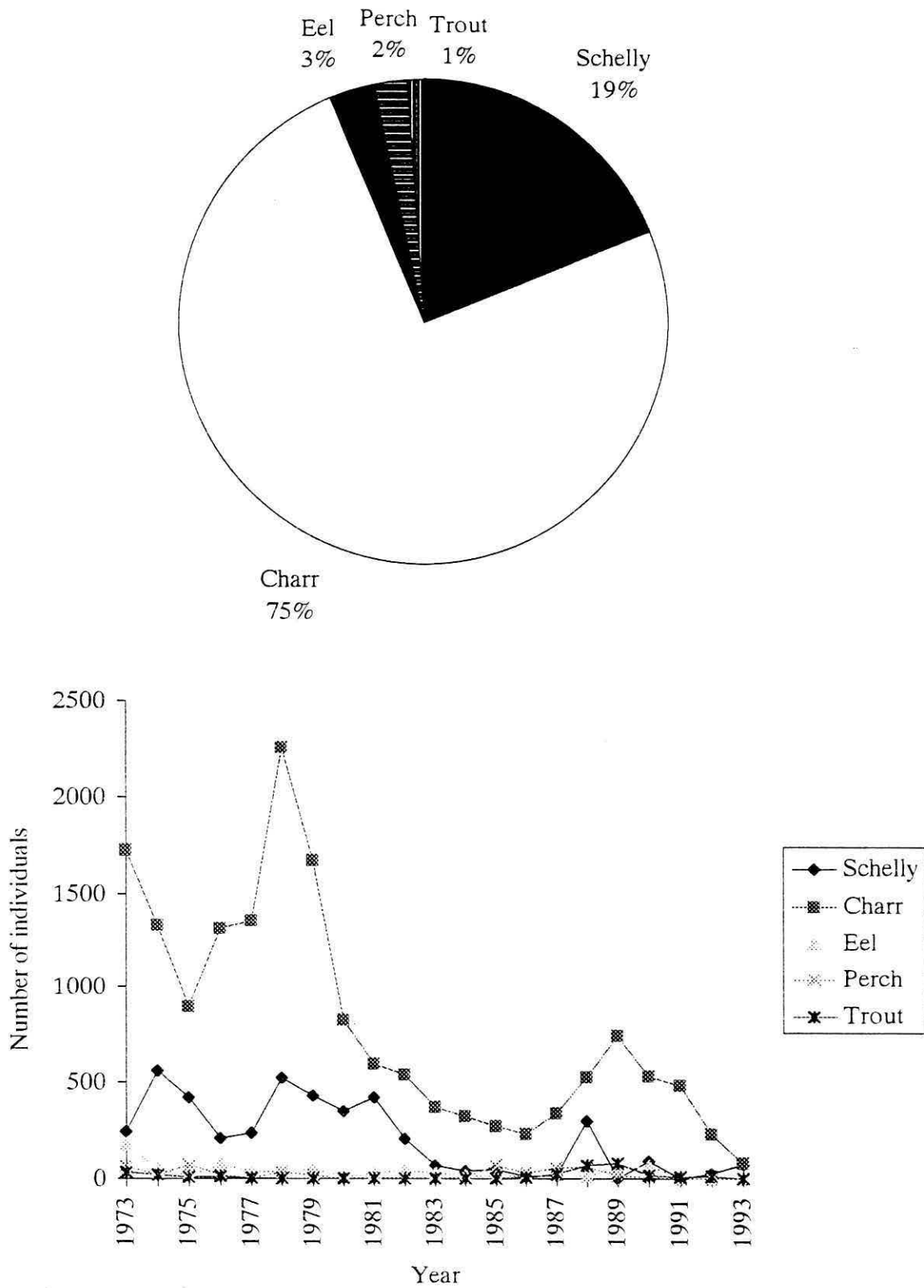
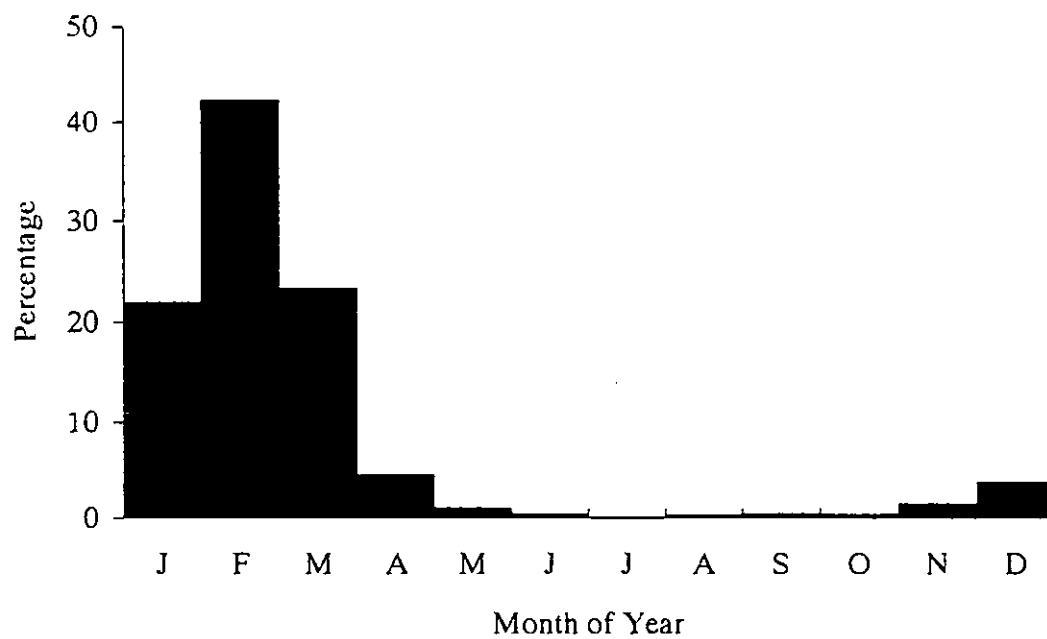


Fig. 5.1 Species composition of the overall Haweswater entrapment catch between 1973 and 1993 inclusive (upper), and the long-term trends in entrapment of schelly, charr, eel, perch and trout over the same period (lower).

Schelly



Charr

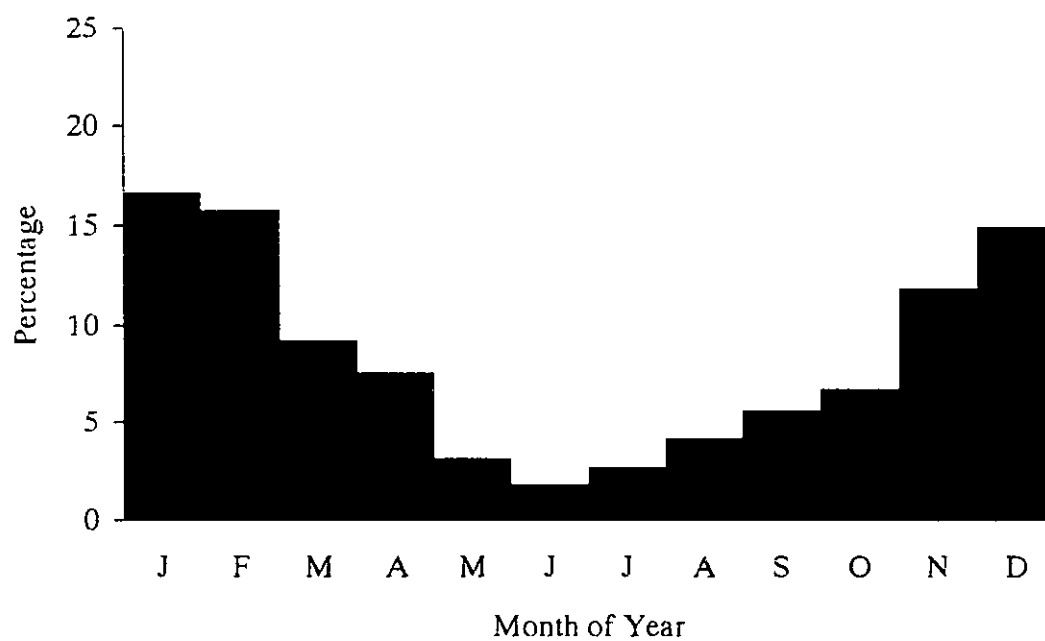


Fig. 5.2 Monthly distributions of schelly and charr entrapment with data pooled from 1973 to 1993 inclusive.

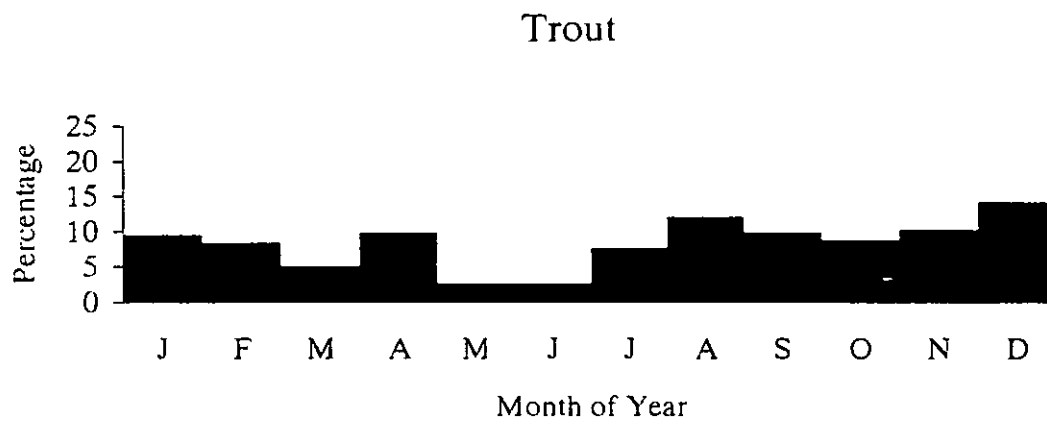
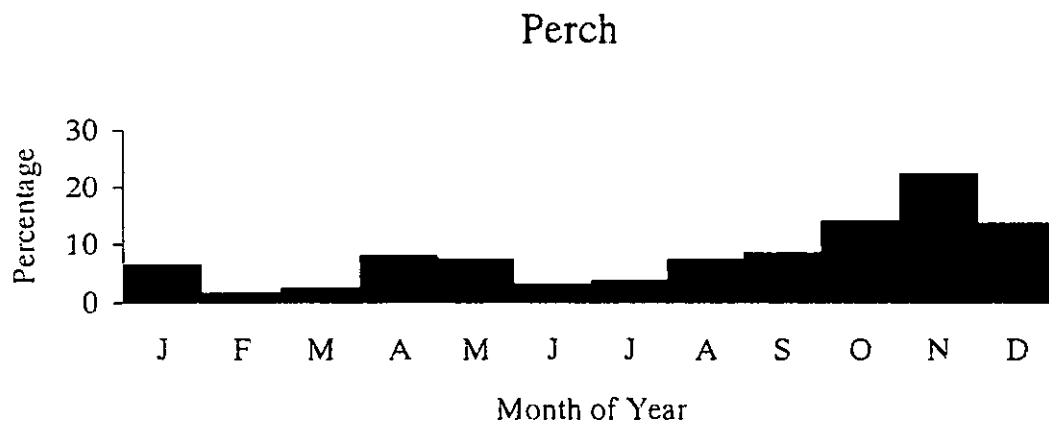
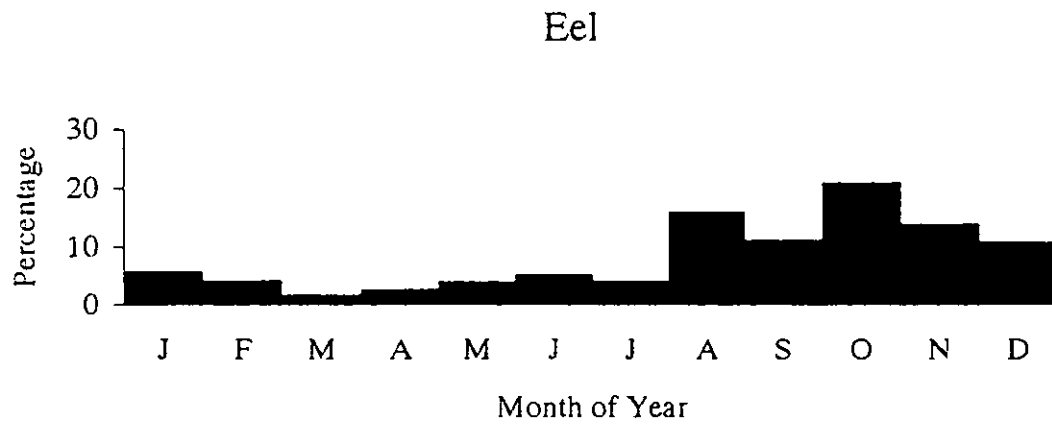


Fig. 5.3 Monthly distributions of eel, perch and trout entrapment with data pooled from 1973 to 1993 inclusive.

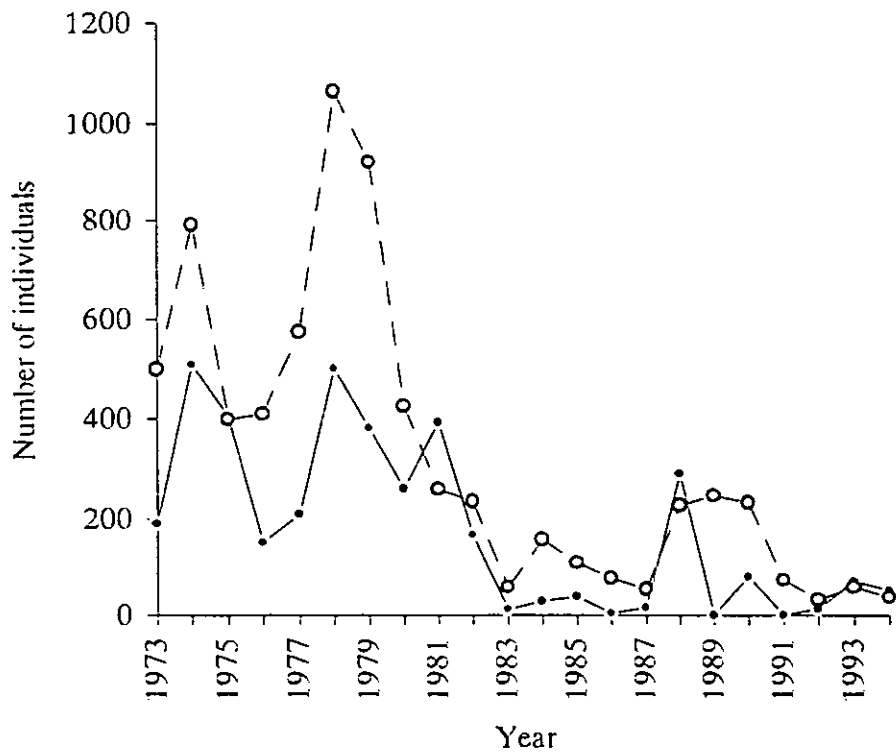
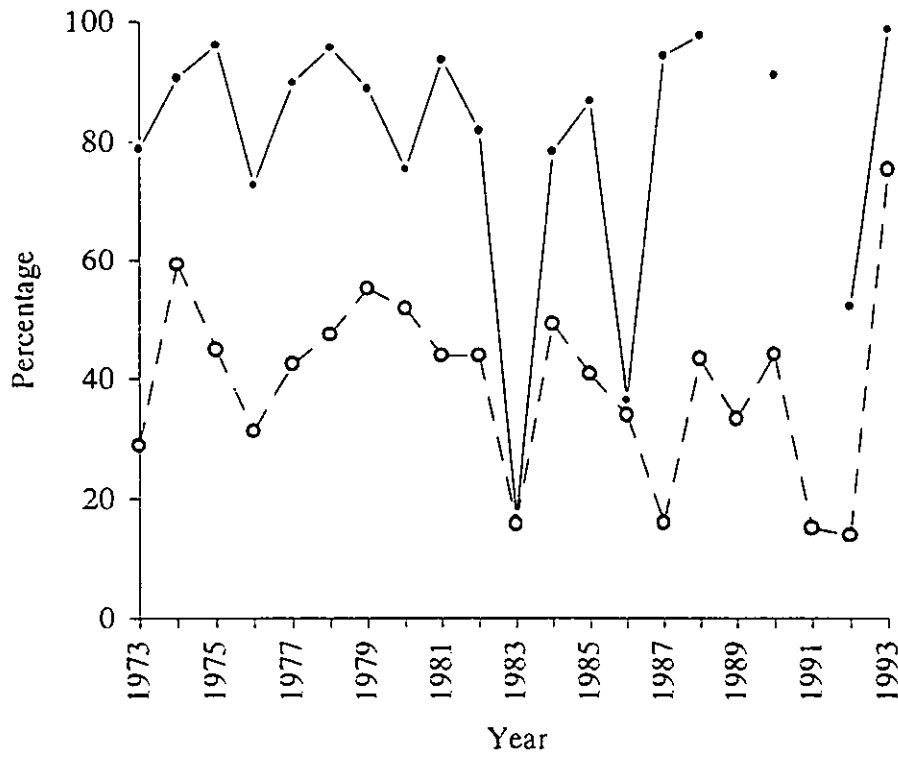


Fig. 5.4 Percentage of annual entrapment occurring during the months January, February and March between 1973 and 1993 inclusive (upper), and the long-term trends in this component of entrapment of schelly (closed symbols with continuous line) and charr (open symbols with broken line) over the same period (lower).

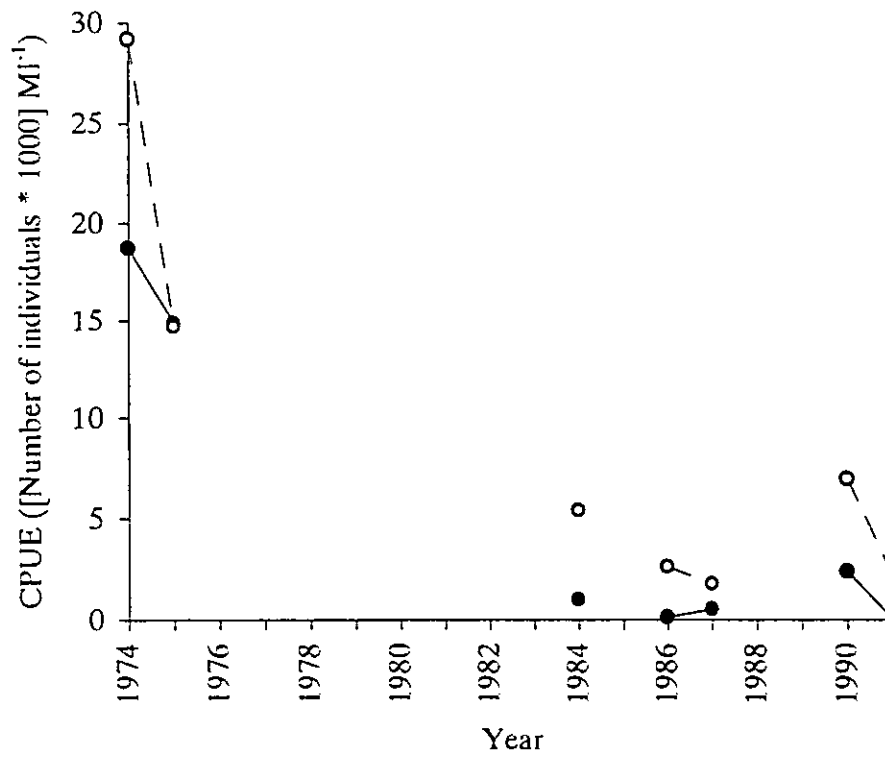


Fig. 5.5 Long-term trends in the catch-per-unit-effort (CPUE) in terms of numbers entrapped with respect to volume of water abstracted of schelly (closed symbols with continuous line) and charr (open symbols with broken line) from Haweswater during January, February and March between 1974 and 1991. Note that only intermittent abstraction data are available from NWW.

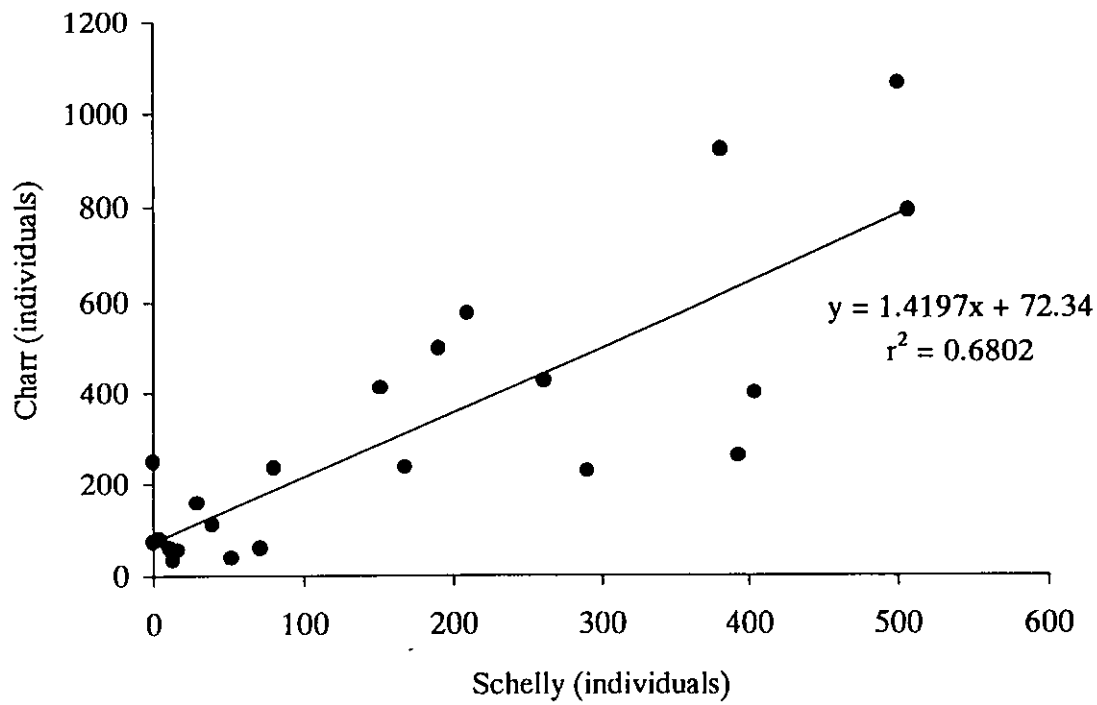
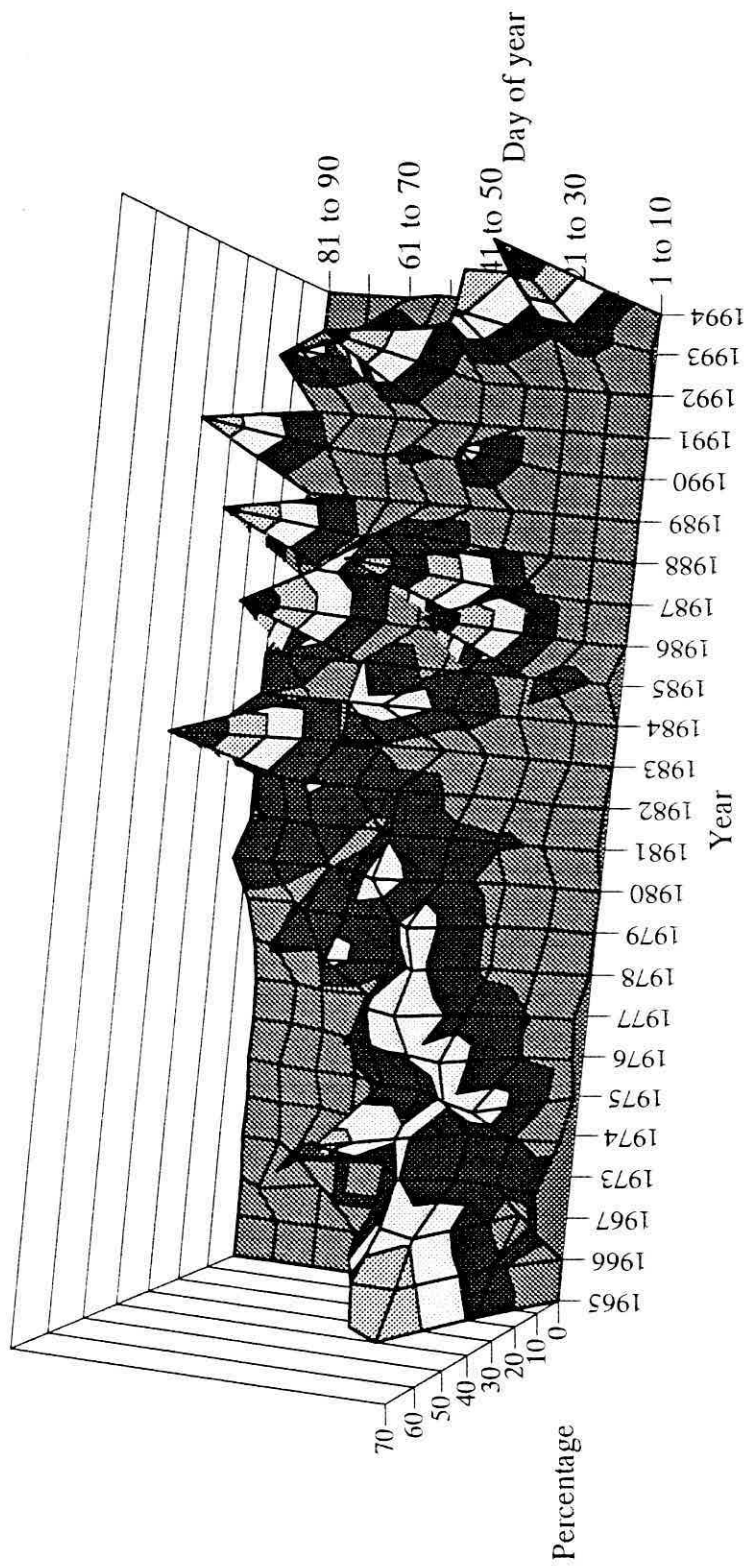


Fig. 5.6 Relationship between the total numbers of schelly and charr entrapped during January, February and March of each year between 1973 and 1994 inclusive. The regression line is significant at the 1% level.

Fig. 5.7 Summary of the daily distribution of schelly entrapment during January, February and March (covering the first 90 days of the year) for the years 1965, 1966 and 1967 (Data from Bagenal, 1970) and 1973 to 1994.



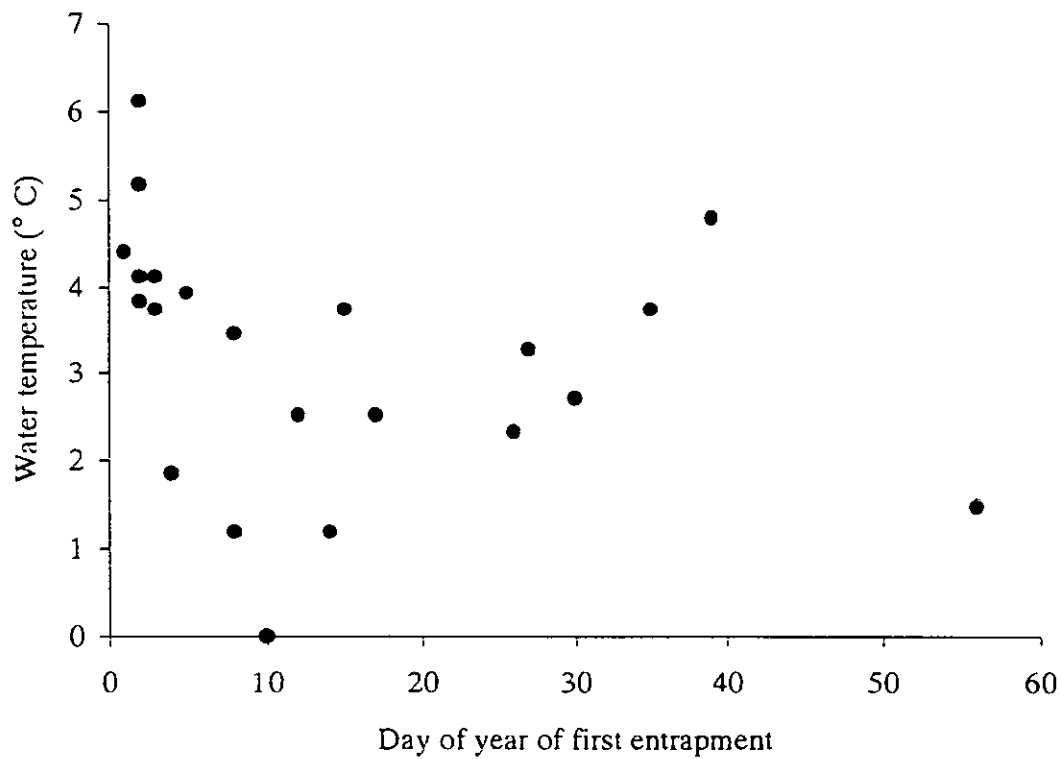
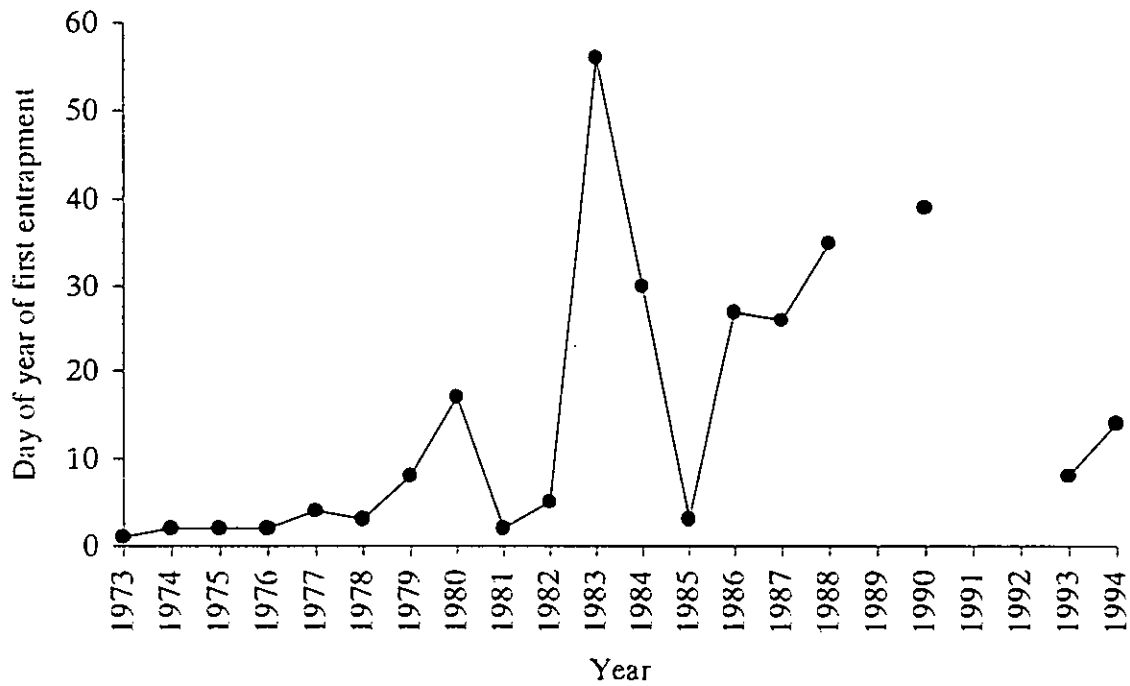


Fig. 5.8 Long-term trend in the day of year of first schelly entrapment between 1973 and 1994 (upper), and its relationship with lake temperature over the same period (lower). The temperature data are reconstructed from a regression with Windermere temperatures, for which the IFE holds a long-term data.

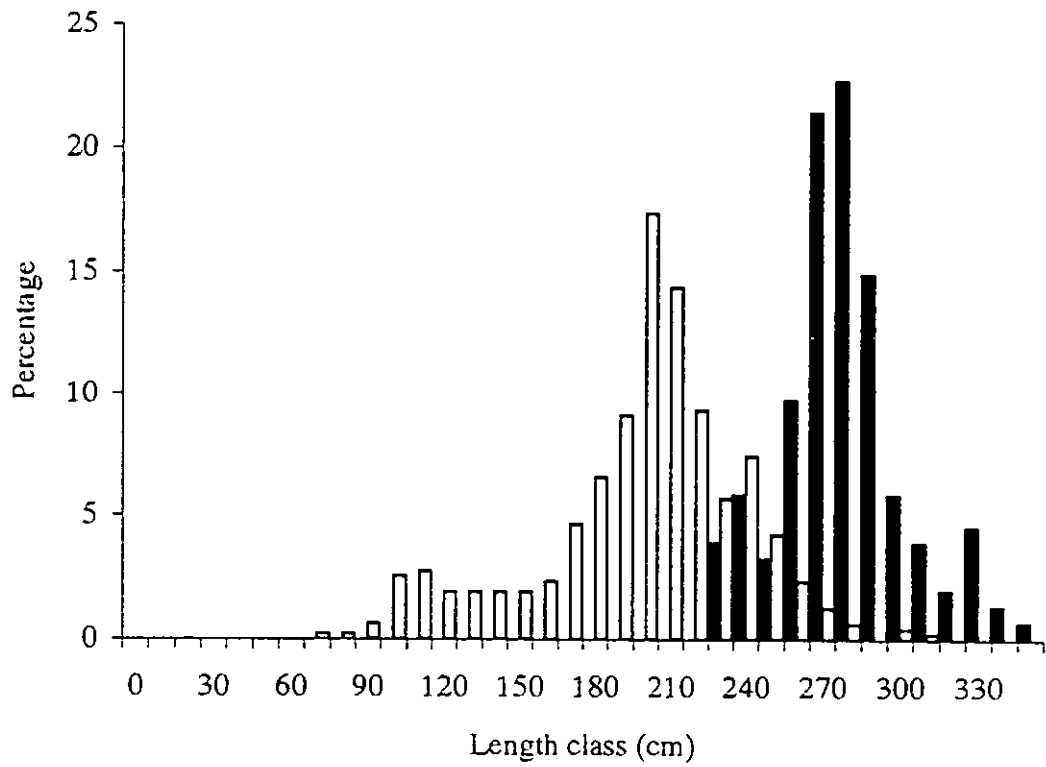


Fig. 6.1 Length frequency distributions of all schelly (closed bars, N = 154) and charr (open bars, N = 472) collected by entrapment during the present study (November 1991 to March 1994, inclusive).

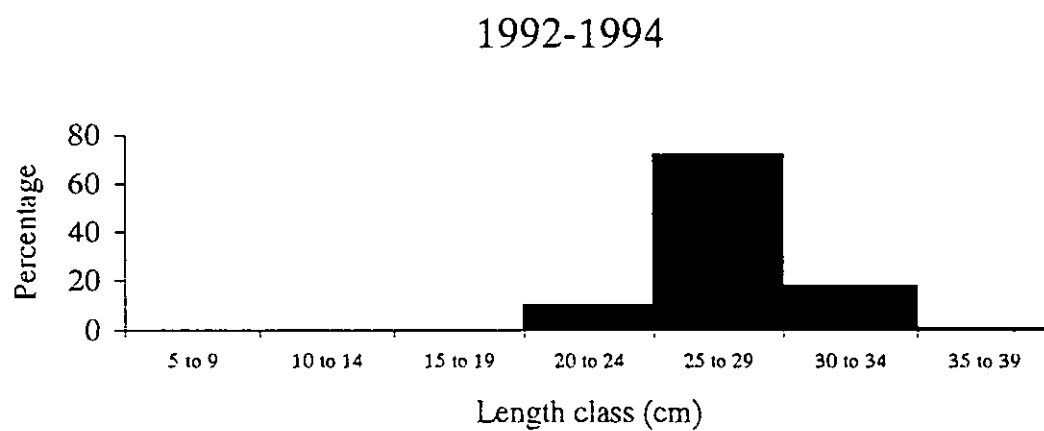
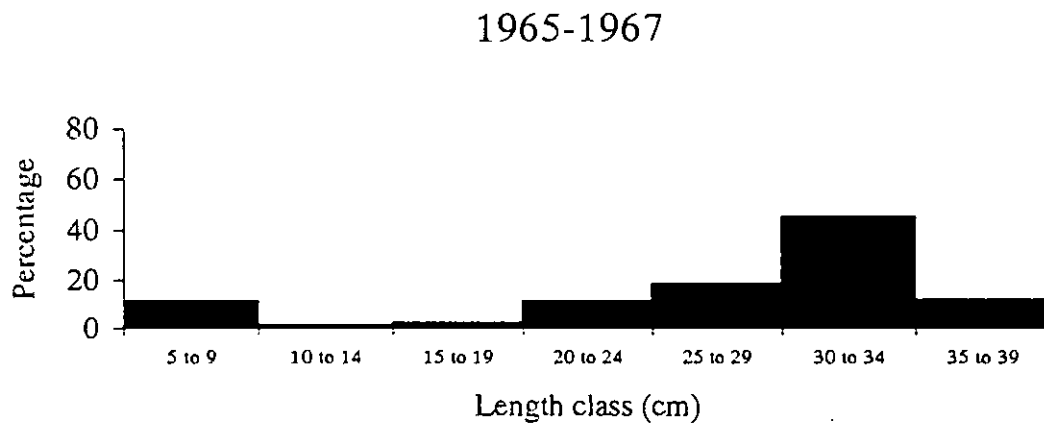


Fig. 6.2 Length frequency distributions of schelly entrapped during 1965-1967 (N = 188) and during 1992-1994 (N = 154). Data from the earlier period and length classes are taken from Bagenal (1970).

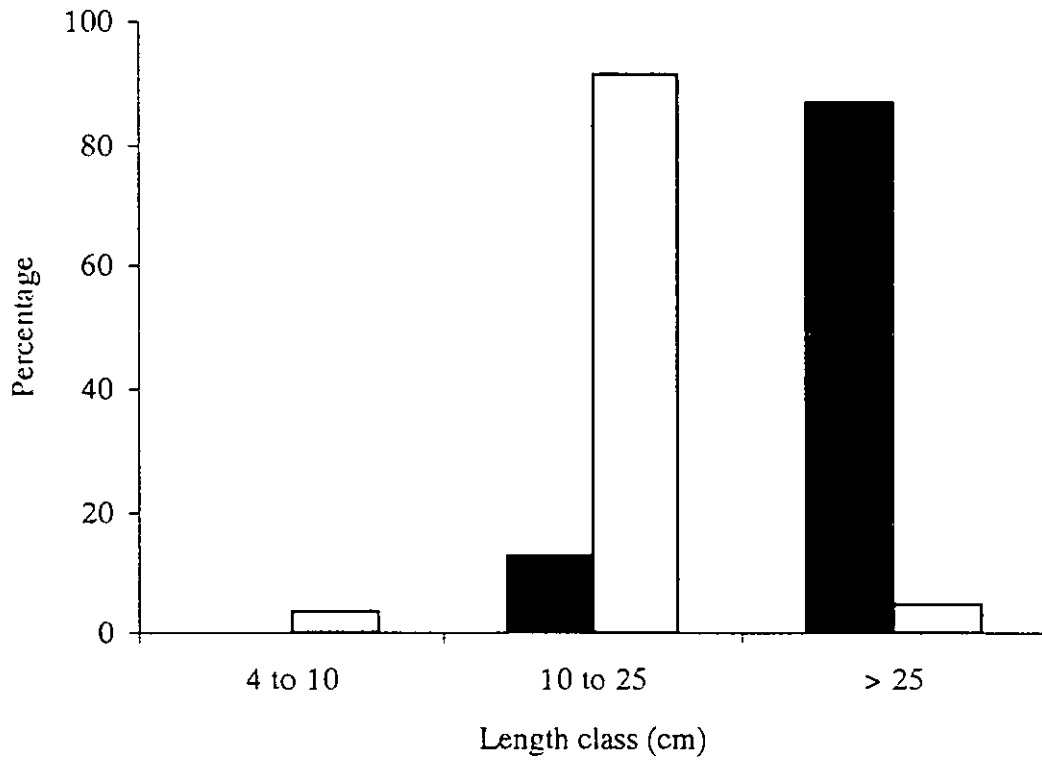


Fig. 6.3 Length frequency distributions grouped into size classes corresponding with the small, medium and large fish groups of the echo-sounding analyses of Chapter 2, of all schelly (closed bars, N = 154) and charr (open bars, N = 472) collected by entrapment during the present study (November 1991 to March 1994, inclusive).

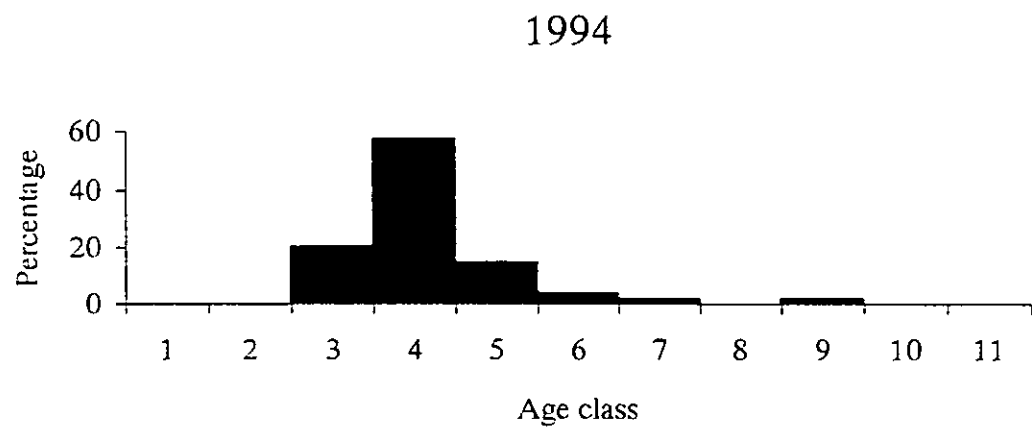


Fig. 6.4 Age frequency distributions of schelly entrapped during the main entrapment periods (January, February and March) of 1992 (N = 24), 1993 (N = 57) and 1994 (N = 64).

1965-1967



1992-1994



Fig. 6.5 Age frequency distributions of schelly entrapped during 1965-1967 (N = 188 from Bagenal, 1970) and during the main entrapment periods (January, February and March) of 1992-1994 (N = 145).

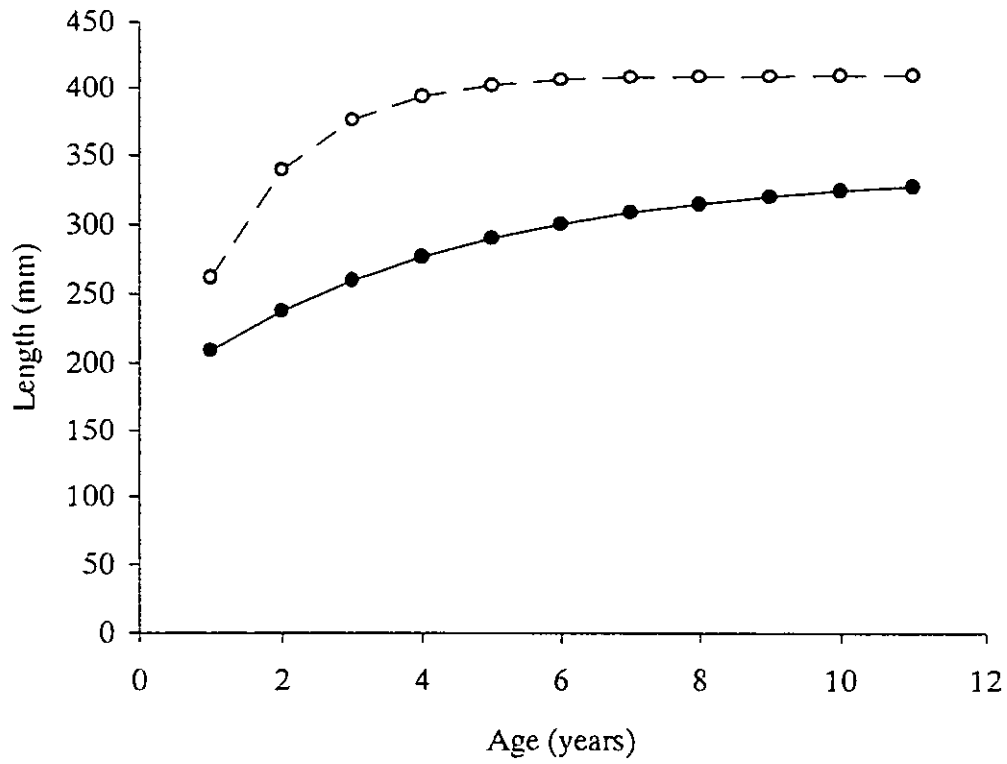


Fig. 6.6 von Bertalanffy growth curves for shell length (mm) versus age (years) for shells entrapped during the main entrapment periods (January, February and March) of 1992-1994 (closed symbols with continuous line) and during 1965-1967 (open symbols with broken line, data from Bagenal, 1970).

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