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# MONITORING THE FISH POPULATIONS OF WINDERMERE, 2010

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Contract Start Date: 1 April 2007
Report Date: 31 March 2011
Report To: Environment Agency (North West Region)
CEH Project No: NEC03461
CEH Report Ref No: LA/NEC03461/8

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**EXECUTIVE SUMMARY**

1. The Arctic charr (*Salvelinus alpinus*) is widely recognised as a species of extremely high biodiversity conservation value in the U.K. and is listed on the U.K. List of Priority Species and Habitats of the U.K. Biodiversity Action Plan (www.ukbap.org.uk). At the same time, it is one of the very few lake fish species in the U.K. to be exploited on a commercial or semi-commercial basis. In Windermere, where populations of spring- and autumn-spawning Arctic charr exist in the north and south basins of the lake, this nationally rare and environmentally intolerant species faces significant local pressures.

2. The objectives of the present study were to monitor the Arctic charr populations of the north and south basins of Windermere by day and night hydroacoustic surveys throughout 2010, to survey the lake's other major fish species by gill netting during the autumn of 2010, to examine 2010 catch and effort data from the lake's Arctic charr fishery, and finally to examine selected components of long-term fish population data for Arctic charr, perch (*Perca fluviatilis*) and pike (*Esox lucius*) collected outside the present project by CEH from 1990 to 2010.

3. During the 2010 hydroacoustic surveys, in the north basin the maximum observed abundance of total fish was 1838.0 fish $ha^{-1}$ in July and was driven primarily by changes in the abundance of small fish in the upper water column which peaked at 1776.0 fish $ha^{-1}$ in the same month. In the south basin, the maximum observed abundance of total fish was 2410.0 fish $ha^{-1}$ at night in July and was again due primarily to the abundance of small fish in the upper water column which peaked at 2338.7 fish $ha^{-1}$ at night in the same month.

4. In a longer-term context, total fish abundance recorded by hydroacoustics has shown a marked increase in both basins, since 1997 in the south basin and since 1999 in the north basin, although with considerable variability in recent years. In both cases, changes have been driven primarily by increases in small fish in the upper water column. The abundance of large fish in the upper water column during the day, i.e. the best hydroacoustic assessment of the stock exploited by the Arctic charr fishery, declined markedly after 1991, showing some temporary and limited recovery in the north basin in the late 1990s before entering a period of relative stability. Such individuals have been relatively stable in recent years in the south basin. However, gill-netting data reveals that substantial numbers of these hydroacoustic targets in the south basin are likely to originate not from Arctic charr, but from an expanding roach (*Rutilus rutilus*) population.

5. A total of 422 fish was sampled by survey gill netting at Windermere in 2010, comprising 6 (1.4% by numbers) brown trout (*Salmo trutta*) (length 128 to 225 mm, weight 27 to 127 g), 384 (91.0% by numbers) perch (length 44 to 329 mm, weight 1 to 655 g), 6 pike (1.4% by numbers) (length 165 to 657 mm, weight 44 to 2820 g), 25 (5.9% by numbers) roach (length 43 to 300 mm, weight1 to 565 g) and 1 (0.2% by numbers) tench (*Tinca tinca*) (length 325 mm, weight 633 g). The prevalence of roach represents a small decrease from the equivalent figure of 7.5% recorded in 2009 and, taken with the hydroacoustics data, may be argued to suggest that the increased roach population is now beginning to fluctuate in abundance. Whatever the finer details of its current population dynamics, it is clear that following its apparent introduction by anglers live-baiting for pike at least as long ago as the 1890s, the roach has now become established as an abundant component of the fish community in both

basins of the lake. The present gill-net survey notably failed to record any common bream, which in 2009 had comprised 2.3% of the fish community. However, two individuals were sampled by other nets set in the south basin of the lake at the same time as the present gill-net survey. It thus appears that the common bream population of Windermere, which almost certainly is also an introduced species, is now also expanding. Finally, the 2010 gill-net survey was also remarkable because it produced the first record of tench within the present monitoring programme in the form of a single individual from the south basin. Although little can be concluded from the observation of a single fish, it is possible that alongside roach and common bream this third cyprinid is now also beginning to increase in abundance.

6. Mean Arctic charr fishery Catch-Per-Unit-Effort (CPUE) in the north basin (0.58 fish $h^{-1}$) was more than twice that of the south basin (0.24 fish $h^{-1}$) during 2010, and both had declined substantially from their 2009 values (north basin 0.97 fish $h^{-1}$, south basin 0.88 fish $h^{-1}$). Fishery performance in the north basin thus continued its medium-term decline and reached its lowest value on record, while the performance in the south basin showed an even greater year-on-year fall and also reached its lowest value on record. Within data from 1990 to 2010, where available, a significant relationship existed between Arctic charr fishery CPUE and the abundance of large fish in the upper water column during the day revealed by hydroacoustics in the north basin, but not in the south basin where it is suggested numbers of large roach are now also registered by hydroacoustic survey.

7. A CPUE of Arctic charr of 0.6 fish $net^{-1}$ $day^{-1}$ recorded during November 2010 in scientific gill netting on a spawning ground in the north basin of Windermere continued a dramatic decrease observed almost continuously since 1990. Significant relationships exist

between such scientific CPUE for Arctic charr and the CPUE of the fishery for this species in the north basin, and between it and the abundance of large fish in the upper water column during the day revealed by hydroacoustics in the north basin. The CPUE of scientific perch sampling by trapping in the north and south basins, and by inference the population abundance of this species, showed no overall trend during the period from 1990 to 2010. The same was true for pike sampled by gill netting in the south basin, although CPUE of this piscivore in the north basin showed some increase up to 2000 but has since been decreasing such that in 2010 it was only slightly higher than that of the south basin.

8. Although present data are inadequate to allow any conclusions to be drawn, the increase and spread of the roach population of Windermere out from inshore to offshore habitats is a concern on the grounds of potential competitive interactions between this cyprinid and Arctic charr for the zooplanktonic prey resources of the epilimnion. Furthermore, this cyprinid is likely to be favoured by any future increase in the degree of eutrophication of either basin or by continued increases in water temperature associated with climate change. Notably, it now appears to be being joined in its expansion by the closely related and similarly introduced cyprinid common bream.

9. With respect to the Arctic charr fishery itself, there is no evidence that this source of mortality has any significant population impact. In contrast, eutrophication-associated water quality issues, particularly in the south basin but now also to some extent in the north basin, give rise to more concern. A recent deterioration in oxygen conditions in the lower hypolimnion of the south basin during the late summer brings such levels near to or beyond the tolerance limits of Arctic charr and may have provoked some movement out of this basin.

10. The present hydroacoustic monitoring programme, together with data from the Arctic charr fishery and scientific gill netting of spawning Arctic charr, indicates Arctic charr populations in overall marked decline in both the north and south basins of Windermere over the last approximately 20 years. It may also be noted that the present day Arctic charr populations now face pressures from eutrophication and, potentially, from the expanded roach populations and climate change.

11. A series of recommendations was made for future research outside the present monitoring programme, including continuation and development of the current Environment Agency log book scheme for the Arctic charr fishery, further analysis of existing hydroacoustic data with respect to echo strength, further analysis of existing data from roach population surveys, study of potential competitive interactions between roach and Arctic charr, investigation of temperature-induced delays in Arctic charr spawning time, modelling of the habitat volumes of Windermere inhabitable by Arctic charr as a function of predicted climate changes and predicted algal responses including the development of deep-water anoxia, and a multivariate analysis of the long-term Arctic charr abundance data in relation to environmental data. Some of these recommendations are currently being undertaken by CEH and collaborators within a three year project investigating the response of the Windermere food web to species invasion mediated by climate change (see www.windermere-science.org.uk).

# CHAPTER 1  INTRODUCTION

## 1.1  Background

The Arctic charr (*Salvelinus alpinus*) is widely recognised as a species of extremely high biodiversity conservation value in the U.K. (Maitland *et al.*, 2007) and is listed on the U.K. List of Priority Species and Habitats of the U.K. Biodiversity Action Plan (www.ukbap.org.uk). At the same time, it is one of the very few lake fish species in the U.K. to be exploited on a commercial or semi-commercial basis. In Windermere, where populations of spring- and autumn-spawning Arctic charr exist in the north and south basins of the lake (Partington & Mills, 1988), it has been recognised for some time that this nationally rare and environmentally intolerant species face significant local pressures (e.g. Mills *et al.*, 1990).

The Arctic charr has been studied extensively in Windermere since the 1940s, principally by the Freshwater Biological Association (FBA) up to 1989 and subsequently by the Centre for Ecology & Hydrology (CEH) and its immediate predecessor the Institute of Freshwater Ecology. Much of the work in the former period was summarised by Mills & Hurley (1990), while Winfield *et al.* (2004) extended this to include a summary of work carried out since 1989. More recently, a synthesis of trends in the Windermere Arctic charr populations up to 2005 is given by Winfield *et al.* (2008a). Although Mills (1989) concluded that in the 1980s the Arctic charr fishery was too small to have any significant population impact, an interpretation still held for 2004 in a recent assessment of the Arctic charr in Windermere by Winfield *et al.* (2005a), greater concern arises with respect to eutrophication-associated water quality issues in the lake's south basin (Mills *et al.*, 1990; Reynolds & Winfield, 2002). This situation has become further complicated in recent years by species introductions or expansions, particularly of the roach (*Rutilus rutilus*) (Winfield & Durie, 2004; Winfield *et al.*, 2008a; Winfield *et al.*, 2011), which have resulted in dramatic changes in the fish community of Windermere. Roach is now a major component of the littoral fish community and also occurs in the epilimnion in increasing numbers in both basins, leading to concern over, amongst other things, potential competition for food with the Arctic charr populations (Winfield *et al.*, 2005a; Winfield *et al.*, 2008a).

Given concerns over this situation, under a project addressing the European Union Urban Waste Water Treatment Directive the Environment Agency (EA) commissioned CEH to continue a 1989-onwards hydroacoustic monitoring of the Arctic charr populations of Windermere begun by Baroudy (1993). This project was subsequently expanded to include gill-netting activities, the examination of catch data from the Arctic charr fishery, and the consideration of extracts of data from existing long-term gill-netting programmes. The project was most recently reported for 2009 by Winfield *et al.* (2010).

## 1.2 Objectives

The objectives of the present study were to monitor the Arctic charr populations of the north and south basins of Windermere by day and night hydroacoustic surveys throughout 2010, to survey the lake's other major fish species by gill netting during the autumn of 2010, to examine 2010 catch and effort data from the lake's Arctic charr fishery, and finally to examine selected components of long-term fish population data for Arctic charr, perch (*Perca* *fluviatilis*) and pike (*Esox lucius*) collected outside the present project by CEH from 1990 to 2010.

# CHAPTER 2 METHODS

## 2.1 Approach

The main approach of the present study was to continue monthly hydroacoustic surveys, begun in 1989 by Baroudy (1993), targeted at the Arctic charr populations of the north and south basins (May, July and September surveys were undertaken within the present project, while those of the remaining months were undertaken outside the present project by CEH) and to survey the lake's other major fish species by gill netting during the autumn of 2010. These activities were augmented by the examination of data from the lake's Arctic charr fishery and the examination of selected components of long-term Arctic charr, perch and pike population data collected outside the present project by CEH from 1990 to 2010. The latter continues a long-term study initiated in the 1940s by FBA.

## 2.2 Hydroacoustics

### 2.2.1 Field work

Hydroacoustic surveys were carried out using a BioSonics DT-X echo sounder with a 200 kHz split-beam vertical transducer of beam angle 6.5° operating under the controlling software Visual Acquisition Version 6.0.1.4318 (BioSonics Inc, Seattle, U.S.A.). Throughout the surveys, data threshold was set at -130 dB, pulse rate at 5 pulses $s^{-1}$, pulse width at 0.4 ms, and data recorded from a range of 2 m from the transducer. In addition to the real-time production of an echogram through a colour display on a laptop computer, data were also recorded to hard disc. The system was deployed from a 10.0 m launch powered by a 90 horse power outboard engine and moving at a speed of approximately 2.7 m $s^{-1}$, depending on wind conditions. The transducer was positioned approximately 0.5 m below the surface of the water. Navigation was accomplished using a Trimble Model PRO/XRS DGPS (Differential Global Positioning System) (www.trimble.com) with accuracy to less than 1 m, while a JRC Model DGPS212 DGPS (www.jrc.co.jp) with accuracy to less than 5 m inputted location data directly to the hydroacoustic system where they were incorporated into the recorded hydroacoustic data files. Prior to the surveys, the hydroacoustic system had been calibrated using a tungsten carbide sphere of target strength (TS) -39.5 dB at a sound velocity of 1470 m $s^{-1}$.

At approximately monthly intervals, hydroacoustic surveys were undertaken during both day and night using zig-zag designs incorporating three transects in the lake’s north basin and five transects in its south basin (Fig. 1, Table 1). North basin surveys were run in the general direction of from the south to the north, while those of the south basin were run from the north to the south. This gave a ratio of coverage (length of surveys : square root of research area) of 3.1:1.

Surveys as described above were carried out at approximately monthly intervals on 19 February, 11 March, 13 April, 11 May, 1 June, 6 July, 12 August, 28 September, 26 October and 18 November 2010. During the summer months, some surveys carried on into the early minutes of the subsequent day. No surveys were undertaken in January and December due to ice cover, with the night surveys of February being abandoned for the same reason. The night survey of the south basin in June was also abandoned due to mist.

2.2.2 Laboratory examination and analysis

Subsequent data analysis in the laboratory was performed by trace formation, also known as fish tracking, using SonarData Echoview Version 3.40.47.1551 (Myriax, Hobart, Australia, www.echoview.com) with a target threshold of -70 dB.

Data analysis involved the water column of each transect being divided into 1 m deep strata from a depth of 2 m below the transducer down to the lake bottom. Fish counts were converted to fish population densities expressed as individuals per hectare of lake surface area for each basin transect by the use of a spreadsheet incorporating the insonification volume for each depth stratum.

Estimates of target strengths produced by Echoview were converted to fish lengths using the relationship described by Love (1971),

$$TS = (19.1 \log L) - (0.9 \log F) - 62.0$$

where TS is target strength in dB, L is fish length in cm, and F is frequency in kHz. In order to maintain compatibility with the long-term analysis of hydroacoustic data from Windermere begun by Baroudy (1993), a breakpoint of –43 dB was used to pool targets into two length classes of small (i.e. less than 200 mm) and large (equal to or greater than 200 mm) fish. These classes approximately equated to below and above the minimum length of Arctic charr that can be taken by the Arctic charr fishery. In addition, data from each 1 m depth strata were combined to produce figures for total water depths and for those above and below 20 m, reflecting the fact that the Arctic charr fishery only operates to a depth of 20 m. The above calculations of fish population densities were thus produced for small, large and total fish.

As 2010 was the ninth year in which the BioSonics DT-X (or its functionally equivalent predecessor the DT6000) echo sounder had been used in the present monitoring as a replacement for an older and less sophisticated Simrad EY M echo sounder, all fish population densities produced using the newer system were converted to values that would have been recorded by the Simrad machine using a series of inter-calibration relationships determined during 2003 (CEH, unpublished data). Only these converted values are presented and considered in this report.

## 2.3 Gill netting

### 2.3.1 Field work

A gill-netting survey was carried out on 28 (four north basin sites), 29 (three south basin sites) and 30 (one north and two south basin sites) September 2010 using 10 basic (i.e. bottom set) Norden survey gill nets and 2 pelagic (i.e. surface set) Norden survey gill nets. Note that, for consistency, a further nine nets set at additional sites are not reported or considered here because they were not deployed within the annual sampling programme of the present project but as part of a more extensive survey undertaken at intervals of 5 years by CEH. The basic version of the Norden survey gill net is of a monofilament design (measuring approximately 1.5 m deep and 30 m long with 12 panels of equal length of bar mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm) and was set singly for approximately 24 hours at five sites in each basin ranging in depth from approximately 4 m to the deepest point of each basin, i.e. 64 m in the north basin and 44 m in the south basin) (Table 1, Fig. 1). This design of net, which was previously known as the Nordic survey gill net (Appelberg, 2000), has become widely adopted throughout Europe as a standard survey net. In addition, a single pelagic version of the Norden survey gill net was set for approximately 24 hours at the deepest site of each basin. This version of the Norden survey gill net measures approximately 6.0 m deep and 27.5 m long, with 11 panels of equal length of bar mesh sizes 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm. All captured fish, with the exception of any large pike or salmonids still in good condition which were measured (fork length, mm) before being released alive, were taken directly to the laboratory where they were frozen to await future processing.

#### 2.3.2 Laboratory examination and analysis

After being partially thawed from storage at -20 °C, all fish were enumerated, measured (fork length, mm) and weighed (total wet, g). Left opercular bones were removed for potential subsequent age determination, although this has not been carried out within the present project.

### 2.4 Arctic charr fishery data

Catch (in numbers of Arctic charr) and effort (in time fished) data for 2010 were acquired from a total of 11 Arctic charr anglers through the EA log book scheme and used to calculate

Catch-Per-Unit-Effort (CPUE, in numbers of fish $angler^{-1}$ $hour^{-1}$) for Arctic charr for each day fished in the north and south basins. Summary statistics for these data (i.e. means and 95% confidence limits) were then put into a long-term context by comparing them with equivalent data from 1990 (the earliest year with complete hydroacoustic data) to 2001 from one angler, 2002 to 2003 from a second angler in the north basin only, and 2004 to 2009 from the EA log book scheme.

## 2.5 Related long-term fish population data

Data were taken from the 1990 (the earliest year with complete hydroacoustic data) to 2010 components of a population monitoring programme for Arctic charr, perch and pike conducted outside the present project by CEH, continuing a long-term study initiated in the 1940s by FBA.

Firstly, data were sourced from a long-term monitoring programme for Arctic charr undertaken since 1939 using a gill net of bar mesh size 32 mm repeatedly set overnight at a depth of approximately 2 m on a spawning ground in the north basin (Low Wray Bay 1939 to 1973 (Latitude 54º 24.174’ N, longitude 2º 57.652’ W), North Thompson Holme 1975 to 2010 (Latitude 54º 21.993’ N, longitude 2º 56.293’ W)). These data were used to calculate CPUE (in numbers of fish $net^{-1}$ $day^{-1}$) of Arctic charr for the month of November from 1990 to 2010.

Secondly, data were sourced from the long-term monitoring programme for perch undertaken since 1943 using traps of hexagonal mesh wire netting of mesh size 12 mm at a depth of approximately 2 to 7 m at Green Tuft (Latitude 54º 24.515’ N, longitude 2º 57.944’ W) and Lakeside (Latitude 54º 17.032’ N, longitude 2º 57.045’ W) in the north and south basins, respectively. Further methodological details are given in Paxton & Winfield (2000). These data were used to calculate CPUE (in numbers of fish $trap^{-1}$ $week^{-1}$) of perch in the north and south basins from 1990 to 2010.

Thirdly, data were sourced from the long-term monitoring programme for pike undertaken since 1943 using gill nets of bar mesh size 64 mm at a depth of approximately 4 to 5 m at numerous locations in the north and south basins. Further methodological details are given in Paxton & Winfield (2000). These data were used to calculate CPUE (in numbers of fish $net^{-1}$ $day^{-1}$) of pike in the north and south basins from 1990 to 2010.

# CHAPTER 3 RESULTS

## 3.1 Hydroacoustics

Fig. 2 presents the population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded during day hydroacoustic surveys in 2010, while Fig. 3 presents equivalent data from night surveys. During the day, total abundance peaked at 194.2 fish $ha^{-1}$ in November. This overall pattern was driven primarily by changes in the abundance of small fish in the lower water column which peaked at 130.8 fish $ha^{-1}$ in November. During the night, total abundance peaked at 1838.0 fish $ha^{-1}$ in July and was driven primarily by changes in the abundance of small fish in the upper water column which peaked at 1776.0 fish $ha^{-1}$ in the same month.

Fig. 4 puts the above day data into a long-term context by presenting the population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded from 1989 to 2010. Total fish abundance in 2010 did not approach the highest level on record observed in 2008, but it was comparable with levels observed in 2006, 2007 and 2009. From 1989 to 1991, total fish abundance was driven primarily by changes in the numbers in the upper water column, but subsequently it has been driven primarily by changes in the numbers in the lower water column. Furthermore, from 1989 to 1991 the variation in total fish abundance was driven primarily by large fish in the upper water column, but subsequently it has been driven primarily by small fish in the lower water column. The abundance of large fish, which was driven by numbers in the upper water column from 1989 to 1991, decreased in the mid 1990s, increased in the late 1990s, and then decreased again for subsequent years where it has been relatively stable with the limited exception of 2005.

Fig. 5 puts the above night data into a long-term context by presenting population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded from 1989 to 2010. Total abundance in 2010 was much higher than in 2009 and thus similar to that of 2008. Recent trends have been driven primarily by the abundance of small fish in the upper water column. The abundance of large fish showed similar values to recent years, other than the unusually high levels of 2008, and was driven by a near equal combination of abundances in the upper and lower water column.

Finally with respect to the north basin, Fig. 6 presents again, this time alone for clarity, the population abundance of large fish in the upper water column of the north basin recorded during the day from 1989 to 2010. As noted above, the abundance of such fish, which is the most appropriate hydroacoustic measure of stock exploited by the Arctic charr fishery (but see discussion), declined markedly after 1991, showing some temporary and limited recovery in the late 1990s before entering a period of relative stability.

Fig. 7 presents population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded during day hydroacoustic surveys in 2010, while Fig. 8 presents equivalent data from night surveys. During the day, total abundance peaked at 622.6 fish $ha^{-1}$ in June and was driven primarily by a near equal combination of abundances of small fish in the upper and lower water column which peaked at 322.1 fish $ha^{-1}$ in June and at 371.2 in July, respectively. During the night, total abundance peaked at 2410.0 fish $ha^{-1}$ in July. Again as in the north basin, this pattern was driven primarily by changes in the abundance of small fish in the upper water column which peaked at 2338.7 fish $ha^{-1}$ in the same month.

Fig. 9 puts the above day data into a long-term context by presenting population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded from 1989 to 2010. Total abundance has increased markedly since 2002, driven in most years primarily by the abundance of small fish in the lower water column, although there is some suggestion of a decline in the maximum values observed in recent years. The abundance of large fish was driven primarily by numbers in the upper water column from 1989 to 1996, but has subsequently been influenced equally by abundance in both parts of the water column and has been relatively stable for a number of years.

Fig. 10 puts the above night data into a long-term context by presenting population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded from 1989 to 2010. Total abundance has shown a marked increase since 1997 in terms of annual maxima, which, as in the later corresponding long-term increase in the north basin, has been driven primarily by increases in small fish in the upper water column. However, total abundance in 2010 was similar to that seen in 2009 and thus also similar to the values seen in the 2000s before the very high levels of 2008. The abundance of large fish, driven primarily by abundance in the lower water column up to approximately 2002 and subsequently by abundance in the upper water column, was relatively low and thus did not continue the slight tendency to increase in terms of annual maxima previously observed since approximately 2000.

Finally with respect to the south basin, Fig. 11 presents again, this time alone for clarity, the population abundance of large fish in the upper water column of the south basin recorded during the day from 1989 to 2010. As noted above, the annual minimum of such fish, which is the most appropriate hydroacoustic measure of stock exploited by the Arctic charr fishery (but see discussion), has been relatively stable in recent years although there was no clear within-year maximum in 2010.

As an overall summary of the relative abundances of total fish in the two basins of Windermere, Fig. 12 presents the ratio of abundance in the north basin to that in the south basin recorded during day and night. During the day, relative abundance was almost always greater in the north than in the south up to 2002, after which the difference has been less consistent and somewhat seasonal although values for 2005 and 2008 showed some features in common with most pre-2002 years. During the night, relative abundance was almost always greater in the north than in the south up to 1996, after which the reverse has largely been the case.

### 3.2 Gill netting

A total of 422 fish was sampled by survey gill netting at Windermere in 2010, comprising 6 (1.4% by numbers) brown trout (*Salmo trutta*) (length 128 to 225 mm, weight 27 to 127 g), 384 (91.0% by numbers) perch (length 44 to 329 mm, weight 1 to 655 g), 6 pike (1.4% by numbers) (length 165 to 657 mm, weight 44 to 2820 g), 25 (5.9% by numbers) roach (length

43 to 300 mm, weight1 to 565 g) and 1 (0.2% by numbers) tench (*Tinca tinca*) (length 325 mm, weight 633 g) (Table 2).

In the north basin, perch and roach comprised 87.7 and 10.0%, respectively, of all fish while in the south basin the corresponding figures were 92.5 and 4.1%, respectively. The single tench was found in the south basin where it comprised 0.3% of all fish.

### 3.3 Arctic charr fishery data

Fig. 13 presents annual CPUE for the Arctic charr fisheries of the north and south basins of Windermere from 1990 to 2010, although no data are available for the south basin in 2002 and 2003.

During 2010, CPUE in the north basin ranged from 0.00 to 2.00 fish $h^{-1}$, with an overall mean of 0.58 fish $h^{-1}$ with lower and upper 95% confidence limits of 0.47 and 0.70 fish $h^{-1}$, respectively. In a longer-term context, these figures represent a decrease from corresponding values for 2009 and are the lowest within the overall dataset for this basin. For Arctic charr in the south basin in 2010, CPUE ranged from 0.00 to 1.00 fish $h^{-1}$, with an overall mean of 0.24 fish $h^{-1}$ with lower and upper 95% confidence limits of 0.10 and 0.38 fish $h^{-1}$, respectively. In a longer-term context, these figures show a marked decrease from those of 2009 and are the lowest within the overall dataset for this basin.

For both basins combined in 2010, CPUE ranged from 0.00 to 2.00 fish $h^{-1}$, with an overall mean of 0.52 fish $h^{-1}$ with lower and upper 95% confidence limits of 0.42 and 0.62 fish $h^{-1}$, respectively.

Fig. 14 presents the relationships between the above data and corresponding hydroacoustic data on the annual maximum abundance of large fish in the upper water column during day. In the north basin, the relationship was significant and strong (ANOVA: $F_{1,19} = 47.257$, $p < 0.001$, $r^2 = 0.713$), but in the south basin it was non-significant and weak (ANOVA: $F_{1,17} = 2.337$, $p > 0.10$, $r^2 = 0.121$).

**3.4 Related long-term fish population data**

Fig. 15 presents annual CPUE for Arctic charr (data available for north basin only), perch (both basins) and pike (both basins) in scientific biological sampling of Windermere from 1990 to 2010. CPUE of Arctic charr in the north basin has displayed a general decline over this period such that by 2010 it was only 0.6 fish $net^{-1}$ $day^{-1}$ which is 1.1% of its 1990 value. In contrast, CPUE of perch in both basins showed no overall trends. CPUE of pike in the south basin has also shown little overall trend, although there is a slightly declining trend in recent years. However, the generally higher CPUE of pike in the north basin showed considerable increase up to 2000 but thereafter decreased such that in 2010 it was only slightly higher than that of the south basin.

Fig. 16 presents relationships from 1990 to 2010 between annual CPUE for Arctic charr in scientific biological sampling of the north basin of Windermere and corresponding hydroacoustic data on the annual maximum abundance of large fish in the upper water column during day, and between the same and annual CPUE for Arctic charr in the Arctic charr fishery of the north basin. The relationship was both significant and strong for both hydroacoustic data (ANOVA: $F_{1,19} = 70.846$, $p < 0.001$, $r^2 = 0.788$) and Arctic charr fishery CPUE (ANOVA: $F_{1,19} = 29.188$, $p < 0.001$, $r^2 = 0.606$).

# CHAPTER 4 DISCUSSION

## 4.1 Hydroacoustics

Before discussing the present hydroacoustic results of 2010, it is appropriate and useful to consider some of the findings of offshore and inshore gill netting conducted previously in Windermere outside the present monitoring programme.

Activities in this area were undertaken in 2004 in offshore habitats within the project reported by Winfield *et al.* (2005a), which summarised their and earlier findings as follows. The occurrence of Arctic charr, brown trout, perch and roach in this time and place was expected given the observations of earlier years (e.g. Winfield & Durie, 2004). However, the sampling of significant numbers of roach at the offshore surface site of the north basin in 2004 by Winfield *et al.* (2005a) was a new and concerning development, reflecting a similar development in the south basin but with a time delay of several years. The offshore bottom site, i.e. the hypolimnion, of the north basin was thus left as the only habitat in Windermere dominated by Arctic charr. In the south basin, perch and roach dominated the offshore surface site, while fish were absent from the offshore bottom site of the south basin at the time of gill netting as a result of low oxygen levels (see below).

Activities in this area in 2005 were conducted in inshore habitats as a third extensive gill-net survey, previous ones being in 1995 and 2000, of the developing roach population. Although analysis of the resulting data has so far been restricted to considerations of CPUE and aspects of individual lengths, these surveys have indicated that following an initial expansion in the south basin roach have now colonised the entire littoral zone of Windermere (Winfield *et al.*, 2008a). A fourth survey of this kind was completed in September 2010, comprising the 12 survey gill nets of the present study augmented by a further nine nets set at additional sites in the two basins of the lake. In total, these 21 nets resulted in the sampling of 1066 fish comprising 6 brown trout, 2 common bream (*Abramis brama*), 939 perch, 15 pike, 103 roach and 1 tench (CEH, unpublished data).

The colonisation of offshore surface habitats of Windermere by roach, and the now confirmed presence of perch in the same locations, poses clear complications for the interpretation of hydroacoustic data which in itself cannot differentiate between species. On the basis of studies undertaken elsewhere, roach in particular are known to undertake horizontal migrations out of the littoral zone and into open water at night (e.g. Winfield & Townsend, 1988), although the degree to which this behaviour is shown is highly dependent on the prevailing environmental conditions. Recent decreases in water clarity in Windermere reported by Maberly *et al.* (2008) will only tend to increase the occurrence of this phenomenon. Furthermore, both roach and perch are also known from studies elsewhere (e.g. Winfield *et al.*, 1993) to make seasonal migrations to deeper water during the autumn, after which they may remain in the lower water column of the deeper areas of lake until the following spring and thus, in the present context, be recorded as small and large echoes in water depths below 20 m over the winter months.

The above gill-netting observations mean that only hydroacoustic data from the deep areas of the north basin during non-winter months can now safely be assumed to originate almost exclusively from Arctic charr. In contrast, data from the upper water column of both basins are becoming increasingly compromised by numbers of roach, perch and perhaps now also common bream (*Abramis brama*) (see below). With further effort, some clarification of the present 2002 to 2010 hydroacoustic data could be made by a more refined analysis with respect to individual echo strength because the vast majority of the roach and perch recorded in the offshore sites have been relatively small (CEH, unpublished data). Similar analysis of 2001 and earlier hydroacoustic data is unjustified because of a much poorer individual echo strength resolution capability of the older, single-beam echo sounder used in those years.

Finally with respect to the gill netting conducted outside the present monitoring programme, comment is also appropriate on the fact that no fish at all were recorded at the offshore bottom site of the south basin during the gill netting of 2 September 2004, while in previous summers Arctic charr had been the dominant species at this site. However, vertical profiles taken by Maberly *et al.* (2005) on 31 August 2004 revealed that the local oxygen level near this time had fallen to 2.81 mg $L^{-1}$ while water temperature was 8.3 ºC. Baroudy & Elliott (1994a) reported that at 5 to 10 ºC the lower incipient lethal levels of oxygen for Arctic charr parr were 1.8 to 2.0 mg $L^{-1}$, suggesting that the lower hypolimnion of the south basin had become uninhabitable or nearly so for this species in the late summer of 2004. This issue has subsequently been investigated further in an analysis of long-term oxygen, temperature and more limited fish vertical distribution data up to 2004 by Jones *et al.* (2006) and Jones *et al.* (2008) and has been found to be a significant and increasing issue in the south basin of the lake. Subsequent water quality sampling by Maberly *et al.* (2008) revealed that levels still remained near the tolerance limits of Arctic charr.

During 2010, month to month variations in the abundance of fish in the open water of the two basins of Windermere revealed by the hydroacoustic surveys showed patterns with some similarity to, but also some differences from, those observed in earlier years and discussed in general terms by Winfield *et al.* (2004). Detailed examination of monthly observations for 2010 showed that day total fish abundance was driven in the north basin by changes in the numbers of small fish in the lower water column and in the south basin by changes in the numbers of small fish in both the upper and lower water column. In the south basin, the annual peak occurred in June as it did in 2009, but in the north basin it occurred not in the same month but in November. These latter observations represent a return to the broad pattern observed in 2008, when total fish abundance peaked in October in the north basin but in June in the south basin. The reason or reasons for these differing patterns is or are presently unknown.

For both basins throughout 2010, night abundances of total fish were driven by changes in the abundance of small individuals in the upper water column. Combined with the day observations, this is a typical pattern for lake fish communities in which small fish often spend the day in the refuge of physical structure in shallow inshore areas, where they are not detected by vertical hydroacoustics, or at depth in areas of reduced light levels before migrating to surface offshore waters at dusk to feed on zooplankton (see review by Winfield (2004)). This persistent night-time domination by small individuals in the upper water column was also seen in previous years. Furthermore, the monthly patterns of small fish abundance observed in the two basins, which reflects the recruitment of underyearling fish into the small fish size category, were generally similar with a summer peak in abundance as previously seen in many earlier years.

Longer-term analysis of hydroacoustic data from 1989 to 2010 reveals that the fish communities of the two basins of Windermere have shown dramatic and contrasting changes in abundance in recent years.

In the north basin during day, total fish abundance in 2010 did not approach the highest level on record observed in 2008, but it was comparable with levels observed in 2006, 2007 and 2009. This observation gives further support to the suggestion of Winfield *et al.* (2010) that 2008 was an exceptional year in terms of fish abundance. The shift from variation in total fish abundance being driven primarily by large fish in the upper water column from 1989 to 1991 to subsequently being driven by small fish in the lower water column is consistent with an interpretation of an increasing importance of roach in the fish community. The abundance of large fish recorded in the upper water column during the day has shown a considerable decrease since 1991, showing some temporary and limited recovery in the late 1990s before entering a period of relative stability in recent years. As this is the fish size, water column location and time of day of exploitation of the Arctic charr fishery of the north basin, the clear implication is that the exploitable stock of this fishery has substantially declined over the overall monitoring period.

Even more marked changes have been observed in the north basin during night. Total fish abundance in 2010 was much higher than in 2009 and while it was not as high as in 2008 it was thus similar to values observed previously in the 2000s, with these trends having been driven primarily by the abundance of small fish in the upper water column. Again, these observations are consistent with those expected under an initially increasing and now possibly fluctuating roach population. The night numbers of large fish, which were themselves driven by abundance of individuals in the upper and lower water column in 2010, have generally tended to decrease since approximately 1998.

Similar changes are evident within the long-term hydroacoustic data of the south basin of Windermere, although they are both on an earlier time scale and more marked in magnitude.

In the south basin during day, total fish abundance has increased markedly since 2002, driven in most years primarily by the abundance of small fish in the lower water column, although there is some suggestion of a decline in the maximum values observed in recent years. As in the north basin, the annual minima of large fish abundance are greater in recent years, which again could result from increased numbers of roach. The abundance of large fish recorded in the upper water column during the day displayed a considerable decrease from the beginning of the data set to the late 1990s, but has subsequently been relatively stable. As this is the fish size, water column location and time of day of exploitation by the Arctic charr fishery of the south basin, the implication is that the exploitable stock of this fishery has stabilised following a decline in the middle of the monitoring period. However, the recording in recent years of significant numbers of large roach in the upper water column of the south basin summarised by Winfield *et al.* (2005a) means that the identity of these echoes cannot safely be assumed to be exclusively Arctic charr. This issue is considered again below.

Changes observed in the south basin have been even more marked during night, where total abundance has shown a marked increase since 1997 in terms of annual maxima, which, as in the later corresponding long-term increase in the north basin, has been driven primarily by increases in small fish in the upper water column. However, total abundance in 2010 was similar to that seen in 2009 and thus also similar to the values seen in the 2000s before the very high levels of 2008. As for the north basin, these changes are consistent with those expected under an increasing and now possibly fluctuating roach population. In contrast, the night numbers of large fish, which were driven primarily by abundance in the lower water column up to approximately 2002 and subsequently by abundance in the upper water column, were relatively low in 2010 and thus did not continue the slight tendency to increase in terms of annual maxima previously observed since approximately 2000.

Relative total fish abundance in the two basins of Windermere, between which individual fish are largely free to migrate, has changed dramatically over the monitoring period. Initially, total fish abundance was consistently higher in the north basin, after which numbers in the south basin showed a relative increase in the early to mid 1990s. This relative increase of total fish abundance in the south basin, coming so soon after a reduction in local phosphorus discharge, was interpreted by Elliott *et al.* (1996) to be the result of a movement of Arctic charr from the north to the south basin, rather than as a result of actual population growth for which there had been insufficient time. This relative increase in total fish abundance in the south basin continued after the analysis of Elliott *et al.* (1996) such that total fish were almost always relatively more abundant in the south basin until approximately 2002, after which the difference has been less consistent and somewhat seasonal although values for 2005 and 2008 showed some features in common with most pre-2002 years. However, over this same time period, the roach population of the south basin is known to have been increasing dramatically and has now been followed by a similar increase in the north basin. Although extensive offshore gill-net data are unavailable for the duration of this period, it is highly likely that the relative increase of total fish in the south basin in the late 1990s was due at least in part to an increase in roach abundance.

Given the relatively recent deterioration in water quality of the south basin reported by Maberly (2008) and considered in detail with specific reference to Arctic charr requirements by Jones *et al.* (2006) and Jones *et al.* (2008), a feasible interpretation of recent Arctic charr data from hydroacoustics, scientific gill netting and Arctic charr fishery performance is that such fish have again shown a mass migration between the two basins of the lake. Although again in response to changing water quality in the south basin as observed in the mid 1990s by Elliott *et al.* (1996), this time the movement appears to be a response to deterioration rather than improvement and is generally in the reverse direction of from the south basin to the north basin.

In summary, although some spatial component of the hydroacoustic data can still be robustly attributed to Windermere's Arctic charr populations, i.e. the deep-water offshore component of the north basin, the now lake-wide expansion of the roach population has significantly compromised the interpretation of all other components. However, recent improvements in hydroacoustic technology mean that some of the uncertainties involved could, with appropriate additional time resources, be resolved by further analysis of data collected in 2002 and subsequently. Furthermore, the fish communities of Windermere's north and south basins are now in such a state of change that future hydroacoustic monitoring must be accompanied by periodic biological sampling to identify the fish species responsible for detected echoes. The contrasting monthly hydroacoustic observations recorded from the two basins only emphasise the need for such activities.

### 4.2 Gill netting

The gill-net survey of 2010 confirmed the continued widespread distribution of roach in Windermere and the wide range observed in individual lengths suggests the presence of a substantial number of year classes. Its constitution of 5.9% of the overall fish community represented a small decrease from the value of 7.5% recorded in 2009 (Winfield *et al.*, 2010), which was itself a small increase over the equivalent figure of 5.1% recorded in 2008 (Winfield *et al.*, 2009). All three of these figures from the last three years are markedly lower than the value of 27.1% observed in 2007 (Winfield *et al.*, 2008b). Like the hydroacoustics data discussed above, these patterns may be argued to suggest that the increased roach population is now beginning to fluctuate in abundance. Whatever the finer details of the current population dynamics of roach in Windermere, it is clear that following its apparent introduction by anglers live-baiting for pike at least as long ago as the 1890s (Watson, 1899), the roach has now become established as an abundant component of the fish community in both basins. Interestingly, a recent analysis of the diet of pike sampled between 1976 and 2009 found the first appearance of roach in 1996 in the south basin and in 2000 in the north basin (Winfield *et al.*, in press).

The present gill-net survey notably failed to record any common bream, which in 2009 had comprised 2.3% of the fish community (Winfield *et al.*, 2010) and had thus shown some increase over the 0.3% recorded in 2008 (Winfield *et al.*, 2009). However, it must be noted that these statistics are based on just a very few individuals which have been confined to the south basin. This relative scarcity of common bream is also reflected in the fact that while none were recorded in the present gill-net survey, two individuals were sampled by the other nets set at the same time as part of a more extensive survey undertaken at intervals of 5 years (CEH, unpublished data). As before, these individuals were recorded exclusively from the south basin. In addition, an analysis by Winfield *et al.* (2011) of the numbers of large common bream taken in the long-term pike gill-netting programme first recorded them in the south basin in 1999 with a substantial increase since 2007, followed by their appearance for the first time in the north basin in 2009. Moreover, the recent analysis of the long-term diet of pike in Windermere first recorded common bream as a prey item in 2007 (Winfield *et al.*, in press). It thus appears that the common bream population of Windermere, which almost certainly is also an introduced species, is now also expanding.

Finally, the 2010 gill-net survey was also remarkable because it produced the first record of tench within the present monitoring programme in the form of a single individual in the south basin. Writing approximately four decades ago, Le Cren *et al.* (1972) noted that tench were rare and localised in Windermere and since that time only one other individual has been recorded by scientific sampling in the lake, specifically from the south basin during the long-term monitoring programme for pike (CEH, unpublished data). Although little can be concluded from the observation of a single fish, it is possible that alongside roach and common bream this third cyprinid is now also beginning to increase in abundance.

### 4.3 Arctic charr fishery data

During 2010, the mean fishery CPUE for Arctic charr in the north basin of Windermere of 0.58 fish $ha^{-1}$ was more than twice that of 0.24 fish $h^{-1}$ found in the south basin. For the north basin, this represented a marked decrease from the corresponding value of 0.97 fish $h^{-1}$ recorded in 2009 (Winfield *et al.*, 2010), which was itself substantially down from the value of 1.14 fish $h^{-1}$ seen in 2008 (Winfield *et al.*, 2009). In the south basin, the 2010 value was substantially less than the 0.88 fish $h^{-1}$ recorded in 2009 (Winfield *et al.*, 2010) and 0.53 fish $h^{-1}$ seen in 2008 (Winfield *et al.*, 2009). Fishery performance in the north basin thus continued its medium-term decline in 2010 and reached its lowest value on record, while the performance in the south basin showed an even greater year-on-year fall and also reached its lowest value on record. These observations and the overall mean CPUE for both basins of 0.52 fish $h^{-1}$ give cause for considerable and increasing concern. Although this may be tempered to some degree by the observation that between 1932 and 1947 fishery CPUE (unspecified for basin) was consistently below 1.0 fish $h^{-1}$ and had a mean of approximately 0.5 fish $h^{-1}$ (Mills & Hurley, 1990), Le Cren *et al.* (1972) noted that the performance of the Arctic charr fishery in the 1940s had become relatively poor, with the apparent reason for the decline being earlier over-fishing of the Arctic charr populations.

Thus, present CPUE in the Arctic charr fishery of Windermere is at its lowest level on record. The reason, or more likely reasons, for this changing fortune of the fishery, i.e. an initial relatively low CPUE when records were first made in the 1930s and 1940s, followed by an increase to relatively high levels (particularly in the 1980s as shown by Winfield *et al.* (2005a)), and then a decrease to relatively low levels again, are likely to be complex as discussed by Winfield *et al.* (2008a). An increase in pike abundance (Winfield *et al.*, 2008c) and decreases in oxygen concentrations at depth (Jones *et al.*, 2006; Jones *et al.*, 2008) may be two of a number of local factors driving this observed decline. Whatever the underlying reasons, the performances of the Arctic charr fisheries of the two basins have undoubtedly shown clearly declining fortunes in recent years, with performance becoming particularly poor in the south basin.

Using a temporal subset of the present Arctic charr fishery CPUE and hydroacoustic data from 1990 to 1999, Elliott & Fletcher (2001) found a strong and significant ($r^2 = 0.76$, $p < 0.01$) relationship for the north basin, but a much weaker and non-significant ($r^2 = 0.14$, $p > 0.05$) relationship for the south basin, a difference for which they suggested the relatively greater abundance of brown trout in the offshore areas of the south basin could be responsible. In the present analysis, with the dataset extended to run from 1990 to 2010 (where data availability allows), the relationship in the north basin remained strong and increased in significance ($r^2 = 0.713$, $p < 0.001$), while that in the south basin weakened and remained non-significant ($r^2 = 0.121$, $p > 0.10$). The brown trout populations of Windermere's north and south basins are known from anglers' catches to have decreased markedly in recent years, even though objective data are unknown to the authors, and thus this species is now unlikely to be a complication in the interpretation of hydroacoustic data. In contrast, the increased roach population of the south basin, where large individuals now occur in the offshore surface waters, is a more likely reason for the observed deterioration in the local relationship between Arctic charr fishery CPUE and hydroacoustic data.

### 4.4 Related long-term fish population data

The CPUE of Arctic charr of 0.6 fish $net^{-1}$ $day^{-1}$ recorded during November 2010 in scientific gill netting on one of their spawning grounds in the north basin of Windermere continued a dramatic medium-term decrease observed almost consistently since the start of the present dataset in 1990. In a more extended analysis of data from 1939 to 2004, Winfield *et al.* (2005a) showed that recent low values follow corresponding CPUEs in excess of 50.0 fish net$^{-1}$ day$^{-1}$ in the 1960s, 1970s and 1980s. Furthermore, analysis of recent CPUE and length frequency distributions by Winfield *et al.* (2005a) indicated that in 2004 the population was in a period of relatively low recruitment to the spawning stock, the individual members of which were consequently of a relatively large size. This of course gives cause for concern but, and again as for the CPUE of the fishery, this is tempered to some degree by the observation by Winfield *et al.* (2005a) that in the late 1930s and early 1940s this CPUE was consistently less than 10.0 fish net$^{-1}$ day$^{-1}$ and included the pre-2007 lowest value on record of 2.1 fish net$^{-1}$ day$^{-1}$. Thus, the CPUE of Arctic charr on one of their spawning grounds in the north basin has now declined to the extent that it has become somewhat similar to the level originally observed in the environmentally-near-pristine Windermere, although it may be noted that in the 1940s the Arctic charr fishing had deteriorated from earlier performances (Le Cren *et al.*, 1972) and the 2010 value has joined the 2008 level of 0.6 fish net$^{-1}$ day$^{-1}$ as being the joint lowest on record. Note that unlike north basin hydroacoustic and Arctic charr fishery CPUE data which can both be inflated by the immigration of individuals from the south basin, the spawning site fidelity of this species in Windermere (Partington & Mills, 1988) means that, unless other factors have changed significantly, the observed decrease in CPUE of scientific gill netting for this species in the north basin can only indicate a true decrease in the abundance of the native north basin fish natal to this site.

Given that both the scientific gill netting and the fishery for Arctic charr in the north basin of Windermere have shown similar long-term trends since the 1930s, it is not surprising that a strong and significant statistical relationship exists between these two measures. It is therefore justifiable to conclude, as did Elliott & Fletcher (2001) for data up to 1999, that both measures still provide a valid assessment of the adult Arctic charr population exploitable by the fishery. A similar conclusion, again as previously drawn by Elliott & Fletcher (2001) for data up to 1999, can also again be drawn with respect to the hydroacoustic data given the strong relationship between it and the scientific gill-netting CPUE described here for data from 1990 to 2010.

The CPUE of scientific perch sampling by trapping in the north and south basins of Windermere, and by inference the population abundance of this species, showed no overall trend during the period from 1990 to 2010. Significant variation, including an indication of recent high recent recruitment, was displayed and was very similar in the two basins. Thus, although studies elsewhere have shown that a high abundance of roach can depress perch populations through competition for food (Persson, 1991), there is no indication that this is presently happening in Windermere. It is also concluded that the observed marked and basin-specific changes in hydroacoustic data for total fish over this same period described above cannot be attributed to population changes in perch, even though this species is known to occur in numbers in the surface waters of the south basin.

Pike in the south basin of Windermere showed little overall trend in the CPUE of scientific gill netting directed at this species, although 2010 continued a slightly declining trend observed in previous years. Changes were more apparent for this species in the north basin where the generally higher CPUE showed considerable increase up to 2000, but thereafter decreased such that in 2010 it was only slightly higher than that of the south basin. However, in the context of hydroacoustic analysis, the numbers of piscivores such as pike in any lake fish community are typically at least an order of magnitude lower than planktivores such as Arctic charr. Consequently, even if pike are responsible for some echoes recorded by the hydroacoustic surveys this source of error is likely to be negligible. However, the importance of an increased pike population in the present context could be manifested by an increased predation pressure on spawning Arctic charr (Winfield *et al.*, 2008a), on which the Windermere populations are known to feed extensively (Winfield *et al.*, in press).

### 4.5 Closing remarks

The present hydroacoustic monitoring programme, together with two sources of independent data from the Arctic charr fishery and scientific gill netting of spawning Arctic charr, indicates that the Arctic charr populations of Windermere are in marked decline in both the north and south basins over a timeframe of the last approximately 20 years. Furthermore, longer-term data for the fishery and scientific gill netting show that CPUE values have now returned to the vicinity of the levels exhibited in the 1930s and 1940s, at which time the Arctic charr populations were apparently considerably depressed by the effects of earlier over-fishing (Le Cren *et al.*, 1972). Even though such over-fishing has not occurred for many decades, the scientific sampling of 2010 still produced fishery CPUE values equalling or exceeding the lowest on record. Furthermore, in contrast to those of the 1940s, the present day Arctic charr populations face continuing pressures from eutrophication and additional potential pressures from the expanded roach populations and climate change (Winfield *et al.*, 2008a).

With respect to the Arctic charr fishery itself, Mills (1989) concluded that in the 1980s this source of mortality was too small to have any significant population impact. Winfield *et al.* (2005a) concluded that there is no reason to suppose that the situation is any different in more recent years. Incidentally, although objective data are apparently lacking, Winfield *et al.* (2005a) also considered it to be extremely unlikely that a recent reported decline in the brown trout population of Windermere is attributable in any way to the local fishery for this species.

In contrast, eutrophication-associated water quality issues in the south basin of Windermere have given real concern with respect to the Arctic charr for a number of years (e.g. Mills *et al.*, 1990). Although improvements to the treatment of sewage entering the south basin improved oxygen conditions at depth in the late 1990s, it is clear that this has not progressed as far as a return to the lake's original condition and in fact there has been some further deterioration in recent years (Maberly, 2008). As a result, and as considered in more detail by Winfield *et al.* (2005a), Jones *et al.* (2006) and Jones *et al.* (2008), oxygen conditions in the lower hypolimnion of the south basin of Windermere are now near to or exceed the tolerance limits of Arctic charr.

Although present data are inadequate to allow any conclusions to be drawn, the increase and spread of the roach population of Windermere out from inshore to offshore habitats is a concern on the grounds of potential competitive interactions between this cyprinid and Arctic charr for the zooplanktonic prey resources of the epilimnion (Winfield & Durie, 2004). This cyprinid is likely to be favoured by any future increase in the degree of eutrophication and/or temperature of Windermere, and now appears to be being joined in its expansion by the closely related and similarly introduced cyprinids common bream and, possibly, tench.

Finally, some comment is appropriate on the potential of climate change to impact coldwater species such as Arctic charr. The recent increase in the temperature of Windermere and its possible adverse effect on Arctic charr by delaying spawning are discussed in detail by Winfield *et al.* (2005a) and Jones *et al.* (2006), although data are again presently insufficient to allow any robust conclusions to be drawn. In addition to having a potential impact on subsequent hatching success, if it is of sufficient magnitude such a delay in spawning could also reduce the validity of using November CPUE of spawning Arctic charr as a measure of their relative abundance. In addition, increased temperature also interacts with oxygen conditions to accelerate habitat decline with respect to species such as Arctic charr, which in Windermere is likely to become significant in the lower water column of the south basin during the late summer. This issue together with possible positive effects of increased temperature on recruitment by roach were considered in the analyses of Jones *et al.* (2006) and Jones *et al.* (2008) and were concluded to be highly significant.

Experimental studies by Baroudy & Elliott (1994b) led these authors to conclude that Arctic charr are amongst the least resistant of salmonids to high temperatures. These temperature tolerances are such that they are of considerable consequence for the spatial distribution of at least Arctic charr in Windermere.

Several areas of further work can be recommended in both fundamental and applied fields relevant to the Arctic charr and other fish populations of Windermere. In terms of monitoring, a number of these areas such as continuation of the long-term programmes for spawning Arctic charr, perch, pike and water quality are already planned by CEH, while others such as continuation of the hydroacoustic surveys would benefit greatly from the continuation of the present support from EA.

Additional recommended activities outside the long-term monitoring programmes noted above are discussed in detail by Winfield *et al.* (2005a) and so will only be considered briefly here.

For the Arctic charr fishery itself, it is recommended that the current log book scheme run by EA is continued and developed, potentially to include a detailed length and age analysis of the catch.

The recommendation by Winfield *et al.* (2005b) of the analysis of long-term oxygen, temperature and more limited fish vertical distribution data has now been completed in large part by Jones *et al.* (2006) and Jones *et al.* (2008), although resources did not permit a recommended more refined analysis with respect to echo strength and hence individual fish length. The latter is still highly desirable.

For the roach population increase, two areas of research are apparent.

Firstly, it is recommended that further analysis of the samples and results of the four major surveys of the roach population undertaken by CEH in 1995, 2000, 2005 and 2010 is completed. Although some of these data have already been analysed by Winfield *et al.* (2008c), others such as individual growths rates and year-class strengths remain unstudied. Such work, which could also include further examination of appropriate samples collected under the present project, would greatly improve our understanding of the population dynamics of roach in Windermere. Some aspects of this work are currently being undertaken by CEH and collaborators within a three year project investigating the response of the Windermere food web to species invasion mediated by climate change (see www.windermere-science.org.uk).

Secondly, it is recommended that a study be made of potential competitive interactions between roach and Arctic charr for the zooplanktonic prey resources of the epilimnion, including an assessment of current and historic growth patterns of the latter species by the examination of new and archived material. Again, some aspects of this work are currently being undertaken within the Windermere food web project described above.

Note that the recommendation by Winfield *et al.* (2005b) that the long-term temperature records of Windermere are analysed in the context of spawning and other requirements of roach has now been completed by Jones *et al.* (2006). In addition, in the context of the recent deterioration in water quality in the south basin of Windermere reported by Maberly (2008), an initial exploration of the potential involvement of roach through impacts on zooplankton was recently completed by Maberly *et al.* (2008) although much more work remains to be done with respect to this question. Such activities are also currently being undertaken within the Windermere food web project described above.

For climate change, several of the research suggestions made above already impinge on this issue and the recommendation by Winfield *et al.* (2005b) that a detailed analysis be undertaken of the long-term water temperature for Windermere in the context of the spawning and other requirements of Arctic charr has now been largely completed by Jones *et al.* (2006). However, as raised above it would now be appropriate to revisit the possibility of an induced delay in spawning time which could reduce the validity of using November CPUE of spawning Arctic charr as a measure of their relative abundance. In addition, the progress made by Jones *et al.* (2006) now allows action on the recommendation by Winfield *et al.* (2005b) that modelling of the habitat volumes of Windermere inhabitable by its brown trout and Arctic charr populations should be carried out as a function of predicted climate changes and predicted algal responses, including the development of deep-water anoxia.

Finally, and running across all of the above areas, it is recommended that a multivariate analysis is undertaken of the long-term Arctic charr abundance data in relation to environmental data including water temperature, nutrient levels, zooplankton abundance, pike abundance and potentially other features of the Windermere environment. Such analyses have recently been performed with respect to the long-term patterns of perch (Paxton *et al.*, 2004) and pike (Paxton *et al.*, 2009) recruitment in Windermere, and in doing so have identified the key driving factors.

**ACKNOWLEDGEMENTS**

We are indebted to the late Mr John Cooper and to Mr Bruce Dobson for allowing us to use their records of Arctic charr fishing effort and catches, and to Ben Bayliss, Graeme McKee, and colleagues of the Environment Agency for organising the current log book scheme for Arctic charr anglers on Windermere and allowing our use of 2004 to 2010 data from it. Prior to his recent retirement, Cameron Durie of the Environment Agency provided much appreciated support for this monitoring programme. We also thank our colleagues Mitzi De Ville, Heidrun Feuchtmayr and Paul Hodgson for assistance in the field during the night hydroacoustic surveys. Finally, we are grateful to the Freshwater Biological Association for their joint stewardship of the invaluable long-term data on the fish populations of Windermere.

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Table 1. GPS locations for 8 hydroacoustic transects and 10 gill-netting sites used at Windermere. Locations are given in degrees and decimal minutes.

| Event | Latitude (North) | Longitude (West) |
|---|---|---|
| Transect 1 start | 54, 22.000 | 2, 56.340 |
| Transect 1 end | 54, 23.480 | 2, 56.330 |
| Transect 2 start | 54, 23.480 | 2, 56.330 |
| Transect 2 end | 54, 24.030 | 2, 57.550 |
| Transect 3 start | 54, 24.030 | 2, 57.550 |
| Transect 3 end | 54, 24.830 | 2, 57.610 |
| Transect 4 start | 54, 20.320 | 2, 56.370 |
| Transect 4 end | 54, 19.780 | 2, 56.700 |
| Transect 5 start | 54, 19.780 | 2, 56.700 |
| Transect 5 end | 54, 19.160 | 2, 56.660 |
| Transect 6 start | 54, 19.160 | 2, 56.660 |
| Transect 6 end | 54, 18.950 | 2, 57.340 |
| Transect 7 start | 54, 18.950 | 2, 57.340 |
| Transect 7 end | 54, 18.050 | 2, 57.070 |
| Transect 8 start | 54, 18.050 | 2, 57.070 |
| Transect 8 end | 54, 17.670 | 2, 57.340 |
| Site 1 (Green Tuft) | 54, 24.448 | 2, 57.799 |
| Site 2 (Off High Wray Bay) | 54, 23.798 | 2, 57.530 |
| Site 3 (North Basin Deep) | 54, 23.826 | 2, 57.110 |
| Site 4 (White Cross Bay) | 54, 23.616 | 2, 56.333 |
| Site 5 (Rayrigg Bay) | 54, 22.357 | 2, 55.275 |
| Site 6 (Chicken Rocks) | 54, 21.085 | 2, 55.939 |
| Site 7 (Rawlinson Nab) | 54, 19.620 | 2, 57.013 |
| Site 8 (South Basin Deep) | 54, 18.865 | 2, 57.088 |
| Site 9 (Off Silver Holme) | 54, 18.598 | 2, 57.377 |
| Site 10 (Lakeside) | 54, 17.032 | 2, 57.045 |

Table 2. Numbers of fish individuals recorded in the gill-net survey of Windermere on 28, 29 and 30 September 2010. The basic (bottom set) version of the Norden survey gill net was used at all sites, together with its pelagic (surface set) version at North Basin Deep and South Basin Deep sites only. The catches of the latter are identified by (P).

| Site | Brown trout | Perch | Pike | Roach | Tench | Total |
|---|---|---|---|---|---|---|
| Site 1 (Green Tuft) | 0 | 5 | 0 | 2 | 0 | 7 |
| Site 2 (Off High Wray Bay) | 0 | 1 | 0 | 0 | 0 | 1 |
| Site 3 (North Basin Deep) | 0 | 0 | 0 | 0 | 0 | 0 |
| Site 3 (North Basin Deep) (P) | 2 | 0 | 0 | 0 | 0 | 2 |
| Site 4 (White Cross Bay) | 0 | 66 | 0 | 7 | 0 | 73 |
| Site 5 (Rayrigg Bay) | 0 | 42 | 1 | 4 | 0 | 47 |
| Site 6 (Chicken Rocks) | 0 | 18 | 2 | 6 | 1 | 27 |
| Site 7 (Rawlinson Nab) | 1 | 80 | 1 | 1 | 0 | 83 |
| Site 8 (South Basin Deep) | 0 | 0 | 0 | 0 | 0 | 0 |
| Site 8 (South Basin Deep) (P) | 3 | 0 | 0 | 5 | 0 | 8 |
| Site 9 (Off Silver Holme) | 0 | 36 | 0 | 0 | 0 | 36 |
| Site 10 (Lakeside) | 0 | 136 | 2 | 0 | 0 | 138 |
| Total | 6 | 384 | 6 | 25 | 1 | 422 |

Fig. 1. Windermere showing the locations of 8 hydroacoustic transects (continuous lines) and 10 gill-netting sites (closed circles). GPS locations are given in Table 1. Redrawn with permission from Ramsbottom (1976).

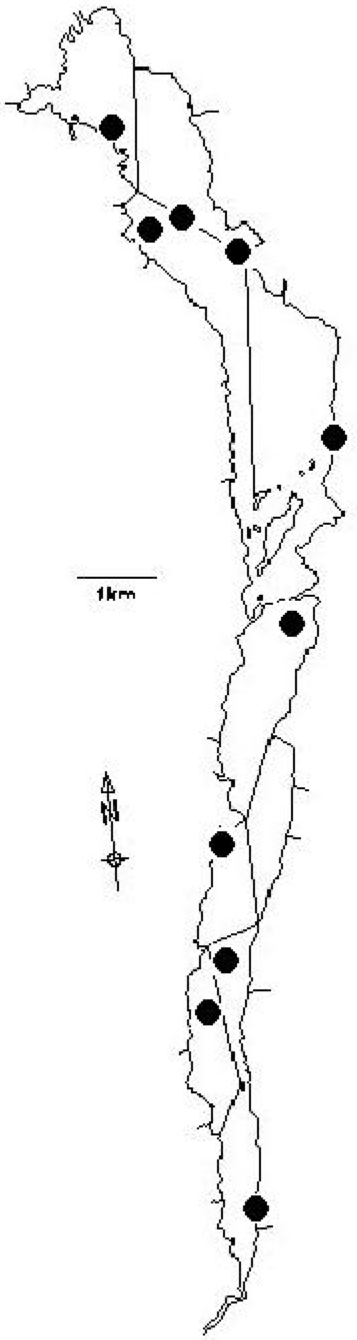
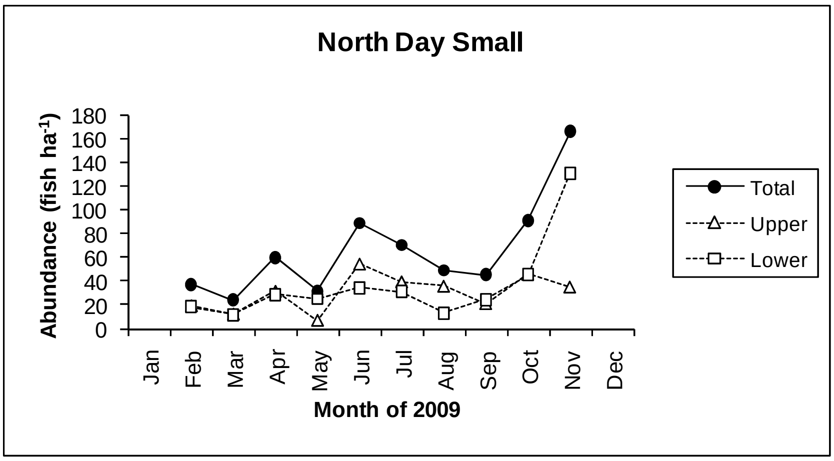
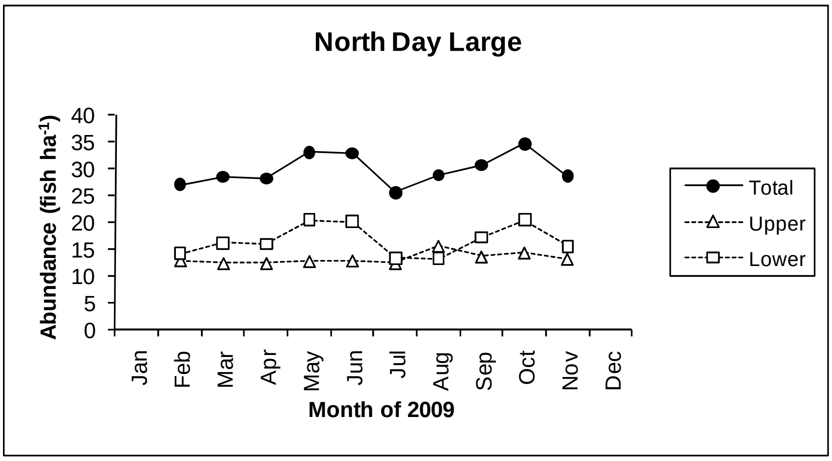


Fig. 2. Population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded during day hydroacoustic surveys in 2010.



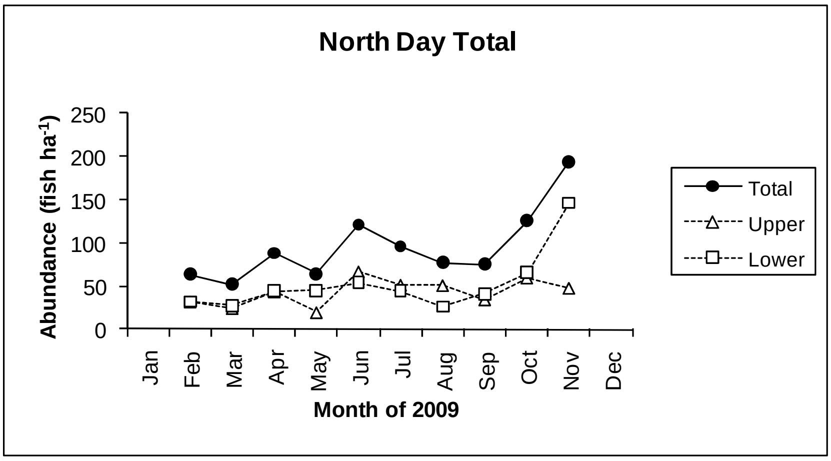
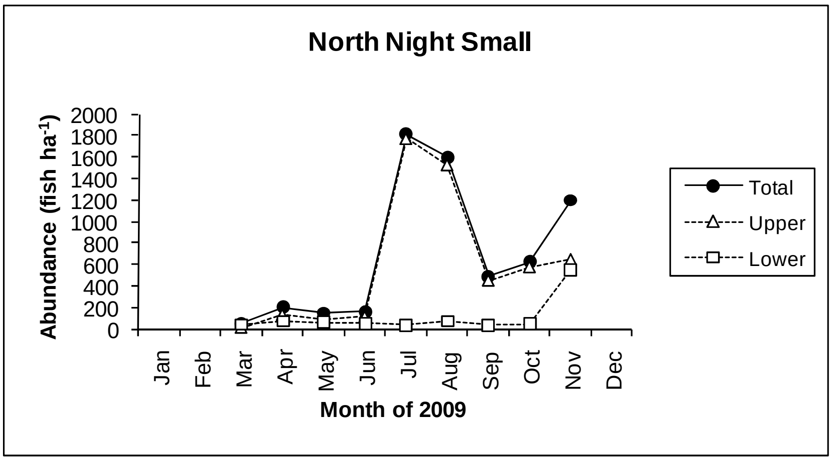
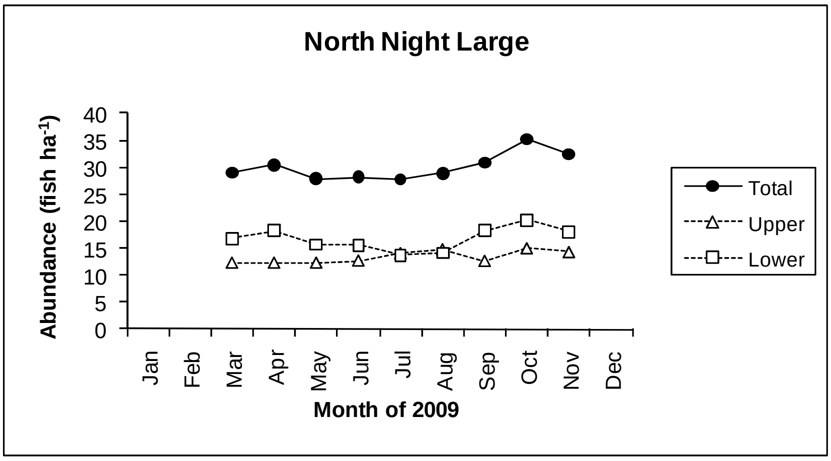



Fig. 3. Population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded during night hydroacoustic surveys in 2010.



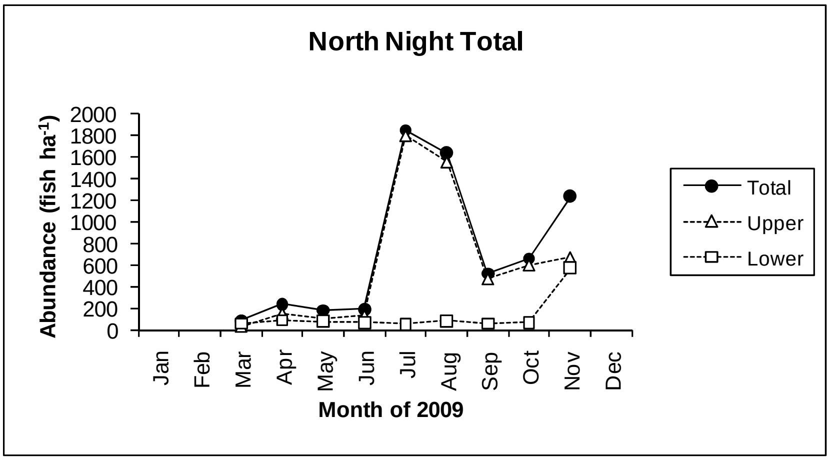
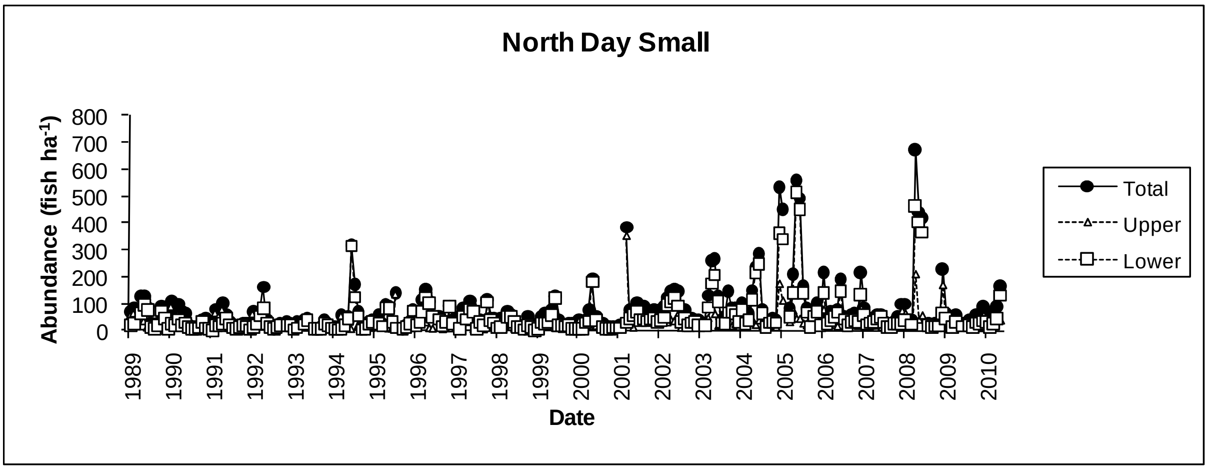
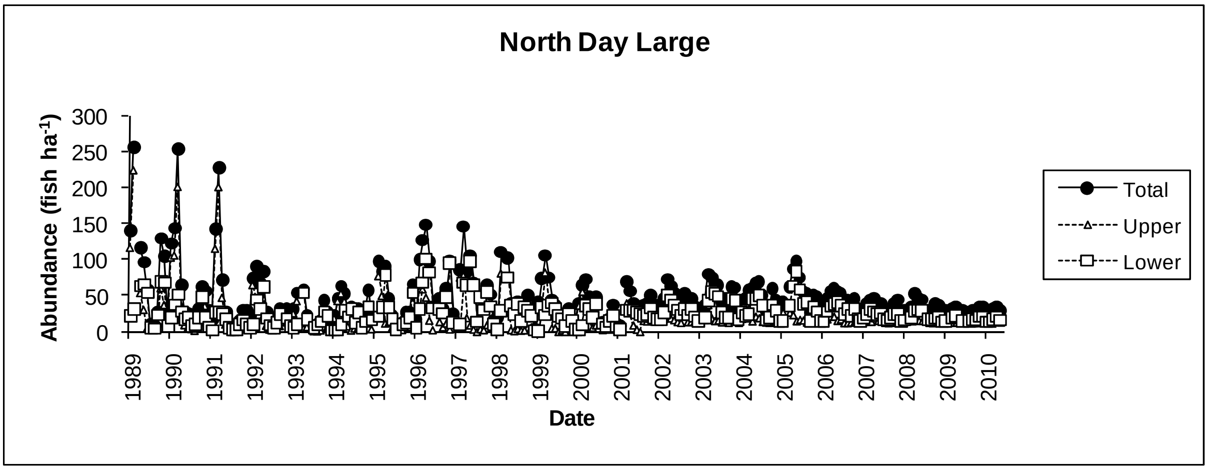



Fig. 4. Population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded during day hydroacoustic surveys from 1989 to 2010.



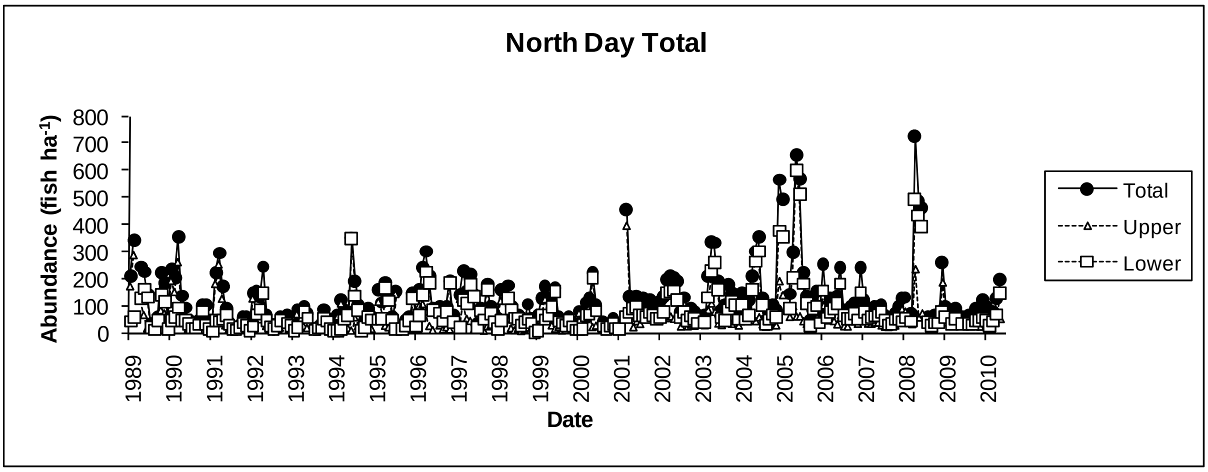
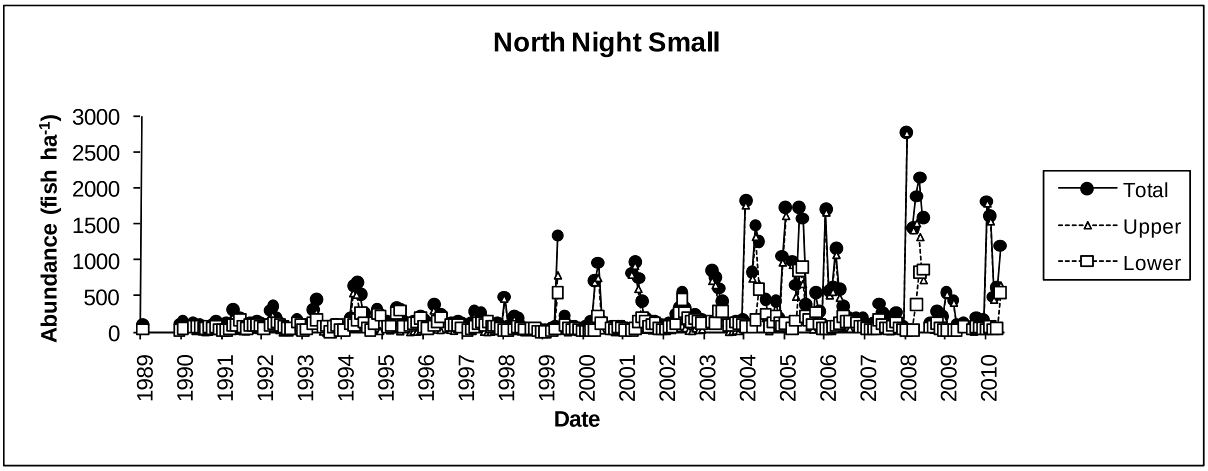
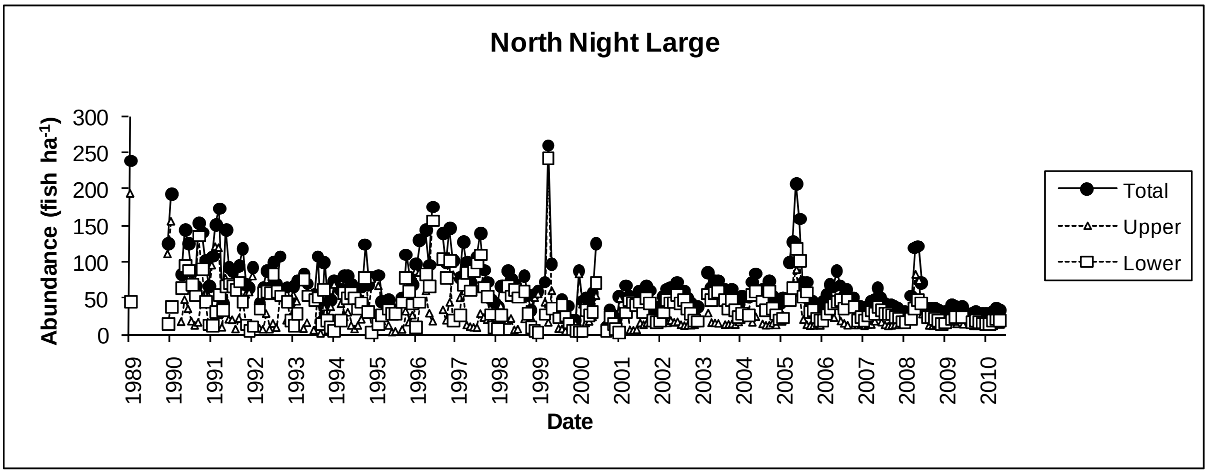



Fig. 5. Population abundance of small, large and total fish in the upper, lower and total water column of the north basin of Windermere recorded during night hydroacoustic surveys from 1989 to 2010.



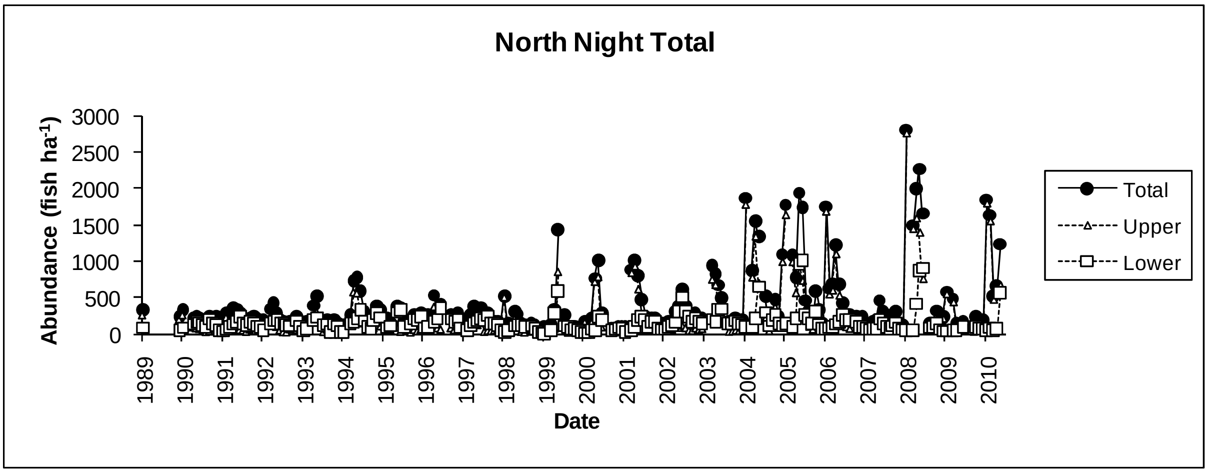



Fig. 6. Population abundance of large fish in the upper water column of the north basin of Windermere recorded during day hydroacoustic surveys from 1989 to 2010, i.e. fish of the size taken in the Arctic charr fishery, in the part of the water column exploited by the fishery and at the time of day of the fishery.

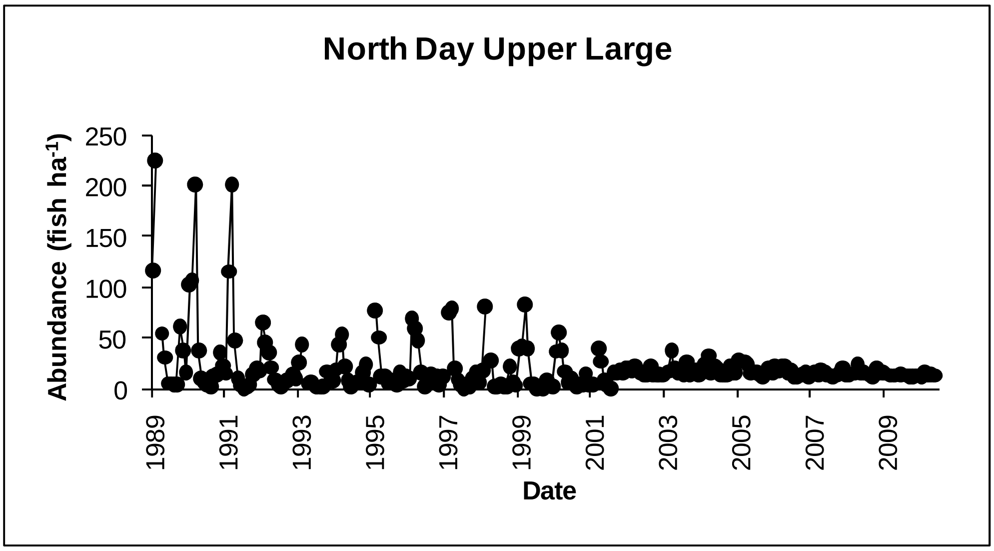
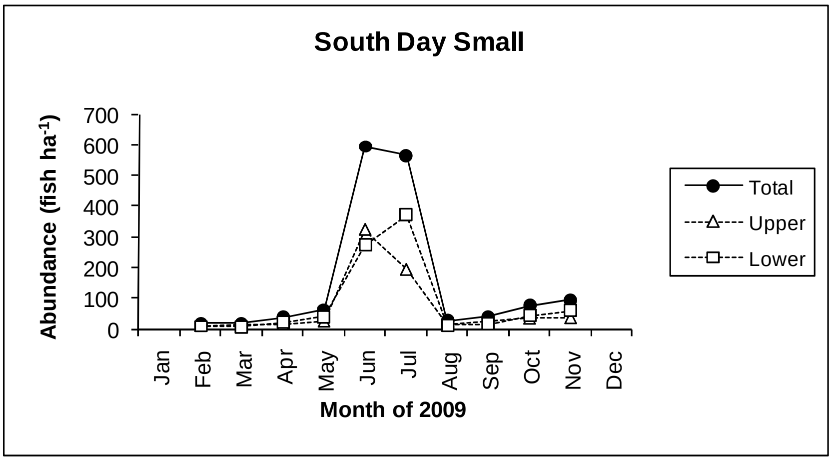
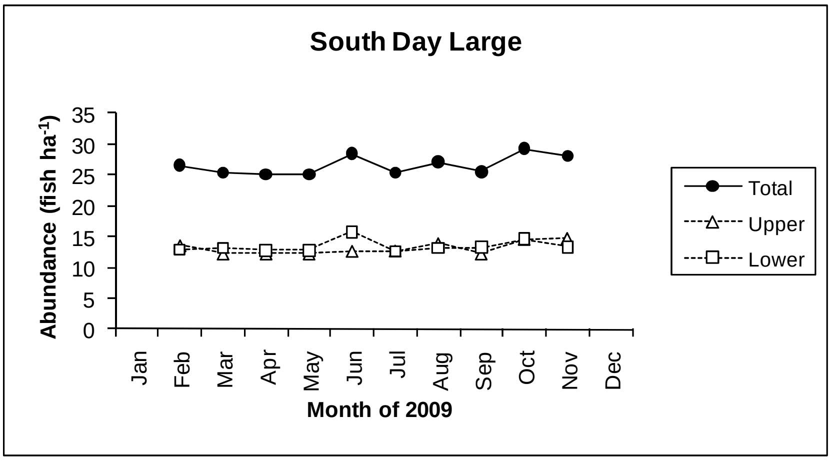


Fig. 7. Population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded during day hydroacoustic surveys in 2010.



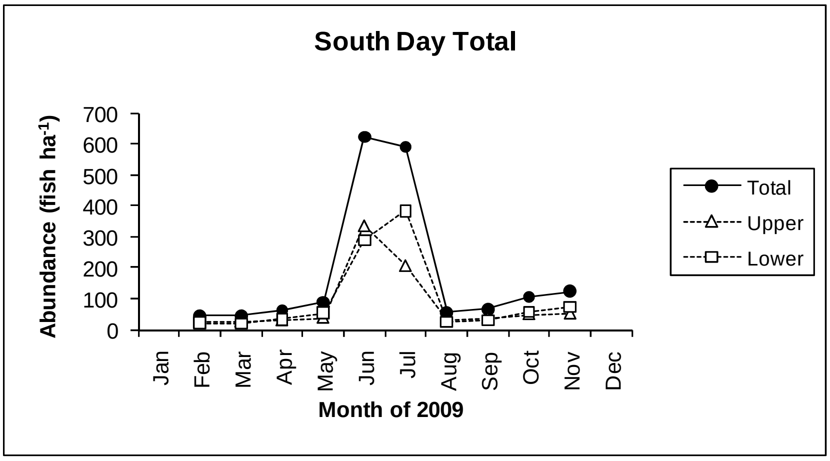
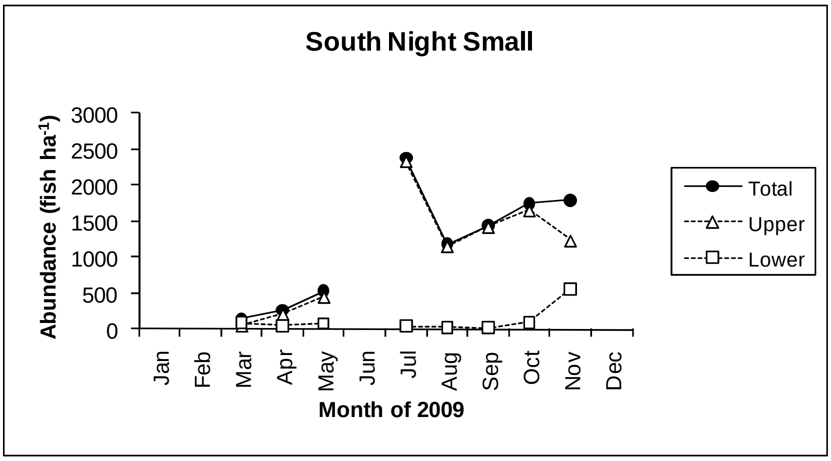
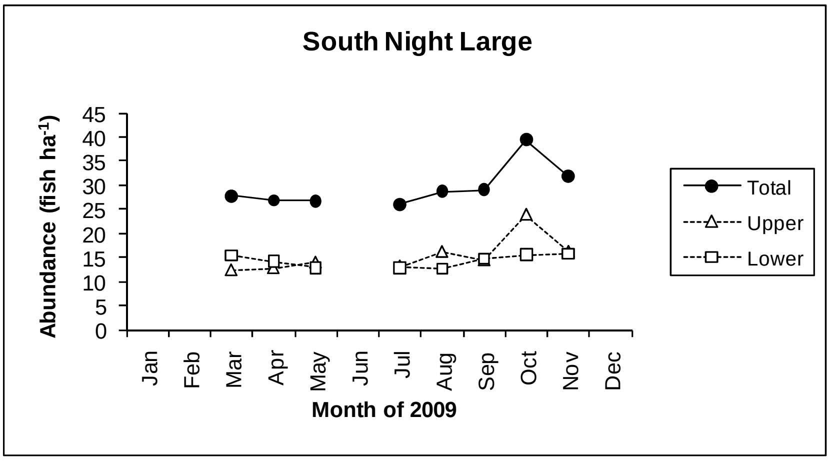



Fig. 8. Population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded during night hydroacoustic surveys in 2010.



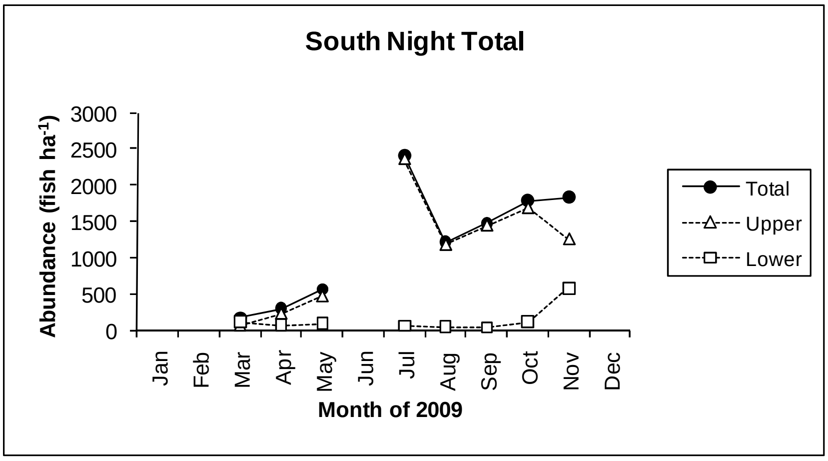
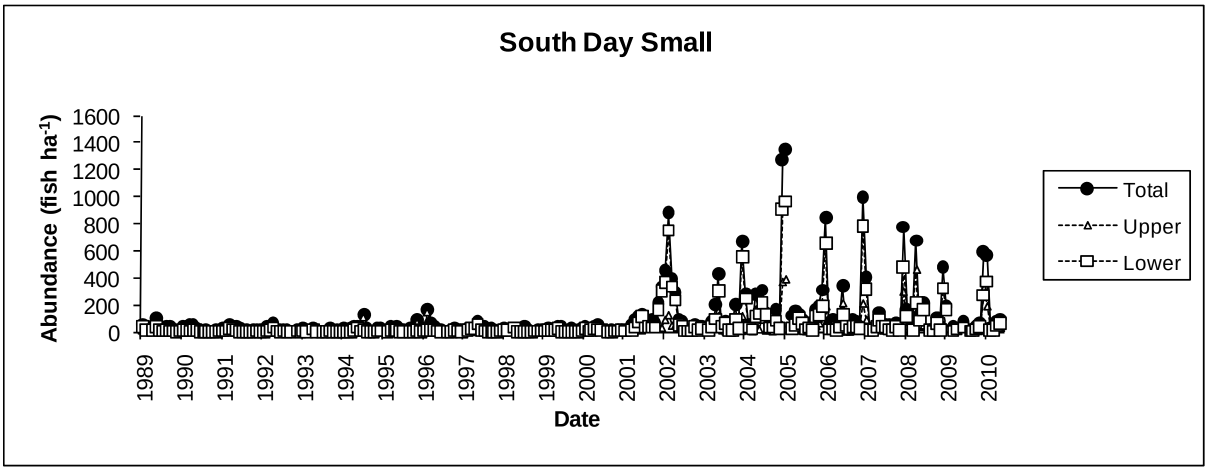
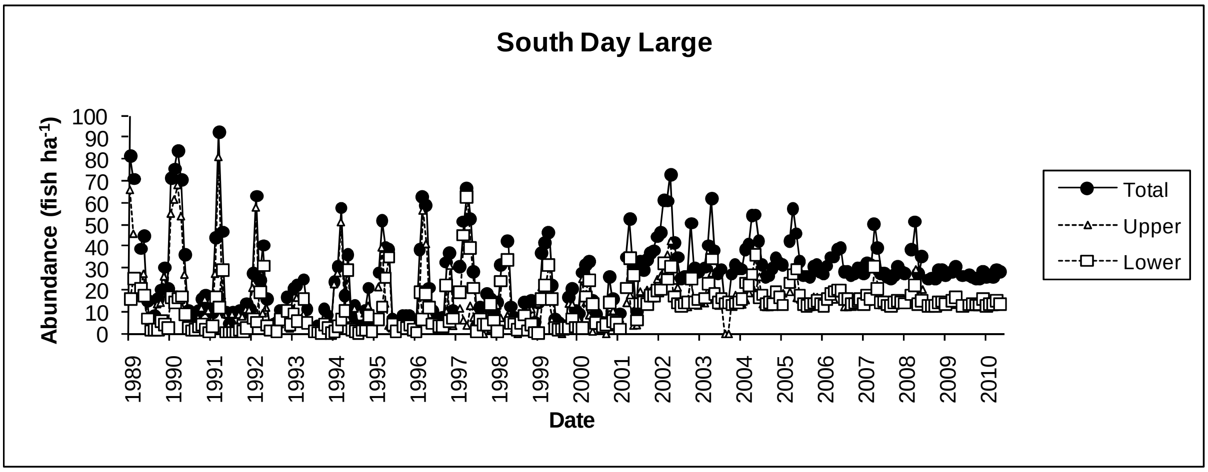



Fig. 9. Population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded during day hydroacoustic surveys from 1989 to 2010.



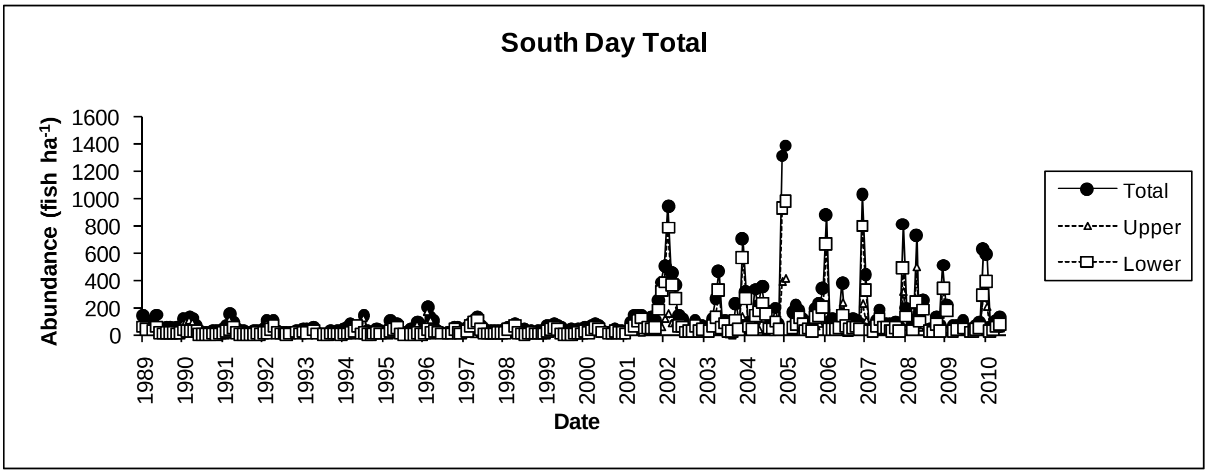
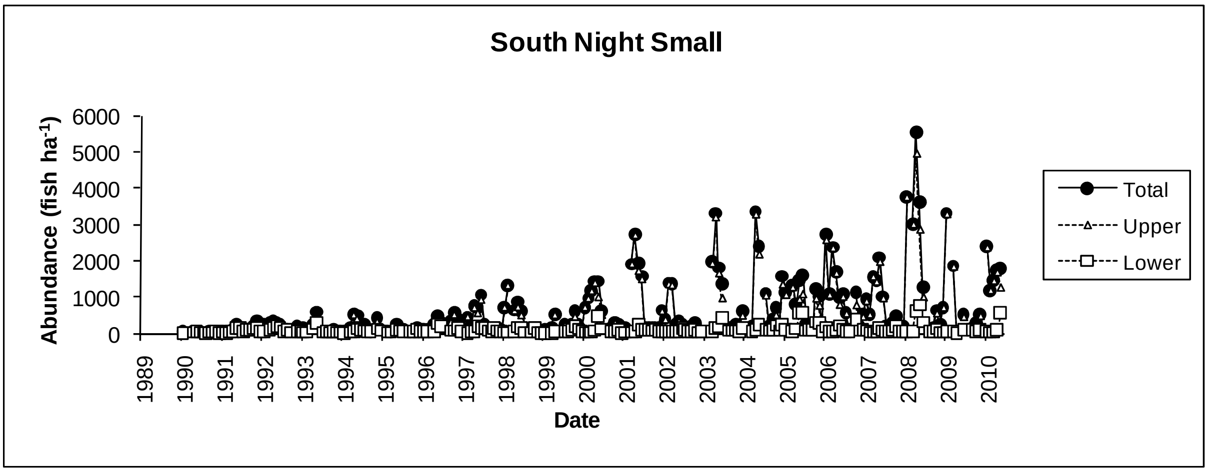
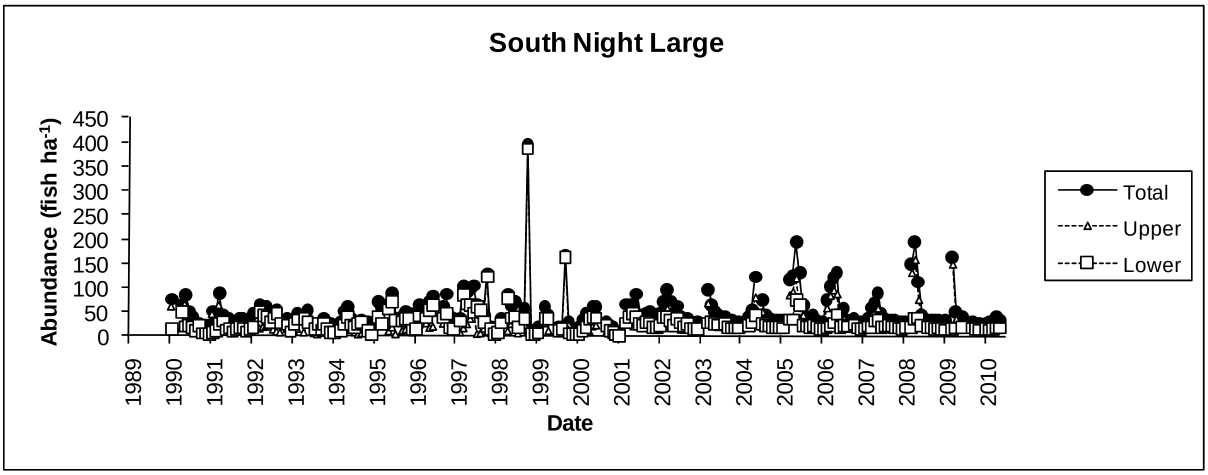



Fig. 10. Population abundance of small, large and total fish in the upper, lower and total water column of the south basin of Windermere recorded during night hydroacoustic surveys from 1989 to 2010.



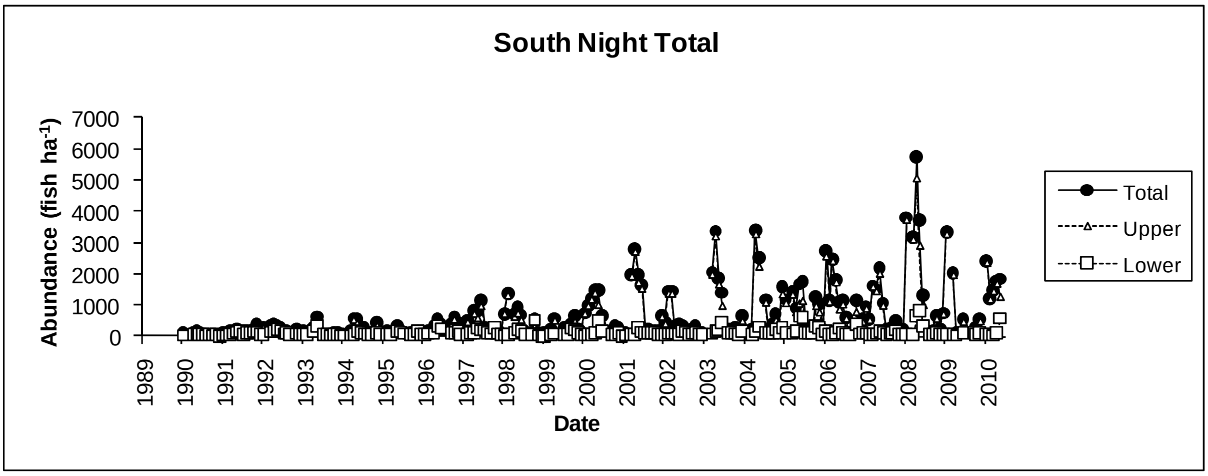



Fig. 11. Population abundance of large fish in the upper water column of the south basin of Windermere recorded during day hydroacoustic surveys from 1989 to 2010, i.e. fish of the size taken in the Arctic charr fishery, in the part of the water column exploited by the fishery and at the time of day of the fishery.

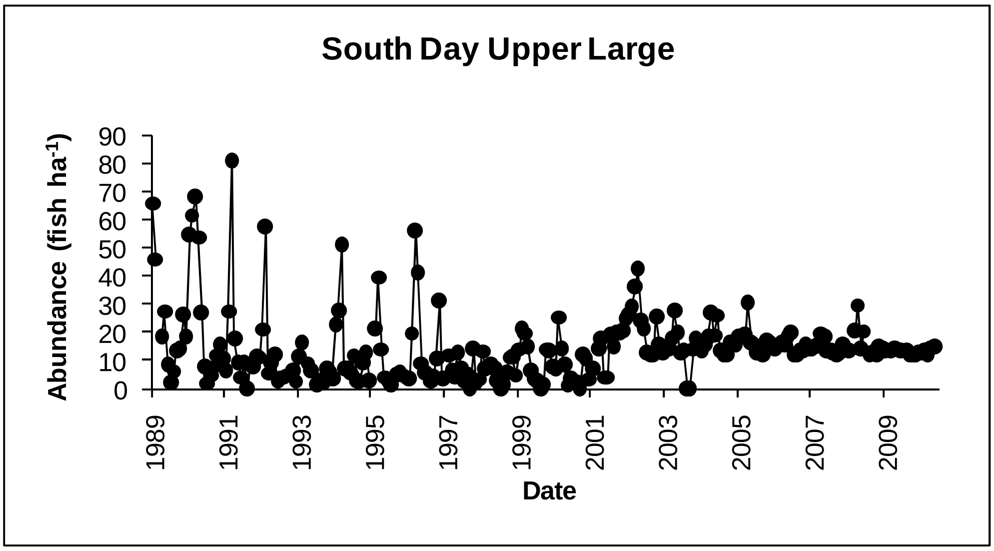
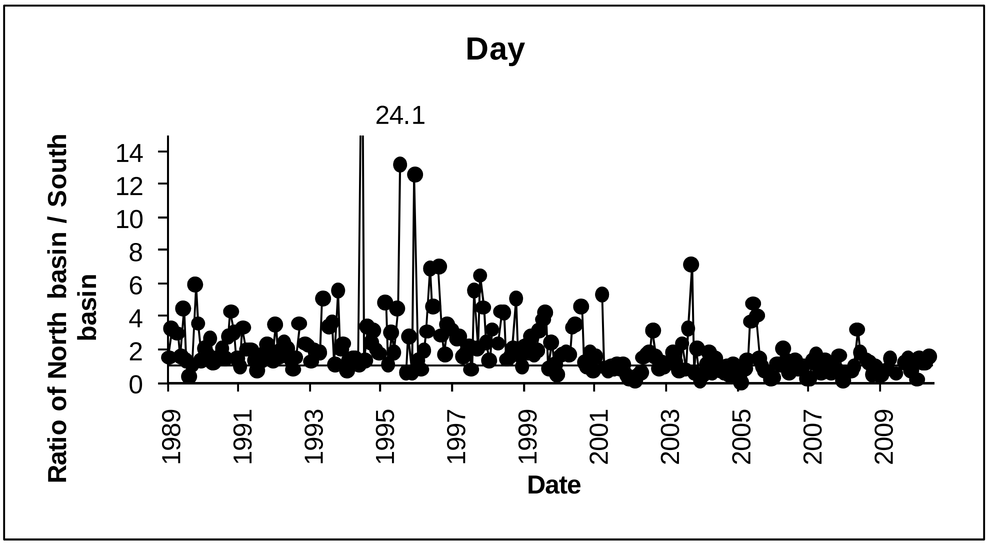


Fig. 12. Ratio of the population abundance of total fish in the total water column of the north basin to that of total fish in the total water column of the south basin of Windermere recorded during day and night hydroacoustic surveys from 1989 to 2010. The horizontal lines indicate unity.



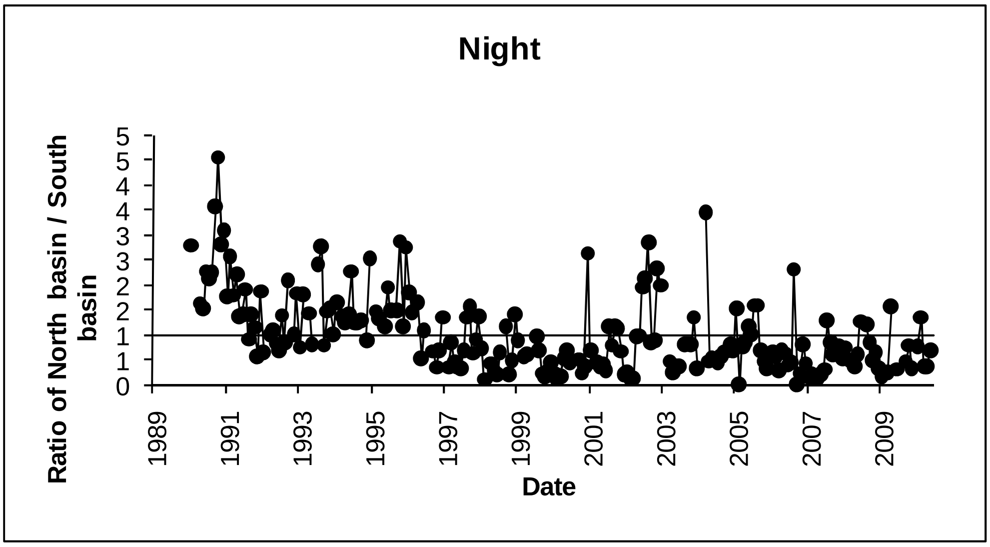
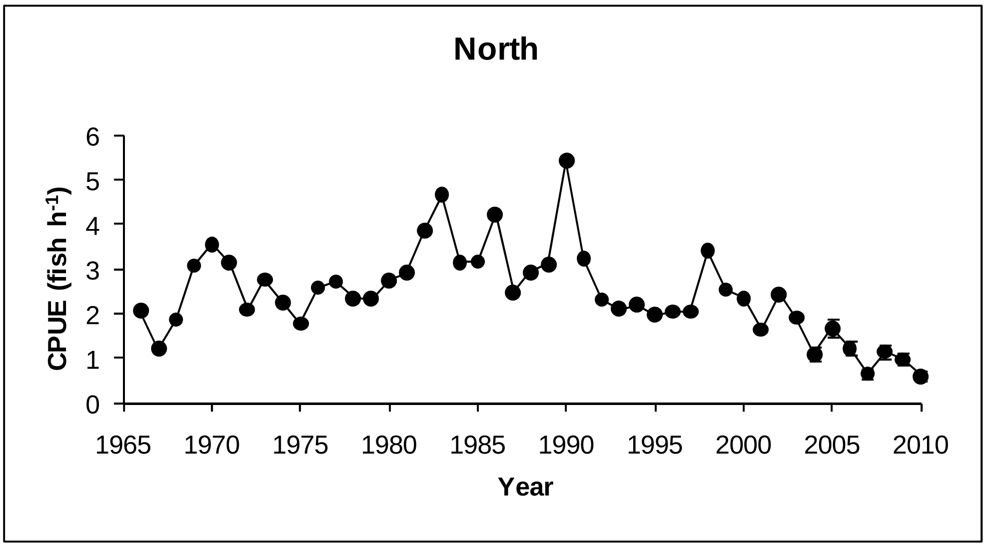



Fig. 13. Annual Catch-Per-Unit-Effort (CPUE) for Arctic charr in the Arctic charr fisheries of the north and south basins of Windermere from 1990 to 2001 (data held by CEH for one angler), 2002 to 2003 (data held by CEH for a second angler in the north basin only) and 2004 to 2010 (data from the EA log book scheme for 16, 17, 13, 13, 18, 14 and 11 anglers in 2004, 2005, 2006, 2007, 2008, 2009 and 2010, respectively). The latter seven data points are given ± 95% confidence limits.



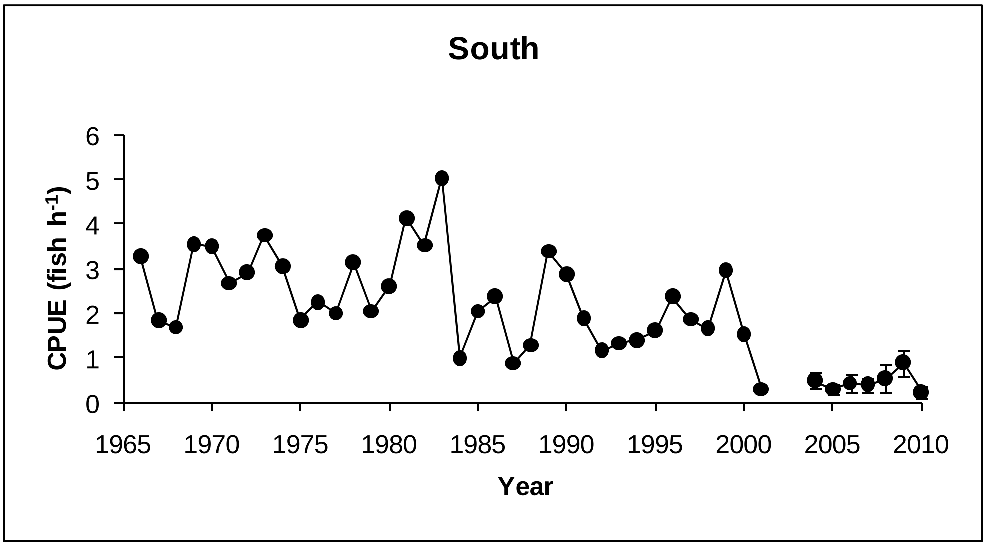
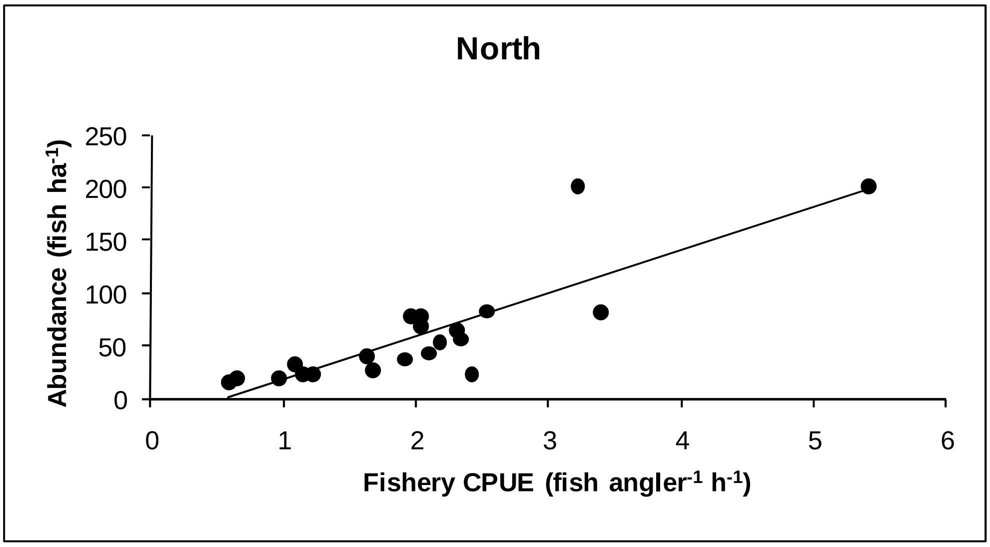



Fig. 14. Relationships between annual Catch-Per-Unit-Effort (CPUE) for Arctic charr in the Arctic charr fisheries of the north and south basins of Windermere and corresponding hydroacoustic data on the annual maximum abundance of large fish in the upper water column during day. Data are from 1990 to 2010 in the north basin, and from 1990 to 2001 and 2004 to 2010 in the south basin. Full statistics are given in the text.



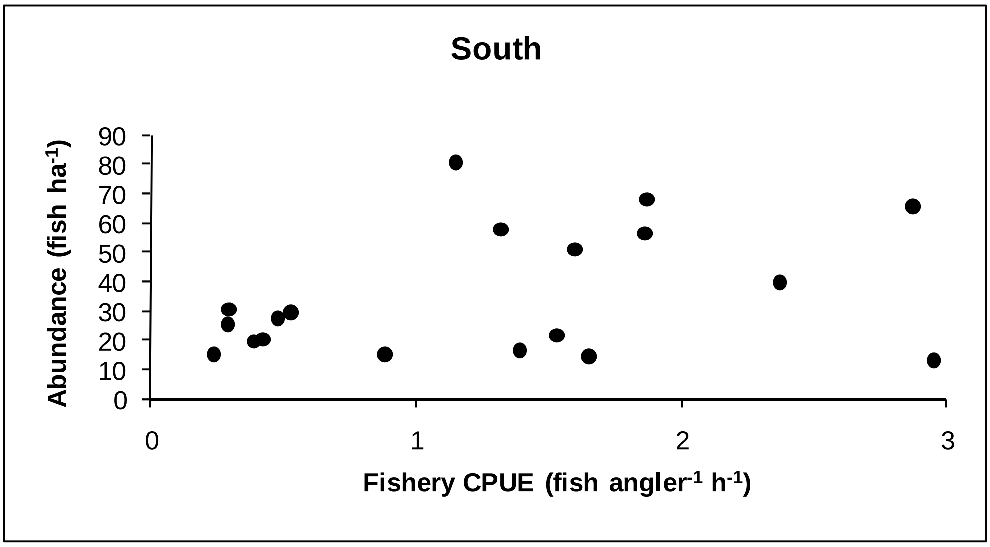
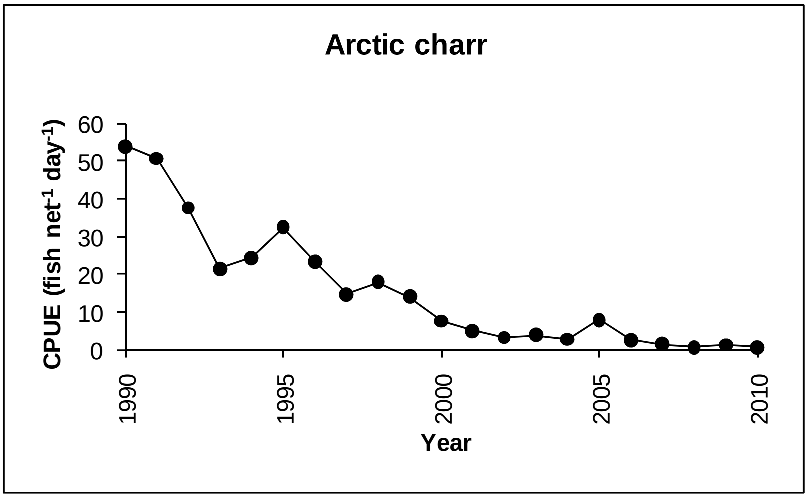
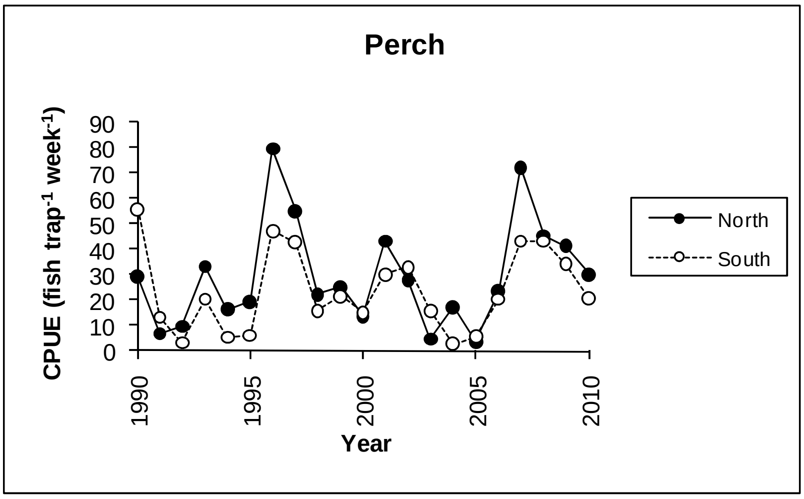



Fig. 15. Catch-Per-Unit-Effort (CPUE) for Arctic charr (data available for north basin only), perch (both basins) and pike (both basins) in scientific biological sampling of Windermere from 1990 to 2010. Data from the long-term monitoring programme begun by FBA and continued since 1989 by CEH.



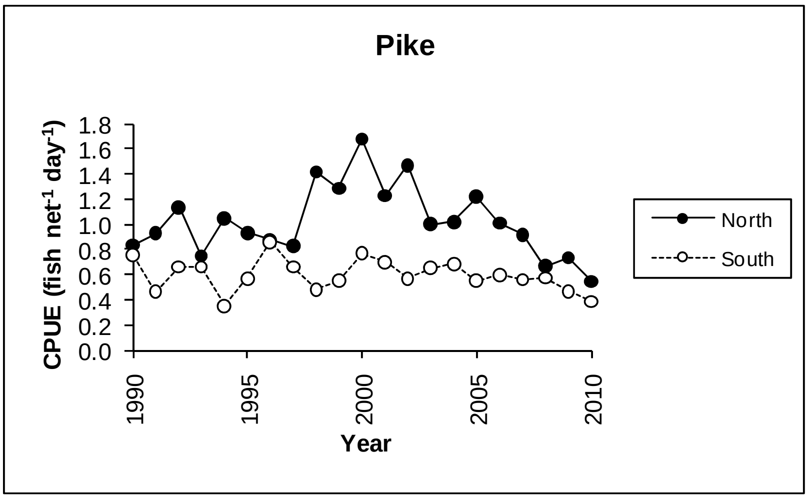



Fig. 16. Relationships between annual Catch-Per-Unit-Effort (CPUE) for Arctic charr in scientific biological sampling of the north basin of Windermere and corresponding hydroacoustic data on the annual maximum abundance of large fish in the upper water column during day, and between the same and annual Catch-Per-Unit-Effort (CPUE) for Arctic charr in the Arctic charr fishery of the north basin. Data are from 1990 to 2010. Full statistics are given in the text.