## SPECIAL ISSUE CHARR

# The Arctic charr (Salvelinus alpinus) populations of Windermere, UK: population trends associated with eutrophication, climate change and increased abundance of roach (Rutilus rutilus)

Ian J. Winfield  $\cdot$  Janice M. Fletcher  $\cdot$ J. Ben James

Received: 13 October 2006 / Accepted: 29 January 2007 / Published online: 14 March 2007 Springer Science+Business Media B.V. 2007

Abstract The north and south basins of Windermere in the English Lake District, UK, support autumn- and spring-spawning populations of Arctic charr, Salvelinus alpinus, which have been studied since the 1930s. Continuous investigations of the population dynamics of Arctic charr at this lake have involved gill netting since 1939, collection of fishery catch-per-unit-effort data since 1966, and hydroacoustic surveys since 1990. Analysis of these and associated long-term data on the abiotic environment and other components of the fish communities revealed recently contrasting fortunes of the Arctic charr populations of the north and south basins, the latter of which has been significantly impacted by eutrophication while both basins have shown elevated water temperatures and increasing roach, Rutilus rutilus, populations. Despite the introduction of phosphate stripping in 1992 and some subsequent initial improvement, the hypolimnion of the south basin still remains significantly eutrophicated and the fishery catch-per-unit-effort in this basin is now at record low levels. In addition, the spatial distribution of roach has expanded to form

J.B. James

significant components of the fish communities of inshore and offshore surface habitats, where this cyprinid may compete with Arctic charr for zooplanktonic prey. It is concluded that the Arctic charr populations of Windermere, particularly those of the south basin, currently face a number of significant environmental pressures and continued management action is required to ensure their survival.

## Keywords Population dynamics

Hydroacoustics · Invasive species · Conservation · Fisheries

## Introduction

The Arctic charr, Salvelinus alpinus, is often a major component of fish communities of lakes throughout its holarctic range, particularly in more northern latitudes where it may dominate and exist as several morphs exploiting different ecological niches (e.g. Sandlund et al. [1992\)](#page-10-0). However, towards its southern limits it is typically sympatric with numerous other fish species which, together with other features of the natural environment, result in its within-lake distribution becoming more limited and usually restricted to offshore areas outside the spawning season (e.g. Mills [1989](#page-10-0)). Environmental problems such as eutrophication, climate change and species

I. J. Winfield  $(\boxtimes)$   $\cdot$  J. M. Fletcher  $\cdot$ 

Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK e-mail: ijw@ceh.ac.uk

introductions are likely to have relatively greater impacts on Arctic charr in these more southern areas. Understanding and intelligently managing these significant issues requires reference to fish population and environmental datasets of long duration. Unfortunately, where such rare data do exist they usually relate to Arctic charr populations significantly influenced by fisheries activities (e.g. Klemetsen et al. [2002\)](#page-10-0), which makes their interpretation complex.

The locality of Windermere, UK, is a notable exception to the above pattern. The autumn- and spring-spawning Arctic charr populations which inhabit the north and south basins of this lake have been studied extensively since the 1930s and show no impacts from a very small, semi-commercial, plumb-line fishery (Mills [1989\)](#page-10-0). Aspects of the early part of this work were summarised by Mills and Hurley ([1990\)](#page-10-0), while Elliott and Baroudy ([1995\)](#page-10-0) extended coverage into the 1990s by which time the lake had suffered significant environmental problems for a number of years. In particular, nutrient enrichment had led to increased levels of phosphate which were leading to increasingly frequent anoxia in the south basin and thus concerns for its Arctic charr populations (Mills et al. [1990\)](#page-10-0). Notably, the lake's scarce cyprinid populations showed no increase during this period of eutrophication (Mills et al. op. cit.). This environmental deterioration was instrumental in provoking the introduction of tertiary chemical stripping of phosphate at the lake's two sewage treatment plants in April 1992.

Phosphate stripping reduced concentrations of soluble reactive phosphorus in the south basin to levels comparable with those of the early 1970s (Parker and Maberly [2000\)](#page-10-0) and produced an apparently encouraging and swift response in the Arctic charr populations (Elliott et al. [1996\)](#page-10-0). However, as eutrophication levels were being addressed with at least some degree of success in the 1990s, the temperature of the lake was increasing to the extent that it impacted on the spawning time of perch, Perca fluviatilis (Winfield et al. [2004\)](#page-10-0). At the same time, a population of the cyprinid roach, Rutilus rutilus, which had apparently been introduced in the early 1900s (Watson [1925\)](#page-10-0) but previously remained localised and rare, began to increase significantly and raised concern

over potential competitive impacts on Arctic charr (Winfield and Durie [2004](#page-10-0)). Although the problem of eutrophication was being tackled in Windermere, its Arctic charr populations now faced further potential problems in the forms of climate change and roach expansion.

The objectives of the present study were to describe the long-term population dynamics of Arctic charr in Windermere in the context of the pressures imposed by eutrophication and climate change, including reference to the recent and rapid expansion of the roach population.

#### Methods

### Study site

Windermere is situated  $(54^{\circ}22' \text{ N}, 2^{\circ}56' \text{ W}; \text{alti-}$ tude 39 m) in the English Lake District, UK. It comprises a mesotrophic north basin (area 8.1  $km^2$ , maximum depth 64 m) and a eutrophic south basin (area 6.7 km<sup>2</sup>, maximum depth 44 m). The fish community is relatively simple with Arctic charr, Atlantic salmon, Salmo salar, brown trout, Salmo trutta, European eel, Anguilla anguilla, perch, pike, Esox lucius, and in recent years roach constituting major populations, although Pickering ([2001\)](#page-10-0) notes that a further nine minor species are also present. Historically, Arctic charr and perch have dominated offshore (e.g. Frost [1977\)](#page-10-0) and inshore (e.g. Le Cren [2001](#page-10-0)) habitats, respectively. Commercial netting fisheries on Windermere ceased in 1921 (Kipling [1972\)](#page-10-0), leaving as the only extant fisheries a very small semi-commercial, plumb-line fishery for Arctic charr (minimum exploitable length c. 200 mm) and some recreational angling for several other species. Limited numbers of perch and pike are removed each year by traps and gill nets, respectively, in programmes which began in the 1940s as fisheries but which persist as a scientific monitoring programme (Le Cren [2001\)](#page-10-0).

#### Water chemistry and temperature

Water samples were collected from the deepest point of each basin at weekly or fortnightly intervals from 1945 to 2005 and analysed as

described in detail by Parker and Maberly ([2000\)](#page-10-0). These data were used to calculate the mean concentrations of soluble reactive phosphorus during the first 4 weeks of the year for each basin and year as the most appropriate measure of the degree of eutrophication.

Inshore surface water temperature was recorded to an accuracy of  $0.1^{\circ}$ C at c. 09:00 h at near daily intervals from 1933 to 2005 at a location near the middle of Windermere  $(54^{\circ}21.156' \text{ N}, 2^{\circ}56.411' \text{ W})$  and used to calculate annual means.

## Hydroacoustic surveys

Day- and night-time hydroacoustic surveys of the fish populations of the north and south basins of Windermere were conducted at approximately monthly intervals from 1990 to 2005. Full details of the survey transects (zig-zag design, coverage ratio 3.1:1), single-beam system (Simrad EY-M echo sounder with 70 kHz vertical transducer (Simrad Subsea A/S, Horten, Norway)) and data analysis (HADAS (Lindem Data Acquisition Systems, University of Oslo, Norway)) used in the early years of these surveys are given by Baroudy and Elliott ([1993\)](#page-10-0), while Winfield et al. ([2006\)](#page-10-0) describe the more sophisticated split-beam system (BioSonics DT-X echo sounder with 200 kHz vertical transducer (BioSonics Inc, Seattle, USA) and data analysis (Echoview, Sonar-Data, Hobart, Australia)) currently in use on the same transects, including inter-calibrations between the two systems.

For each basin, data were used to calculate the night-time abundance of all detectable fish in the entire water column, which gives the best estimate of total fish abundance in Windermere (Winfield et al. [2007\)](#page-10-0). Data were also used to calculate the day-time abundance of large  $(\geq c$ . 200 mm) fish in the upper 20 m of the water column, which gives the best assessment of the abundance of fish of legally exploitable length in the part of the water column exploited by the Arctic charr fishery, which is itself confined to daylight hours. For each year, summary data for the above two parameters were calculated as means  $\pm 95\%$  confidence limits based on the monthly data.

#### Roach

The recently expanding roach population was sampled in both basins in 1995, 2000 and 2005 using bottom-set survey gill nets set overnight at 15 inshore sites (5 and 10 sites in the north and south basins, respectively) of depth c. 4 m during September. In 1995, each survey gill net was 60 m long and 1.5 m deep and comprised bar mesh sizes of 8, 10, 12, 16, 22, 25, 30, 33, 38 and 43 mm. In 2000, each survey gill net was again 60 m long and 1.5 m deep but comprised bar mesh sizes of 8, 10, 13, 16, 19, 25, 30, 33, 38 and 45 mm. In 2005, each survey gill net was of the standard Norden design, i.e. 30 m long and 1.5 m deep with bar mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm. All catches were frozen at  $-20\textdegree\text{C}$  to await future processing in the laboratory where all individuals were identified to species, measured (fork length, mm) and further examined beyond this study. Data were used to calculate catch-per-unit-effort (CPUE, as number of fish 100  $m^2$  net<sup>-1</sup> day<sup>-1</sup>) of small (<c. 200 mm) and large ( $\geq c$ . 200 mm) roach for each basin for each year.

In addition to the above inshore sampling, information on the roach population was also collected by periodic open-water survey gill netting using standard and pelagic versions of the Norden survey gill net from 2001 to 2004. The pelagic version of this net, which is set floating on the lake surface, is approximately 27.5 m long and 6.0 m deep with bar mesh sizes 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm. One net of each design was set overnight at the deepest points of the north or south basins on a combined total of 19 occasions between 16th May 2001 and 2nd September 2004, thus sampling the offshore surface and bottom fish communities. As for the inshore gill netting, all fish were frozen at  $-20^{\circ}$ C to await future processing in the laboratory as described above.

#### Arctic charr

Arctic charr were monitored in the north basin from 1940 to 2005 using a gill net c. 28 m long and 1.8 m deep (with some minor variations pre-1970s as described in detail by Kipling ([1984\)](#page-10-0)) of bar mesh size 32 mm. The gill net was repeatedly set overnight from October to December of each year at a depth of c. 2 m on a spawning ground (Low Wray Bay 1939–1973 (54°24.174′ N, 2-57.652¢ W), North Thompson Holme 1975– 2004 (54°21.993′ N, 2°56.293′ W)). All fish caught were identified and measured (fork length, mm) before being immediately returned alive, with the rare exception of accidental mortalities which were retained for further examination beyond the present study. These data were used to calculate CPUEs (as number of fish net<sup>-1</sup> day<sup>-1</sup>) of spawning Arctic charr for the month of November of each year, during which catches peaked.

In addition, CPUEs (as number of fish angler<sup>-1</sup> h<sup>-1</sup>) of the Arctic charr fishery in each basin were calculated on an annual basis using catch and effort data provided by one angler from 1966 to 2001, by a second angler for 2002 and 2003 in the north basin only, and by multiple anglers within an Environment Agency log book scheme for 2004 (16 anglers) and 2005 (17 anglers). Although individual trip records are not available for the first angler, the robustness of his summary CPUE data has previously been demonstrated by its significant correlation  $(r = 0.59, P < 0.01)$  with those of another angler and with other assessment methods (Elliot and Fletcher [2001\)](#page-10-0). The later data are likely to be similarly robust because in 2004 they were calculated from 1,146 h of fishing effort expended during 300 fishing trips, while in 2005 the corresponding figures were 1,202 h and 320 fishing trips.

Finally, relationships for each year between the Arctic charr fishery CPUE data and corresponding hydroacoustic data on the mean abundance of large fish in the upper 20 m of the water column during day-time were examined using simple linear regressions.

## **Results**

## Water chemistry and temperature

Mean concentrations of soluble reactive phosphorus during the first 4 weeks of the year showed overall increases between 1945 and 2005 in both the north and south basins (Fig. [1](#page-4-0)). This trend was much more marked in the south basin where it reached a peak of  $28.0 \text{ mg m}^{-3}$  in 1990 almost three times greater than the peak of 10.4 mg m–3 observed in the north basin in 2001.

Inshore surface water temperature varied with no overall trend up to the late 1980s, after which it showed a significant increase (Fig. [1](#page-4-0)). For example, for the period from 1961 to 1990 the overall mean was  $10.4^{\circ}$ C but for 1991–2005 this increased to  $11.5^{\circ}$ C (*t* test assuming unequal variances;  $t = 6.151$ , df = 34,  $P < 0.0001$ ).

## Hydroacoustic surveys

Night-time abundance of total fish in the entire water column increased substantially in both basins from 1990 to 2005 (Fig. [2\)](#page-5-0). Increased values in the north basin were largely restricted to 2004 and later, but in the south basin this increase occurred several years earlier in the late 1990s. In contrast, the day-time abundance of large fish in the upper 20 m of the water column of the north basin decreased markedly in the early 1990s, with the abundance in the south basin showing an initially similar pattern followed by a unique increase after 2001 (Fig. [2\)](#page-5-0).

## Roach

CPUEs of small and large roach increased in the inshore areas of both basins from 1990 to 2005, with increases being relatively greater for small than for large individuals and with large individuals being relatively more abundant in the south than in the north basin (Fig. [3](#page-6-0)). Total roach inshore sample sizes in the north and south basins were 189 and 406 individuals, respectively. In the offshore areas, roach comprised between 0% and 23% of the fish community by numbers at the surface of the north basin with Arctic charr, brown trout and perch also present. In the south basin, roach comprised between 20% and 80% of CPUE at the surface where the same three species plus pike also occurred (Fig. [3](#page-6-0)). At the bottom of the offshore areas, roach were never recorded in either the north basin, where only Arctic charr occurred, or the south basin, where Arctic charr, brown trout and perch were

#### <span id="page-4-0"></span>Fig. 1 Mean

concentrations of soluble reactive phosphorus during the first 4 weeks of the year for the north (closed symbols, continuous line) and south (open symbols, broken line) basins of Windermere from 1945 to 2005 (upper figure), and inshore surface water temperature presented as annual means from 1933 to 2005 (lower figure)



observed (Fig. [3](#page-6-0)). Total fish offshore sample sizes in the north and south basins were 184 and 411 individuals, respectively. No fish were sampled in the bottom offshore area of the south basin in 2004.

## Arctic charr

CPUE of spawning Arctic charr in the north basin increased from 1940 to the mid 1970s, after which it decreased such that by 2000 CPUEs were similar to those of the 1940s (Fig. [4\)](#page-7-0). Annual Arctic charr sample sizes ranged from 23 to 720 individuals, with a total sample size of 16,824 individuals. CPUEs for the Arctic charr fisheries of the north and south basins showed considerable variation between 1990 and 2005, with no marked overall trend in the north basin but a noticeable decline in the south basin in recent years (Fig. [4](#page-7-0)). During 2005, mean CPUE in the north basin was 1.67 fish  $h^{-1}$  (lower and upper 95% confidence limits of 1.47 and 1.87 fish  $h^{-1}$ , respectively) which in the context of the dataset is a relatively low CPUE although it is a slight increase on the level recorded in 2004 which was 1.09 fish  $h^{-1}$  (lower and upper 95% confidence limits of 0.92 and 1.26 fish  $h^{-1}$ , respectively). For Arctic charr in the south basin, mean CPUE in 2005 was 0.30 fish  $h^{-1}$  (lower and upper 95%) confidence limits of 0.18 and 0.42 fish  $h^{-1}$ , respectively) which was lower than the 2004 mean CPUE of 0.48 fish  $h^{-1}$  (lower and upper 95%) confidence limits of 0.29 and 0.67 fish  $h^{-1}$ , respectively). The lowest CPUE for the south basin recorded within the dataset was 0.29 fish  $h^{-1}$  in 2001. Thus, the three lowest recorded CPUEs for <span id="page-5-0"></span>Fig. 2 Night-time abundance of total fish in the entire water column of the north (closed symbols, continuous line) and south (open symbols, broken line) basins of Windermere from 1990 to 2005 (upper figure), and day-time abundance of large ( $\geq c$ . 200 mm) fish in the upper 20 m of the water column of the north (closed symbols, continuous line) and south (open symbols, broken line) basins over the same period (lower figure). Data are presented as means ±95% confidence limits



the south basin have come from the three most recent data points.

The north and south basins displayed contrasting relationships between the above Arctic charr fishery CPUE data and corresponding hydroacoustic data on the abundance of large fish in the upper water column during day-time (Fig. [5\)](#page-8-0). In the north basin, the relationship was significant and strong (ANOVA:  $F_{1,14} = 19.731$ ,  $P < 0.001$ ,  $r^2 = 0.585$ , but in the south basin it was nonsignificant and weak (ANOVA:  $F_{1,12} = 1.043$ ,  $P > 0.10, r^2 = 0.080$ .

## **Discussion**

On a global basis, the Arctic charr and its congeners face a range of environmental pressures (see Magnan et al. [2002a](#page-10-0)). Within Britain and Ireland, a recent review of the status of Arctic charr by Maitland et al. [\(2007](#page-10-0)) identified pollution, eutrophication, acidification, afforestation, engineering, exploitation, aquaculture, introduction of alien species and climate change as specific threats to this species. Understanding the impacts in Windermere of eutrophication, climate change and the recent roach expansion, following its introduction c. 100 years ago, thus has a generic importance beyond informing local conservation and fisheries management.

Although the problem of eutrophication in Windermere has been addressed for over 14 years by phosphate stripping, this action has only been partially successful. Neither the significantly impacted south basin nor the less impacted north basin has been returned to the near pristine

<span id="page-6-0"></span>Fig. 3 Catch-per-unitefforts (CPUE, as number of fish 100 m<sup>2</sup> net<sup>-1</sup> day<sup>-1</sup>) of small ( $<$ c. 200 mm, open bars) and large ( $\geq c$ . 200 mm, closed bars) roach in the inshore areas of the north and south basins of Windermere in 1995, 2000 and 2005 (upper figure), and species compositions by numbers (Arctic charr, closed areas; brown trout, open areas; perch, stippled areas, pike, vertically hatched areas, roach, horizontally hatched areas) of the fish communities at the surface and bottom of the offshore areas of the north and south basins from 2001 to 2004 (lower figure). Note that no fish were sampled in the bottom offshore area of the south basin in 2004. Sample sizes are given in the text



conditions of the 1940s. Furthermore, oxygen concentrations in the hypolimnion of the south basin are once again deteriorating to the low levels observed by Mills et al. [\(1990](#page-10-0)) in the 1980s prior to the introduction of phosphate stripping and were probably responsible for the failure to sample any fish from this habitat in 2004 (ID Jones, Centre for Ecology & Hydrology, unpublished data). The south basin of Windermere is undoubtedly deteriorating as an Arctic charr habitat.

The temperature increase of Windermere evident in recent years may play some role in the above deterioration in oxygen conditions. The warming of the inshore surface water of Windermere described up to 2002 by Winfield et al. ([2004\)](#page-10-0) has clearly persisted, with the 3 years of 2003–2005 having the second, third and eighth highest values since records began in 1933. An examination of the potential effects of climate change on fish habitats including that of lake trout, Salvelinus namaycush, in temperate zone lakes by Janssen and Hesslein ([2004\)](#page-10-0) noted that the impact of oxygen deficits on habitat availability is influenced by lake trophic status. Consequently, through interactions with oxygen availability the impact of increased temperature in Windermere can be expected to be greatest in <span id="page-7-0"></span>Fig. 4 Catch-per-uniteffort (CPUE, as number of fish  $net^{-1}$  day<sup>-1</sup>) of spawning Arctic charr in the north basin of Windermere from 1940 to 2005 (upper figure), together with CPUEs (as number of fish angler<sup>-1</sup>  $h^{-1}$ ) of the Arctic charr fisheries of the north (closed symbols, continuous line) and south (open symbols, broken line) basins from 1990 to 2005 (lower figure). No data are available for the south basin in 2002 and 2003, while data points for 2004 and 2005 are presented as means ±95% confidence limits. Sample sizes, where appropriate, are given in the text



its south basin. Janssen and Hesslein (op. cit.) also identified the potentially negative effects of warmer winters on Salvelinus spp. through effects on incubating eggs, an effect, which has yet to be investigated in Windermere. As predicted by Magnan et al. [\(2002b\)](#page-10-0), the issue of climate change is emerging as a key area for future research on Arctic charr and its congeners.

Despite the limited improvement in eutrophication conditions and the temperature increase noted above, neither of which is likely to increase Arctic charr abundance significantly, total fish abundance in both basins of Windermere recorded by hydroacoustics has increased by almost an order of magnitude since 1990. The most probable explanation is that this increase is due not to Arctic charr, but to expansion of the roach population. In contrast, the post-1990 decreases observed by hydroacoustics in both basins in the day-time abundance of large fish in the upper 20 m of the water column is probably more indicative of the stocks of exploitable Arctic charr, at least in the north basin. Using a temporal subset of the present Arctic charr fishery CPUE and hydroacoustic data from 1990 to 1999, Elliott and Fletcher [\(2001](#page-10-0)) found a strong and significant relationship for the north basin, but a much weaker and non-significant relationship for the south basin, a difference which they suggested was due to the relatively greater abundance of brown trout in the offshore areas of the south basin. In the present analysis, with the dataset extended to run from 1990 to 2005 (where data availability allows), the relationship in the north basin remained strong while that in the south basin weakened and remained non-significant.

<span id="page-8-0"></span>

Fig. 5 Relationships between annual catch-per-unitefforts (CPUE, as number of fish angler<sup>-1</sup> h<sup>-1</sup>) of the Arctic charr fisheries of the north (upper figure) and south (lower figure) basins of Windermere and corresponding hydroacoustic data on the day-time abundance of large  $(\geq c. 200$  mm) fish in the upper 20 m of the water column. Data are from 1990 to 2005 in the north basin, and from 1990 to 2001 and 2004 to 2005 in the south basin. Regression statistics are given in the text

The brown trout populations of Windermere's north and south basins are known from anglers' catches to have decreased markedly in recent years (although objective data are unavailable) and thus this species is now unlikely to be a complication in the interpretation of hydroacoustic data. However, the increased roach population of the south basin, where large individuals now occur in the offshore surface waters, has become a more likely contributor to the poor local relationship between Arctic charr fishery CPUE and hydroacoustic data. In addition, the more restricted ranges of both data types in the south basin also probably contribute to the lack of a significant local relationship between these two measures of abundance. It is possible that the presently strong relationship in the north basin will also deteriorate in the future as the roach

population in that part of Windermere becomes more established and greater in individual size.

The recent expansion in the roach population of Windermere has been remarkable, particularly given that this species was first recorded in the early 1900s following its apparent introduction by anglers live-baiting for pike (Watson [1925](#page-10-0)). Le Cren [\(2001](#page-10-0)) referred to it still being present only in small numbers in some locations in the late 1930s, specifically mentioning the north end of the south basin, while extensive survey gill netting in this basin in 1979 and 1980 by Craig and Fletcher ([1981\)](#page-10-0) failed to record a single specimen. During the early 1990s, recreational angling catches of roach began to increase markedly in the south basin (although objective data are again unavailable), a pattern which is consistent with the hydroacoustic and survey gill-netting data considered above. This increase in the south basin occurred at a time when the local degree of eutrophication was falling rather than rising, as has often been observed in roach expansions elsewhere (see Persson [1991\)](#page-10-0). Furthermore, the subsequent expansion of roach into the north basin was also not associated with any increase in eutrophication. In contrast, it seems more likely that the roach expansion in Windermere is the result of the recent temperature increase which is of a magnitude similar to that identified elsewhere in the UK as being associated with the production of strong year classes of this cyprinid (Nunn et al. [2003\)](#page-10-0).

Arctic charr and roach rarely occur sympatrically and apparently no studies have addressed potential competition between these two planktivores, although the general competitive abilities of this cyprinid for such prey in offshore habitats are well known (see Persson [1991\)](#page-10-0). Furthermore, Langeland and Nost [\(1994](#page-10-0)) have found competitive impacts of an introduced roach population on a native whitefish, Coregonus lavaretus, population, a species which has similar foraging requirements to Arctic charr. The potential for a competitive impact of roach on Arctic charr in Windermere is thus considerable.

The long-term observations on the CPUE of spawning Arctic charr in the north basin of Windermere constitute the only dataset available for this species which covers the entire period of

eutrophication, climate change and roach expansion, although it must be acknowledged that these data relate to only one of six known spawning grounds in the basin. The long-term trend in this spawning CPUE is clearly one of a general increase up to the 1970s and then a decrease to 2005. Previous authors have interpreted the initial population increase as a response to the eutrophication of this basin increasing food availability during the 1950s and 1960s (Mills et al. [1990\)](#page-10-0), augmented by a fishery-induced reduction in pike abundance lowering predation impacts (Kipling [1984;](#page-10-0) Mills et al. [1990\)](#page-10-0). The subsequent Arctic charr population decline, which appeared to start in the 1980s well before the recent temperature increase or roach expansion, may be attributable to increased predation by pike following a population recovery of this major piscivore in both basins (authors' unpublished data). It is both interesting and relevant in a conservation context to note that the decline in spawning CPUE observed through the 1990s has in fact simply returned it to values seen in the near pristine Windermere of the 1940s. The intervening elevated spawning CPUEs from the late 1940s to the late 1990s may thus be an unnatural result of eutrophication and predator reduction.

Continuous CPUE data from the Arctic charr fishery are only available from 1966 to 2005. In the north basin these data showed no marked overall trend, but in the south basin they exhibited some decline in the late 1980s and early 1990s followed by a dramatic decline since 2000. Although contrasting parasite burdens and growth rates (Mills [1989](#page-10-0)) suggest little movement of Arctic charr between the two basins under normal conditions, Elliott et al. [\(1996](#page-10-0)) interpreted an increase in Arctic charr abundance in the south basin during the 1990s to be a response to temporarily improving conditions as individuals dispersed from the refuge of the north basin. It is possible that the more recently deteriorating environmental conditions in the south basin have caused a reverse movement of individuals, resulting in a lowered Arctic charr fishery CPUE in the south basin but inflating Arctic charr fishery CPUE in the north basin. Such a mechanism could explain why the marked decline in spawning CPUE seen in the north basin since c. 1990 was not accompanied by a similarly dramatic decline in local Arctic charr fishery CPUE, i.e. native north basin stocks were being subsidised by immigrants from the south basin.

As for spawning CPUE, it is notable that the present Arctic charr fishery CPUE in the north basin is comparable with a value of 0.47 fish - angler<sup>-1</sup> h<sup>-1</sup> estimated by Mills [\(1989](#page-10-0)) for fishing undertaken mostly in this basin from 1927 to 1942. Corresponding data for the south basin from the same time period are unavailable, leaving the values observed from 2001 onwards as the lowest on record.

## Conclusion

The Arctic charr populations of Windermere face significant environmental pressures from eutrophication, climate change and potentially from competition with an increased roach population. Current Arctic charr abundance in the north basin, where eutrophication is limited and the local roach population has increased only recently, is comparable with that of the near pristine lake of the 1940s. In contrast, the situation is becoming critical in the south basin where eutrophication is much more developed, with associated deepwater hypoxia, and the local roach population increased earlier. Continued lake management in the form of nutrient control to address in particular the problem of deepwater hypoxia is essential to ensure survival of the local Arctic charr populations.

Acknowledgments We would like to thank many past and present colleagues too numerous to name here for their help in the field and laboratory and for allowing our use of their unpublished data. We are indebted to the late John Cooper and to Bruce Dobson for allowing us to use their records of Arctic charr fishing effort and catches, and to Ben Bayliss, Graeme McKee, Jeremy Westgarth and colleagues of the Environment Agency for organising the current log book scheme for Arctic charr anglers and allowing our use of 2004 and 2005 data from it. We appreciate the work of three anonymous reviewers whose thoughts substantially improved our manuscript. We are also grateful to the Freshwater Biological Association for their joint stewardship of the Windermere long-term data. This work was funded by the Natural Environment Research Council, Environment Agency and United Utilities.

#### <span id="page-10-0"></span>References

- Baroudy E, Elliott JM (1993) The effect of large-scale spatial variation of pelagic fish on hydroacoustic estimates of their population density in Windermere (northwest England). Ecol Freshwat Fish 2:160–166
- Craig JF, Fletcher JM (1981) Some results of fishing with survey gill nets in Windermere. Proceedings of the Second British Freshwater Fisheries Conference. University of Liverpool, Liverpool pp 236–244
- Elliott JM, Baroudy E (1995) The ecology of Arctic charr, Salvelinus alpinus, and brown trout, Salmo trutta, in Windermere (northwest England). Nordic J Freshwat Res 71:33–48
- Elliott JM, Fletcher JM, Elliott JA, Cubby PR, Baroudy E (1996) Changes in the population density of pelagic salmonids in relation to changes in lake enrichment in Windermere (northwest England). Ecol Freshwat Fish 5:153–162
- Elliott JM, Fletcher JM (2001) A comparison of three methods for assessing the abundance of Arctic charr, Salvelinus alpinus, in Windermere (northwest England). Fish Res 53:39–46
- Frost WE (1977) The food of charr, Salvelinus willoughbii Gunther, in Windermere. J Fish Biol 11:531–547
- Janssen W, Hesslein RH (2004) Potential effects of climate warming on fish habitats in temperate zone lakes with special reference to Lake 239 of the experimental lakes area (ELA), north-western Ontario. Env Biol Fish 70:1–22
- Kipling C (1972) The commercial fisheries of Windermere. Trans Cumberland Westmorland Antiquarian Archaeol Soc 72:156–204
- Kipling C (1984) Some observations on autumn-spawning charr, Salvelinus alpinus L., in Windermere, 1939– 1982. J Fish Biol 24:229–234
- Klemetsen A, Amundsen P-A, Grotnes PE, Knudsen R (2002) Takvatn through 20 years: long-term effects of an experimental mass removal of Arctic charr, Salvelinus alpinus, from a subarctic lake. Env Biol Fish 64:39–47
- Langeland A, Nost T (1994) Introduction of roach (Rutilus rutilus) in an oligohumic lake: 1. Competition impacts on whitefish (Coregonus lavaretus). Int Ver Theor Ang Lim Verh 25:2113–2117
- Le Cren ED (2001) The Windermere perch and pike project. Freshwat Forum 15:3–34
- Magnan P, Audet C, Glémet H, Legault M, Rodríguez MA, Taylor EB (2002a) Ecology, behaviour and conservation of the charrs, genus Salvelinus. Env Biol Fish 64:1–351
- Magnan P, Audet C, Glémet H, Legault M, Rodríguez MA, Taylor EB (2002b) Developments in the ecology, evolution, and behaviour of the charrs, genus Salvelinus: relevance for their management and conservation. Env Biol Fish 64:9–14
- Maitland PS, Winfield IJ, McCarthy I, Igoe F (2007) The status of Arctic charr Salvelinus alpinus in Britain and Ireland. Ecol Freshwat Fish 16:6–19
- Mills CA (1989) The Windermere populations of Arctic charr, Salvelinus alpinus. Physiol Ecol Jpn Spec Vol
- 1:371–382 Mills CA, Heaney SI, Butterwick C, Corry JE, Elliott JM (1990) Lake enrichment and the status of Windermere charr, Salvelinus alpinus (L.). J Fish Biol (Suppl A) 37:167–174
- Mills CA, Hurley MA (1990) Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (Esox lucius) and Arctic charr (Salvelinus alpinus). Freshwat Biol 23:119–136
- Nunn AD, Cowx IG, Frear PA, Harvey JP (2003) Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? Freshwat Biol 48:579–588
- Parker JE, Maberly SC (2000) Biological response to lake remediation by phosphate stripping: control of Cladophora. Freshwat Biol 44:303–309
- Persson L (1991) Interspecific interactions. In: Winfield IJ, Nelson JS (eds) Cyprinid fishes: systematics, biology and exploitation. Chapman & Hall, London, pp 530– 551
- Pickering AD (2001) Windermere: restoring the health of England's largest lake. Freshwater Biological Association Special Publication No 11. Freshwater Biological Association, Ambleside
- Sandlund OT, Gunnarson K, Jonasson PM, Jonsson B, Lindem T, Magnusson KP, Malmquist HJ, Sigurjonsdottir H, Skulason S, Snorrason SS (1992) The Arctic charr Salvelinus alpinus in Thingvallavatn. Oikos 64:353–364
- Watson J (1925) The English Lake district fisheries. TN Foulis Ltd, London
- Winfield IJ, Durie NC (2004) Fish introductions and their management in the English Lake district. Fish Manage Ecol 11:1–7
- Winfield IJ, Fletcher JM, Hewitt DP, James JB (2004) Long-term trends in the timing of the spawning season of Eurasian perch (Perca fluviatilis) in the north basin of Windermere, UK. In: Barry TP, Malison JA (eds) Proceedings of Percis III: The Third International Percid Fish Symposium. University of Wisconsin Sea Grant Institute, Madison, pp 95–96
- Winfield IJ, Fletcher JM, James JB (2006) The Urban Waste Water Treatment Directive: Monitoring the Arctic charr population of Windermere, 2005. Unpublished Report from Centre for Ecology & Hydrology to Environment Agency, North West Region. LA/C01752/15, 56 pp
- Winfield IJ, Fletcher JM, James JB (2007) Seasonal variability in the abundance of Arctic charr (Salvelinus alpinus (L.)) recorded using hydroacoustics in Windermere, UK, and its implications for survey design. Ecol Freshwat Fish 16:64–69