ARCTIC CHARR (SALVELINUS ALPINUS) IN WINDERMERE (CUMBRIA)

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Introduction

This article commences with a brief introduction to Arctic charr (Salvelinus alpinus (L.)) and its distribution in the British Isles. The history of investigations on charr in Windermere is then presented and, finally, recent trophic changes in the lake and their consequent effects on the salmonid population, are discussed.

The Arctic charr is a holarctic salmonid species that includes both exclusively freshwater and anadromous forms, i.e. fish migrate to sea as juveniles and return to fresh water where they reproduce. It has the most northerly distribution of any freshwater fish. It is frequently anadromous at latitudes north of 60°N but in southerly latitudes only non-migratory stocks occur. The populations of Arctic charr in the British Isles are all non-migratory and are near their southernmost range. Charr are most widespread in Scotland and Ireland, with over 175 lochs in Scotland (Maitland 1992) and over 45 loughs in (mainly) western Ireland (Went 1971) containing charr. In Wales, there are five known lakes containing charr (Maitland & Lyle 1991). The English populations of Arctic charr all occur in the north-west, in the English Lake District. Previously, twelve lakes were reported to contain charr but now only eight (Buttermere, Coniston Water, Crummock Water, Ennerdale Water, Haweswater, Thirlmere, Wastwater and Windermere) are known to contain Arctic charr (Partington & Mills 1988; Maitland & Lyle 1991). Windermere is one of the few lowland lakes (39.3 metres above sea level) at southerly latitudes to contain a substantial population of Arctic charr.

Windermere, the largest natural lake in England, originated some 12,000 years ago and occupies a glacially-excavated valley rock basin. It covers an area of 14.8 km² and has a total length of 17 km. It is divided into a north and south basin by an area of shallow water and islands. The north basin is 8.1 km² and has a mean depth of 25.1 m; the maximum depth is 64 m. The south basin is 6.7 km² with a mean depth of 16.8 m, a maximum depth of 42 m, and has a more extensive littoral than the north basin (Ramsbottom 1976). The two basins differ in their inflow - outflow characteristics but water retention time of the lake as a whole is ca. 9 months (Sutcliffe & Carrick 1983). The main fish assemblage in the lake is one of Arctic charr, brown trout (*Salmo trutta* L.),

186 E. BAROUDY

perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and eels (*Anguilla anguilla* (L.)). Atlantic salmon (*Salmo salar* L.) pass through the lake when migrating to and from the rivers that flow into Windermere.

History of studies on Windermere charr

The Windermere population of Arctic charr has been studied on a continuous basis since the early 1940s. The background to the start of an experimental fishery, mainly for pike and perch but also for charr, is given by Worthington (1950) and Bagenal (1970). Early experimental studies on Arctic charr in Windermere were undertaken mainly by Dr Winifred Frost, who wrote a series of papers from the mid-1940s until her death in 1979, on various aspects of charr biology, including feeding (Frost 1977), homing behaviour (Frost 1963), breeding habits (Frost 1965), growth (Frost 1978; Frost & Kipling 1980) and history (Frost 1952). A summary of the early work is presented in Mills (1989).

The first recorded mention of charr in Windermere was made around 1540 but it was in the mid-17th century that different "sorts" of charr were recognised, based on differences in their breeding behaviour. Frost (1963) confirmed the presence of two distinct populations, autumn spawners and spring spawners, isolated from each other by time and place of spawning. Child (1984) presented the first genetic evidence for the existence of autumn and spring-spawning populations and Partington & Mills (1988) showed that there were at least four races of charr in Windermere, based on genetic, morphometric and meristic characteristics. The four races were from four spawning sites, with each basin having its own race of autumn and spring spawners. Based on this evidence, and considering charr homing behaviour (Frost 1963; Le Cren & Kipling 1963), there may be at least thirteen races of charr in Windermere, as there are thought to be twelve spawning sites in the lake and one in the River Brathay. Separation into autumn and spring spawners is possible (with ca. 95% accuracy) using a discriminant function based on gillraker numbers and length (Partington & Mills 1988). Spring spawners constitute 4 to 6% of the population (Mills 1989).

An extensive paper by Frost (1965) describes the breeding habits of Windermere charr. Autumn spawning occurs from October to December, with peak numbers spawning in November, on the lake bed, in shallow water 1 to 3 m deep. Spring spawning occurs from January to April, with the greatest numbers spawning in mid-February, on the lake bed, in water 15 to 30 m deep. Both autumn and spring spawners require a stony substratum in which to spawn. A day-length of 8.5 hours may trigger spawning. Autumn spawning occurs in both the lake and the afferent River Brathay, but spring spawning occurs only in the lake. The populations mix when the fish are not breeding and they are well dispersed throughout Windermere (Frost 1963).

A more recent study on the egg and juvenile life stages showed there were no

major differences between races for egg incubation times and the percentage of eggs hatching successfully (Baroudy & Elliott 1994a). Although there were no significant differences in the lengths of the female parents, both eggs and alevins were significantly larger for the autumn spawners than for the spring spawners. Relating juvenile survival to the size of the egg and alevin life stages showed that the size of the egg and alevin stages appeared to have a significant effect on subsequent survival and could be responsible for the relatively small proportion of spring spawners in Windermere.

Autumn spawners in the north basin of Windermere are the slowest-growing charr, attaining a length of ca. 307 mm at 10 years of age. Autumn spawners in the south basin and spring spawners in the north basin grow faster, and spring spawners in the south basin are the fastest-growing charr in the lake, attaining a length of ca. 360 mm at 10 years of age (Partington & Mills 1988). Swift (1964) discussed the effect of temperature and oxygen on growth rates of charr and found that the highest growth rates occurred at temperatures between 12 and 16°C.

Both autumn and spring spawners are infected with plerocercoids of cestode tapeworms, *Diphyllobothrium dendriticum* (Nitzch) and *D. ditremum* (Creplin). The level of infection varies with the size and age-classes of the charr but it is generally higher in the north basin than in the south basin and also higher in spring spawners than in autumn spawners (Mills 1989).

Kipling (1984) gives an historical account of the Windermere charr fishery. Commercial netting for Windermere charr started in the 16th century. An estimated 3 tonnes of charr could have been removed annually. Up to the mid-19th century, fish were caught at sustainable levels but then were over-fished. The poor catches resulted in the last commercial netting in 1921. Despite severe exploitation reducing the maximum size of the fish, the Windermere charr stock is considered to have recovered to its former size and abundance (Johnson 1984). Le Cren et al. (1972) proposed that a net fishery could be reintroduced to Windermere and that 2 tonnes might be removed annually as a sustainable yield. The only charr-fishing at present is semi-commercial using plumb lines to catch the fish. Kipling (1984) estimated that 4 tonnes of fish are caught annually using this method.

Population estimates for Windermere charr have been made using mark recapture results obtained from sampling the spawning population (Frost 1965; Kipling & Le Cren 1984; Mills & Hurley 1990) and more recently using results obtained from echo-sounding (Baroudy 1993).

Recent changes in Windermere

Recent changes in the trophic status of Windermere have occurred. This primarily has been due to an input of phosphorus from treated sewage released from treatment works around the lake. The increasing nutrient inputs are

188 E. BAROUDY

related to the increasing resident and tourist population in the area. The consequent eutrophication of the lake is more pronounced in the south basin than in the north basin (Tailing & Heaney 1988). There has been a deterioration in water quality, with reduced levels of oxygen recorded in the hypolimnion in both basins during summer stratification. Anoxic conditions have been recorded in the south basin hypolimnion, but not in the north basin. The low levels of oxygen have been correlated with the sedimenting out and decomposition of filaments of the blue-green alga *Tychonema* (formerly called *Oscillatoria*), especially in the south basin of Windermere during the 1980s (Mills et al. 1990).

In Windermere, higher surface temperatures and decreased levels of oxygen in the hypolimnion during summer stratification, and the possible adverse effects this may have on charr, was cause for concern (Mills 1989; Mills et al. 1990). This, coupled with reports from charr anglers that changes in catches were occurring, prompted a series of investigations (Elliott & Baroudy 1992, 1995; Baroudy 1993; Baroudy & Elliott 1993, 1994a, b, c).

Anglers have reported two changes in fish catches which coincided with the deterioration in water quality since the mid-1980s. Compared with the north, the numbers of charr caught in the south basin declined, and the numbers of trout caught in the south basin pelagic increased. A comparison of three methods used to obtain relative estimates of the charr stocks in Windermere, gill-netting (records available from 1939 until present), anglers' catches (1966 to the present) and echo-sounding (1989 to the present), confirmed that the levels of charr stocks in the south basin had declined, compared with the north basin, and that an increase in trout catches in the south basin pelagic had also occurred. No such change had occurred in the north basin. However, the increase of trout catches was not responsible for the decrease in charr catches in the south basin (Elliott & Baroudy 1992, 1995). In addition, the echosounding results showed that numbers of pelagic fish were greater in the north basin than in the south basin, there were lower numbers of pelagic fish in both basins in winter, and there was a general decline in the numbers of larger fish in more recent years (Elliott & Baroudy 1992, 1995; Baroudy & Elliott 1993).

In order to examine some possible effects of lake stratification and eutrophication on the Windermere charr, their tolerances to elevated temperatures and low oxygen levels were investigated experimentally. The studies were performed on the juvenile stages of charr, which are less mobile than adults; the adults are assumed to be able to move freely to more favourable conditions. The results showed that charr are amongst the least tolerant of salmonids to increased temperatures but amongst the most tolerant to low temperatures. At the highest acclimation temperature, the maximum tolerated temperature was 26.6°C over a 10-minute interval and 22-23°C was tolerated over a period of 7 days. Lower temperature limits were close to 0°C (Baroudy & Elliott 1994b). Investigations on oxygen tolerance showed that

Arctic charr are amongst the most tolerant of salmonids to low oxygen levels, tolerating oxygen levels of 1.8 to 2.4 mg per litre, depending on acclimation temperature (Baroudy & Elliott 1994c). In all cases, there were no differences in results between the races in Windermere but alevins were less tolerant than parr (Baroudy 1993). One of the most vulnerable life stages is the egg (Swift 1965; Elliott & Baroudy 1995) but at the time when the eggs and alevins are on the spawning sites, temperature and oxygen conditions are favourable to both the autumn and spring spawners.

Although nutrient enrichment is not directly harmful to fish, severe cases of eutrophication can be. The associated problems of eutrophication, deoxygenation, siltation and, in some cases, competition, have been shown to be detrimental to some European charr populations (e.g. Laurent 1972; Hartmann 1984; Ruhle 1984; Muller & Meng 1992). Of the threats to European charr, the threat to the survival of Windermere charr is most likely to come from water quality degradation. Considering the worst recorded cases of elevated temperatures and low oxygen levels during lake stratification in Windermere, charr are more likely to be affected by the low oxygen levels. However, investigations into the rate of siltation on spawning sites and the tolerance of eggs to different levels of temperature and oxygen would be useful for future management considerations.

New mechanisms have been installed at the sewage treatment plants around Windermere which should limit the input of phosphorus to the lake. Although this will reduce incoming levels to the lake, its sediments may still act as a source of phosphorus. Therefore it is important to continue monitoring the levels of Arctic charr stocks in the lake in order to detect any further changes in the stocks, and to obtain additional information for the management and conservation of the Windermere charr.

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References

Bagenal, T. B. (1970). An historical review of the fish and fisheries investigations of the Freshwater Biological Association, mainly at the Windermere Laboratory. *Journal of Fish Biology*, 2, 83-101.

Baroudy, E. (1993). Some factors affecting survival and distribution of Arctic charr (*Salvelinus alpinus* (L.)) in Windermere. Unpublished PhD thesis, University of Lancaster.

- Baroudy, E. & Elliott, J. M. (1993). The effect of large-scale spatial variation of pelagic fish on hydroacoustic estimates of their population density in Windermere (northwest England). *Ecology of Freshwater Fish*, 2, 160-166.
- Baroudy, E. & Elliott, J. M. (1994a). Racial differences in eggs and juveniles of Windermere charr, *Salvelinus alpinus*. *Journal of Fish Biology*, 45, 407-415.
- Baroudy, E. & Elliott, J. M. (1994b). The critical thermal limits for juvenile Arctic charr, (*Salvelinus alpinus*). *Journal of Fish Biology*, 45, 1041-1053.
- Baroudy, E. & Elliott, J. M. (1994c). Tolerance of parr of Arctic charr, *Salvelinus alpinus*, to reduced dissolved oxygen concentrations. *Journal of Fish Biology*, 44, 736-738.
- Child, A. R. (1984). Biochemical polymorphism in char *(Salvelinus alpinus L.)* from three Cumbrian lakes. *Heredity*, 53, 249-257.
- Elliott, J. M. & Baroudy, E. (1992). Long-term and short-term fluctuations in the numbers and catches of Arctic charr, *Salvelinus alpinus* (L.) in Windermere (northwest England). *Annates de Limnologie*, 28, 135-146.
- Elliott, J. M. & Baroudy, E. (1995). The ecology of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*, in Windermere (northwest England). *Nordic Journal of Freshwater Research*, 71, (in press).
- Frost, W. E. (1952). Predators on the eggs of char in Windermere. *Salmon and Trout Magazine*, **136**, 192-196.
- Frost, W E. (1963). The homing of charr, *Salvelinus willughbii* (Giinther) in Windermere. *Animal Behaviour*, 11, 74-82.
- Frost, W. E. (1965). Breeding habits of Windermere charr, *Salvelinus willughbii* (Giinther) and their bearing on speciation of these fish. *Proceedings of the Royal Society B*, **163**, 232-284.
- Frost, W. E. (1977). The food of charr, *Salvelinus willughbii* (Giinther) in Windermere. *Journal of Fish Biology*, 11, 531-547.
- Frost, W. E. (1978). The scales of charr, *Salvelinus willughbii* (Giinther) in Windermere and their use for the determination of age and growth. *Journal du Conseil International pour l'Exploration de la Mer*, 38, 208-215.
- Frost, W. E. & Kipling, C. (1980). The growth of charr, *Salvelinus willughbii*, Giinther, in Windermere. *Journal of Fish Biology*, 16, 279-289.
- Hartmann, J. (1984). The chairs *(Salvelinus alpinus)* of Lake Constance, a lake undergoing cultural eutrophication. In *Biology of the Arctic Charr; Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981* (eds L. Johnson & B. L. Burns), pp. 471-486. University of Manitoba Press, Winnipeg.
- Johnson, L. (1984). Charr and man: the philosophy of limited interaction. In *Biology of the Arctic Charr; Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981* (eds L. Johnson & B. L. Burns), pp. 523-486. University of Manitoba Press, Winnipeg.
- Kipling, C. (1984). Charr fisheries in Windermere, England, during the past

- 400 years: organisation and management. In *Biology of the Arctic Charr; Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981* (eds L. Johnson & B. L. Burns), pp. 533-536. University of Manitoba Press, Winnipeg.
- Kipling, C. & Le Cren, E. D. (1984). Mark-recapture experiments on fish in Windermere, 1943-1982. *Journal of Fish Biology*, 24, 395-414.
- Laurent, P. J. (1972). Lac Leman: effects of exploitation, eutrophication and introductions on the salmonid community. *Journal of the Fisheries Research Board of Canada*, 29, 867-875.
- Le Cren, E. D. & Kipling, C. (1963). Some marking experiments on spawning populations of charr. *International Commission for North West Atlantic Fisheries Special Publications*, 4, 130-139.
- Le Cren, E. D., Kipling, C. & McCormack, J. (1972). Windermere: effects of exploitation and eutrophication on the salmonid community. *Journal of the Fisheries Research Board of Canada*, 29, 819-832.
- Maitland, P. S. (1992). The status of Arctic charr *Salvelinus alpinus* (L.) in southern Scotland: a cause for concern. *Freshwater Forum*, 2, 212-227.
- Maitland, P. S. & Lyle, A. A. (1991). Conservation of freshwater fish in the British Isles: the current status and biology of threatened species. *Aquatic Conservation*, 1, 25-54.
- Mills, C. A. (1989). The Windermere populations of Arctic charr, *Salvelinus alpinus*. *Physiology and Ecology*, Japan. Special Volume 1, 371-382.
- Mills, C. A. & Hurley, M. A. (1990). Long-term studies on the populations of perch, *Perca fluviatilis*, pike, *Esox lucius* and charr, *Salvelinus alpinus*. *Freshwater Biology*, 23, 119-136.
- Mills, C. A., Heaney, S. I., Butterwick, C, Corry, J. E. & Elliott, J. M. (1990). Lake enrichment and the status of Windermere charr, *Salvelinus alpinus (L.)*. *Journal of Fish Biology*, 37 (A), 167-174.
- Muller, R. & Meng, H. J. (1992). Past and present state of the ichthyofauna of Lake Lugano. *Aquatic Sciences*, 54, 338-350.
- Partington, J. D. & Mills, C. A. (1988). An electrophoretic and biometric study of Arctic charr, *Salvelinus alpinus* (L.) from ten British lakes. *Journal of Fish Biology*, 33, 791-814.
- Ramsbottom, A. E. (1976). Depth charts of the Cumbrian lakes. *Freshwater Biological Association Occasional Publications*, 33, 1-39.
- Ruhle, C. (1984). The management of Arctic charr (Salvelinus alpinus L.) in eutrophied Lake Zug. In Biology of the Arctic Charr; Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981 (eds L. Johnson & B. L. Burns), pp. 487-492. University of Manitoba Press, Winnipeg.
- Sutcliffe, D. W. & Carrick, T. R. (1983). Chemical composition of water-bodies in the English Lake District: relationships between chloride and other major ions related to solid geology and a tentative budget for Windermere.

192 E. BAROUDY

- Freshwater Biology, 13, 323-352.
- Swift, D. R. (1964). The effect of temperature and oxygen on the growth rate of the Windermere char (*Salvelinus alpinus willughbii*). *Comparative Biochemistry and Physiology*, 12, 179-183.
- Swift, D. R. (1965). Effect of temperature on mortality and rate of development of the eggs of the Windermere char (*Salvelinus alpinus*). *Journal of the Fisheries Research Board of Canada*, 22, 913-917.
- Tailing, J. F. & Heaney, S. I. (1988). Long-term changes in some English (Cumbrian) lakes subjected to increased nutrient inputs. In *Contributions to Algal Biology and Environments in Honour of J. W. G. Lund* (ed. F. E. Round), pp. 1-29. Biopress, Bristol.
- Went, A. E. J. (1971). The distribution of Irish char (Salvelinus alpinus). Irish Fisheries Investigation Series A (Freshwater), 6, 5-11.
- Worthington, E. B. (1950). An experiment with populations of fish in Windermere, 1939-1948. *Proceedings of the Zoological Society of London*, 120,113-149.