THE WINDERMERE PERCH AND PIKE PROJECT:
AN HISTORICAL REVIEW

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Introduction

When the Second World War began in September 1939, the first full-time Director of the FBA, Barton Worthington, wondered how the FBA might help the war effort, and decided that stocks of fish in freshwater lakes might be harvested to enhance the supplies of food in a country subject to blockade. This was the start of a project that has continued since then, and is still continuing, sixty years later. The following account is an attempt to set the background, provide a brief history, review some of the project's scientific achievements, note current developments and hopes for the future, and comment on some aspects of such long-term projects. I shall take some of the scientific results up to 1976, others up to 1998; several of the later developments are still being analysed and interpreted.

The whole project has already resulted in the publication of over one hundred peer-reviewed papers, as well as over sixty reviews, theses, popular articles and unpublished reports. I have not attempted to review all of them, but have merely outlined the main changes in the populations of perch, pike and charr that occurred as a result of the experimental fishery and other influences, and some of the main supporting research. Thus I cite here only some of the principal papers as support for particular points in the text or as examples of the kind of work that has been done.

Background

Charlotte Kipling (1972) has described how commercial net fisheries were carried out on Windermere from the 12th Century until 1921. These were for perch, pike, eels, trout and Arctic charr, with charr the most valuable product. In the latter half of the 19th Century, an increasing demand for charr led to serious overfishing and a reduction in the catches of charr and their average size. The mesh sizes of the nets were reduced until they were catching "minnow-sized" charr and also salmon smolts - which latter catches did not please the salmon fishermen on the River Leven. Some of the proprietors of the fisheries and then the local Board of Conservators (after it had been set up by the Fisheries Act of 1865) sought to control the fisheries. Eventually the Board bought up all the netting rights and stopped all netting in 1921, though a semi-commercial plumb-line fishery for charr continued, and at least one fisherman continued long-lining for pike, eels and big trout. By 1939, the fish
population of Windermere consisted of a dense population of perch *Perca fluviatilis* L., few of which grew larger than 200 mm in length, and a moderate population of pike *Esox lucius* L. feeding mostly on the perch but also eating charr and trout. There was a moderate population of Arctic charr *Salvelinus alpinus* L., a small population of brown trout *Salmo trutta* L., a few roach *Rutilus rutilus* in some locations, and numbers of smaller species such as minnow *Phoxinus phoxinus* L., three-spined stickleback *Gasterosteus aculeatus* L. and bullhead *Cottus gobio* L. Such was the situation when 'Kay' (Kenneth Radway) Allen studied the food and seasonal migration of the perch (Allen 1935) and the growth, food, seasonal cycle and population of the trout (Allen 1938).

The 1930s were also a time when marine fishery biologists were increasingly concerned with the "overfishing problem" - the reduction of catches and decrease in average size of the fish caught in commercial fisheries as a result of fishing too intensively with nets of too small a mesh size (e.g. Graham 1943; Russell 1942). Barton Worthington became Director of the FBA in 1937 after spending time in Africa, some of it when assisting Michael Graham (later Director of the MAF Fisheries Research Laboratory at Lowestoft) in a survey of tilapia fisheries. When the Second World War broke out in September 1939, he immediately started to think of ways in which the FBA could help the war effort.

Perch were among the most abundant edible freshwater fish in British lakes and Allen had shown that they could be caught in large numbers in Windermere, using traps; Worthington also had seen fish traps in use in Africa. In addition, Worthington was a keen fly-fisherman and so concerned to see an improvement in the angling for trout on Windermere. He thought that a reduction in the density of perch (a competitor with the trout for prey) and pike (a predator) would improve the numbers of trout, and charr which were also the subject of a valuable fishery. Finally, intensive fisheries on "virgin" populations of perch and pike might provide scientific information that would illuminate the overfishing problem (Worthington 1950). Thus, there were three good reasons for starting fisheries for perch and pike on Windermere.

**Early history and the fishing operations**

Worthington first concentrated on the perch by employing Noel Hynes (who was just completing a PhD on stoneflies at Windermere) to try out various methods of fishing for perch during the autumn of 1939. These trials confirmed the abundance of perch and that they could be caught by several methods- gill-nets, seines and traps, the latter requiring the minimum of human effort. The autumn of 1939 also saw the start of regular annual sampling of the autumn-spawning charr in Low Wray Bay (Fig. 1).
FIG. 1. North and South basins of Windermere, showing the sites mentioned in the text and Tables 1 and 2. CR = Chicken Rocks; FH = Fisherty How; GT = Green Tuft; LS = Lake Side; LWB = Low Wray Bay; NTH = North side of Thompson Holme; RN = Rawlinson's Nab. Depth contours in metres (Ramsbottom 1976).
FIG. 2. Perch: the upper picture shows a flat-bottomed Windermere perch trap.
FIG. 3. Pike: the upper picture shows a pike gill-net being lifted on Windermere.
In January 1940, a series of traps was set at different depths in a line perpendicular to the shore off Fisherty How, near Wray Castle. The catches in these confirmed the findings of Allen on the migration of perch to water of about 20-metres depth in October and their inshore migration in April, at the end of which they could be caught in very large numbers in the traps while spawning. This series of "pilot" traps was maintained for several years as a guide to the depth at which the traps should be set for the fishery.

Trapping for perch

As a result of these trials, Worthington planned to launch a full-scale fishery in Windermere, using traps, in the spring of 1941. Initially, some 300 traps were manufactured from fencing wire covered with ½ inch (12 mm) mesh wire netting, with a funnel entrance and a small door for removal of the catch. Following trials with traps of different colours, after 1941 all traps were dipped in black tar-varnish to increase both their catches and their life. The first traps made were cylindrical but, after a number were lost from rolling down the steeper slopes of the littoral, they were given flat bottoms. Each trap was provided with a 10-metre rope and two glass floats. Much later, the traps still being used for sampling have been on submerged lines to prevent tampering from inquisitive people in boats (Fig. 2).

Worthington also recruited the help of about thirty volunteers around the lake - mostly charr fishermen or others interested in angling who owned a rowing boat. They were each allocated a "beat" of about twenty traps set along a length of shore, and they were responsible for lifting these on appointed days during the season: in the early years three or more times a week from the last week in April until the end of June; later, just once a week for six weeks from the end of April. A contract was negotiated with a canning factory in Leeds that agreed to buy all the perch and process them into sardine tins to be sold as "Perchines - Lakeland Perch, Britain's most lovely and tasty fresh water fish" (see the front cover illustration). (Actually, by the time they had spawned, been caught in a trap, travelled to Leeds and been canned, the fish were not very tasty; but packing them in Yorkshire relish and tomato ketchup, together with the fact that their purchase did not require many wartime food rationing coupons, helped to sell them!) The coordination of the volunteers and lifting the traps required some organisation; the catches were packed in fish boxes and landed at a small number of centres around the lake from where they were taken to Windermere station to catch over-night trains to Leeds.

After the success of the perch trapping on Windermere in 1941, efforts were made to extend the fishery to other lakes. In 1942, the Ministry of Agriculture and Fisheries organised perch trapping on several other lakes in Cumbria, but these fisheries lasted no more than a year or two. Worthington, through the
angling press and other connections, stimulated several fishing clubs, owners of small lakes and water companies, to start perch trapping, and fisheries were operated for two or three years on several lakes and reservoirs elsewhere in England and Wales and in some Scottish lochs and reservoirs, including Loch Lomond. However, none of these fisheries yielded catches comparable to those on Windermere, and few lasted more than a year or two.

**Gill-netting for pike**

After the successful launch of the perch fishery on Windermere, Barton Worthington instigated trials of a fishery for pike, choosing gill-netting in winter as the method. Winifred E. Frost (affectionately and familiarly known as 'WEF') had succeeded Kay Allen as fish biologist at the FBA and was starting work on eels (another species that had potential for fishery development). Some of her effort was diverted to the pike, and a trial was carried out over the winter of 1943-14. The gill-nets used had a mesh of 5 inches when stretched (64 mm knot to knot) and were 30 yards x 10 feet (27 m x 3 m) in size. They were set on the bottom in shallow water at sites all round the lake, being lifted every two or three days, and were moved to a new site when it appeared that no more pike were being caught (Fig. 3). The mesh was large enough to avoid catching any other species except the very occasional large trout and perch, and, being winter, the nets did not interfere with fishermen's or tourist boats. Most of the pike were sold on the fresh fish market.

**Later history of the fishery**

The principal changes in the fisheries and other important events are summarised in Table 1. In 1941, perch trapping was confined to Windermere North Basin, though towards the end of the season some traps were moved to the top end of the South Basin. More traps were then made and, by the end of the 1942 season, the whole of the lake was fished. The catches made in each successive year declined sharply as the stock of perch was fished out; a classic example of the effect of an intensive new fishery. After the 1947 season, it was decided to cease the large-scale removal of perch from the North Basin, but continue removal in the South Basin. By this time it was no longer economical to sell the perch for canning and subsequent operations were carried out entirely by FBA staff. Removal of perch continued in the whole of the South Basin until after the 1951 season, when it ceased at the southern end; after 1964 removal was discontinued in the rest of the basin.

Some samples of perch to provide data on their size, age and growth were taken from seine-nettings in the summer of 1941 and from trap catches in 1942. From 1943 onwards until the present, larger and more consistent samples have been taken every year from the catches in traps at three places:
Table 1. Chronology of events in the perch-pike project on Windermere, from 1939 to 2000.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Perch</th>
<th>Pike (nd = net-days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1939 autumn</td>
<td>Trials with various methods</td>
<td></td>
</tr>
<tr>
<td>1940 throughout</td>
<td>'Pilot' traps at a range of depths</td>
<td></td>
</tr>
<tr>
<td>1941 April-June</td>
<td>c. 300 traps in NB (North Basin)</td>
<td></td>
</tr>
<tr>
<td>1941 May-July</td>
<td>c. 60 traps in north end of SB (South Basin)</td>
<td></td>
</tr>
<tr>
<td>1942 April-June</td>
<td>c. 365 traps in NB, c. 415 in SB</td>
<td></td>
</tr>
<tr>
<td>1943 April-June</td>
<td>Trapping continued in NB and SB; samples from GT, RN, LS (Fig. 1)</td>
<td>Gill-netting trials, c. 140 nd</td>
</tr>
<tr>
<td>1943 Sept-1944 March</td>
<td>Trapping and sampling continued</td>
<td>Gill-netting, c. 3740 nd</td>
</tr>
<tr>
<td>1944 April-June</td>
<td>Trapping and sampling continued</td>
<td>Gill-netting continued</td>
</tr>
<tr>
<td>1945 April-June</td>
<td>Trapping and sampling continued</td>
<td>Gill-nets frozen; abandoned</td>
</tr>
<tr>
<td>1946 April-June</td>
<td>Trapping and sampling continued</td>
<td>Gill-netting continued</td>
</tr>
<tr>
<td>1947 April-June</td>
<td>Trapping and sampling continued</td>
<td>Gill-netting continued</td>
</tr>
<tr>
<td>1947 Sept-1948 March</td>
<td>Trapping and sampling continued</td>
<td>Gill-netting continued</td>
</tr>
<tr>
<td>1948 April-June</td>
<td>NB, sampling at GT only; counting at 4 other beats;</td>
<td>Gill-netting continued each winter</td>
</tr>
<tr>
<td>1951 April-June</td>
<td>SB, removal and sampling continued</td>
<td></td>
</tr>
<tr>
<td>1948 Sept until</td>
<td></td>
<td>Gill-netting continued each winter</td>
</tr>
<tr>
<td>1956 March</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1952 April-June to</td>
<td>Removal from north end of SB only;</td>
<td>NB only 10 sites fished.</td>
</tr>
<tr>
<td>1964 April-June</td>
<td>Sampling at RN and LS: 2 beats counted</td>
<td>262 nd; SB increased no. of nd</td>
</tr>
<tr>
<td>1956 Sept-1959 March (three winters)</td>
<td></td>
<td>SB only 10 sites fished,</td>
</tr>
<tr>
<td>1959 Sept-1962 March (three winters)</td>
<td></td>
<td>c. 250 nd; NB c. 3000 nd</td>
</tr>
<tr>
<td>1962 Sept-1963 March</td>
<td></td>
<td>Some ice; reduced nd</td>
</tr>
<tr>
<td>1964 April-June</td>
<td>Last removal of perch from north end of SB</td>
<td></td>
</tr>
<tr>
<td>1965 April-June to</td>
<td>Sampling only at GT, RN, LS, CR (Fig. 1)</td>
<td></td>
</tr>
<tr>
<td>1977 April-June</td>
<td>No removal of perch; counting at 7 beats</td>
<td></td>
</tr>
<tr>
<td>1965 Sept-1990 March</td>
<td>Gill-netting continued each winter; reducing number of nd</td>
<td></td>
</tr>
<tr>
<td>1976 January</td>
<td>First signs of perch disease</td>
<td></td>
</tr>
<tr>
<td>1976 April-June</td>
<td>Sampling as usual – disease prevalent</td>
<td></td>
</tr>
<tr>
<td>1977 April-June</td>
<td>Very few perch caught</td>
<td></td>
</tr>
<tr>
<td>1978 April-June onwards</td>
<td>Sample trapping continued at GT, RN, LS, CR – 5 traps each site each spring, continuing to present time</td>
<td></td>
</tr>
<tr>
<td>1990 Sept-December onwards</td>
<td>Gill-netting by now reduced to c. 240 nd each autumn</td>
<td></td>
</tr>
</tbody>
</table>
Green Tuft in the North Basin, and Lakeside and Rawlinson's Nab in the South Basin; from 1965 Chicken Rocks was added to these sampling sites (Fig. 1). For a few years after the end of removal, a few other beats of traps continued to be fished where the perch caught were counted and then returned alive. In one or two years, the presence of strong year-classes allowed these perch to be counted into "small" and "large", the small fish consisting of the new strong year-class.

The pike fishery has continued throughout the period, though there was an overall reduction in fishing effort with time, especially because some of the sites fished in the early years were found to catch no pike, so were abandoned. In the three winters 1956-57, 1957-58 and 1958-59, only ten sites were fished in the North Basin and extra effort was transferred to the South Basin. From 1959-60 to 1961-62, this allocation of fishing effort was reversed with only ten sites being fished in the South Basin. In the 1946-47 season, fishing was abandoned because the lake froze over. Since 1992, fishing effort has been constant at a lower level of effort (Paxton & Winfield 2000). Throughout the pike fishery, all the operations have been carried out by FBA staff, and nearly all the pike were measured, weighed and had opercular bones removed for age determination.

In an attempt to estimate changes in the abundance of autumn-spawning charr, a gill-net has been set each November, from 1939 until 1974 in Low Wray Bay, and since 1975 at the north end of Thompson Holme (Table 2).

<table>
<thead>
<tr>
<th>Date</th>
<th>Event Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1939 autumn</td>
<td>Gill-net set in Low Wray Bay fishing continued in November each year until 1975</td>
</tr>
<tr>
<td>1974 November</td>
<td>Net stolen; no effective fishing</td>
</tr>
<tr>
<td>1975 November</td>
<td>Net moved to north side of Thompson Holme (Fig. 1); net changed to nylon; fishing continued each November to the present</td>
</tr>
</tbody>
</table>

Catch statistics, sampling and research

From the start, Worthington recognised that the fishery would present an opportunity to provide understanding of the effect of new, intensive fisheries on the population dynamics of the fish-species concerned, and on other species in the lake. During the early trials by FBA staff, records were kept of the catches and some attempts were made to sample the populations before much fishing had taken place. A series of monthly seine-nettings was instituted from April until September at a small number of bays in the North Basin. Also, a collection of measurements and scales was made from perch
seined during 1941. Douglas Kimmins (evacuated to Wray Castle with the insect collections of the British Museum (Natural History)), was persuaded to carry out regular sampling of benthic invertebrates.

Unfortunately, many of these early samples of perch have proved to be of very limited value, although some of the material and results from them have been kept. For example, only after the fishery had begun was it realised that, during the spawning season, the traps were highly selective for male perch; for most of the few early samples of perch the sex was not recorded, so these samples have limited value. Furthermore, in late 1942 it was found that the opercular bones of perch are much better than scales for age and growth determination (Le Cren 1947); samples of scales that had been collected in 1941 without accompanying records of sex, or data on length frequencies, proved to be almost useless. (These sampling efforts demonstrate how important it is to do statistical trials and preliminary studies before launching into any field sampling programme; but in wartime, with limited time and resources, this was not always possible.)

Perch

For the fishery itself, records were kept of the number of traps emptied and the weight of fish caught at each lift for each beat of traps (based on the number of full boxes of fish; sample boxes were actually weighed); these have proved to be good basic data on fishing effort and catch. Counts of batch weighings, and samples giving individual lengths and weights, have allowed the catches in weight to be converted, with reasonable accuracy, to numbers. From 1943 onwards, three (later four) groups of traps, each from a different part of the lake, were selected for scientific sampling. At these sites (Fig. 1) every year, all the fish from the regular catches (or a large sample of them) were sexed and measured and opercular bones were removed from subsamples stratified by size and sex.

These samples have allowed the partitioning of catches into age-groups and the estimation of most of the basic statistics for the analysis of population dynamics as well as other aspects of perch biology. Hugo Buchanan-Wollaston (evacuated to Wray Castle from the MAF Lowestoft Fishery Laboratory, where he was a statistician) introduced the technique of "pricking" the lengths of the fish onto waxed graph-paper with a mounted needle. This speeded up the measurement of large numbers of fish and also allowed one to divide the sheet of paper into six groups of fish according to their sex and state of maturity. Special wet-strength paper ruled with 5-mm lines was later obtained, and made waterproof by dipping in melted paraffin wax. The convention of measuring the total length of the perch to the tip of the longest tail finray was also adopted to speed up measurement. It proved to be easy to count up the pricks in each 5-mm column to yield length-frequency distributions.
The fish were divided into six groups: ripe and "running" males, spent males, immature males (rare), ripe females, spent females and immature females. Ripe fish were immediately recognisable, but, towards the end of the season, many of the fish had to be cut open to identify the group to which they belonged. The catches of each sex and maturity group on each date provided information on the phenology of spawning each year - which was found to differ a little from year to year and from one part of the lake to another.

**Pike**

It was soon discovered that the opercular bone could provide good estimates of age and growth for the pike as well as for perch (Frost & Kipling 1959), and full records of fishing effort, catch in weight and numbers, sex and age were made for virtually all the pike caught in the fishery. The numbers of pike involved have been much smaller than the numbers of perch it was found necessary to sample, so the labour of sampling, age determination and analysis has been less. Information on about 154,000 perch and 17,000 pike had been collected up to 2000; most of this includes data on sex, maturity, age, length at the end of each year of life, etc.

**Catch statistics and their analysis**

Much early research effort was spent on development of the methodology, the verification of the accuracy of age and growth determinations (e.g. Le Cren 1947; Frost & Kipling 1959), relating weights to lengths (e.g. Le Cren 1951), assessing the selectivity of various fishing gears (Kipling 1957) and, in particular, the exploration of ways in which the data could be analysed to provide maximum information about the population dynamics of the principal species. Data on the numbers of fish of each sex that had been caught were divided by measures of the fishing effort used to catch them (i.e. the number of traps or settings of gill-nets over the season) to give catch-per-unit-effort or CPUE. This is a basic fishery statistic, often closely related to the population density. The numbers of fish in the population could then be divided into fish of each age, or age-group, from which estimates of mortality rate were obtained. CPUEs of age-groups could be converted into CPUEs of cohorts or year-classes, i.e. fish hatched in a particular year.

One of the main problems in the analysis of these data was their conversion from changes in relative abundance into estimates of actual numbers. For the pike, information from the numbers marked and then recaptured was helpful in this, but much less so in the case of the perch. However, with some ingenuity, Charlotte Kipling was able to use sums of the total numbers of each year-class caught in the fisheries over successive years to derive estimates of the basic variables for both perch and pike (Kipling & Frost 1970; Le Cren et
This technique is known as virtual population analysis and was first used by Fry (1949) on lake trout *Christivomer namaycush* in Lake Opeonogon in Ontario, but was later further developed by Paloheimo (1958) and others.

Another cause of problems in data analysis was the variation in the "catchability" of fish from year to year, further complicated by differences in this between male and female perch. Though possibly influenced by the temperature and light during or before the fishing season, and even perhaps during the previous summer, the cause of such variation has yet to be found and measured; although on the three years when the lake was frozen during the spring, catches of male perch were much reduced. However, it proved possible to adjust the CPUEs for the major variations in catchability. During the spawning season, the behaviour of the male perch leads to many more males than females being caught by the traps, so the trap catches give a very biased estimate of the sex-ratio. Consequently the number of males was much more rapidly reduced than was the number of females. Thus the population dynamics of the two sexes have been analysed separately.

In the pike also, differences between the rates of growth of the two sexes, and differences between the two lake-basins and calendar years, affected the age at which each sex was recruited into the net fishery; many of the females, being slightly fatter and growing slightly faster, were first retained by the gill-nets when a year younger than the males (Frost & Kipling 1967). Marking experiments have shown that perch appear to spawn in the same area in successive years and that there is almost no mixing of the perch between the North and South basins of Windermere. Therefore the two basins have usefully been treated as two separate and different lakes in many of the analyses; the rates of fishing have varied between the basins. The recaptures of tagged pike have shown more movement between the basins, although the pike, too, seem to spawn in the same area in successive years (Kipling & Le Cren 1984).

**Computation and modelling**

Those who nowadays take it for granted that there will be a computer on their desk with which they can analyse data, calculate regressions, conduct tests of significance or model populations, all within a few minutes, must be reminded that all the early analyses of the perch and pike data were carried out by mental arithmetic, and later with a simple electrically-driven mechanical calculator. In about 1960, Liverpool University bought a computer and its Department of Numerical Analysis processed some of the pike data, though punching and verifying the cards then used was a tedious operation - especially when some were lost in a Liverpool gutter when the Department transferred to a new building! More recently, all the perch and pike data have been put onto computer discs in a form that can be handled on a modern PC, and these data are thus now much more accessible for modelling using the
latest methods. It is likely to be a long time, however, before the actual fishing for samples or reading the opercular bones for age and growth can be mechanised. Moreover, the interpretation of computer models will always require a good understanding of the fish's biology as well as a great deal of human intellect and intuition.

It also must be noted that many of the early analyses were carried out before most of the recent developments in statistical analysis, and before it was realised that errors might arise from the original assumption that catches could be treated as normally distributed parametric statistics; the relevance of non-normal distributions to the analysis of catches and samples of organisms had not then been sufficiently realised. 'Tim' (Timothy) Bagenal (1972a,b) showed that a negative binomial best described both the catches of perch in the traps and the catches of pike in the gill-nets, so logarithmic transformations were advisable before analysis. More recently, 'Charlie' (Charles) Paxton & Ian Winfield (2000) have shown that for analysing catches made by the pike-netting programme since 1992, non-parametric statistics are appropriate. However, the early estimations of total populations and biomasses and the changes in them are unlikely to be significantly affected by these developments in statistical analysis.

Changes in the population dynamics of perch

Numbers

As was intended and expected, the initial effects of the intensive perch fishery were to reduce substantially the total catches and the CPUE. In the North Basin, about 50 tonnes of perch had been removed by the end of the 1947 season, after which removal (except for regular samples for scientific analysis) ceased. It is estimated that the population (of two-year-old and older fish) had been reduced from about 2.6 million perch in 1941 to about 0.4 million in 1947 (Le Cren et al. 1977). In the South Basin, removal continued at a reduced rate (over only part of the lake) until 1964. A total of about 70 tonnes was removed, reducing the population from 3.6 million to 1.4 million fish (Fig. 4).

Once removal had ceased it was expected that the numbers of perch would start to increase again, but this was not the case; population numbers remained low until 1957, i.e. for a period of ten years. There was then a spectacular increase with the advent of two very strong year-classes—those of 1955 and 1959 in the South Basin, and 1959 in the North Basin (Fig. 4). The numbers then gradually declined with the mortality of these strong year-classes, stabilising at moderate levels from 1965 to 1976 in the North Basin, but with slightly higher numbers between 1971 and 1975 in the South Basin (Craig et al. 1979).
FIG. 4. Estimated numbers (above) and year-class strengths (below) for perch in the North (•) and South (•) basins of Windermere. (Data from Craig et al. 1979).
FIG. 5. Catch-per-unit-effort, in numbers (above) and estimated biomass of adults, in tonnes (below) for perch in the North (•) and South (♦) basins of Windermere. (Data for CPUE in 1941 to 1998 was provided by Ian Winfield; data for biomass in 1941 to 1976 was taken from Craig et al. 1979).
In 1976 there was a completely unexpected epidemic among the perch (Bucke et al. 1979) which killed about 98% of the adult perch. The primary infective agent of this disease has not yet been identified, though it has been suggested that it is a form of furunculosis (Aeromonas sp.) (des Clers, personal communication); it is also possible that secondary infection with Saprolegnia spp. may have been the ultimate cause of death. From 1977, the CPUEs were very low, but have gradually increased again, with fluctuations, since then (Mills & Hurley 1990) (Fig. 5). There was also a change in the sex ratio, with a reduction in the proportion of males, but this appears to have gradually returned to its original value (Paxton et al. 1999).

Growth and biomass

In 1940 the perch grew slowly; maximum normal body length (von Bertalanffy l) was c. 180 mm (though rare individuals grew much larger (Le Cren 1992)). In 1941, immediately after the first trapping season in the North Basin, there was an increase in the growth rate of adults, and, subsequently, a gradual increase in growth rate in each successive year-class. By the 1955 year-class, the L of females had increased to c. 250 mm, and by the 1967 year-class to c. 300 mm; the male perch grow at a slightly slower rate than the females (Le Cren 1958; Craig 1980). The equivalent weights for lengths are (approximately): 60 g at 180 mm, 185 g at 250 mm and 400 g at 300 mm, so these increasing growth rates had a substantial effect upon the total weight of perch - the biomass. Indeed, by 1957 in the South Basin and 1961 in the North Basin, the biomasses of perch had exceeded those estimated for 1941, before trapping began. In the North Basin the biomass then declined slightly, becoming stable from 1964 until 1976 at about the same level it had been in 1941 - about 55 tonnes. In the South Basin the biomass was similarly fairly stable at the 1941 level of about 80 tonnes from 1965 until 1975 (Fig. 5). Equivalent estimates of growth rate and biomass are not yet available for the years since 1976, but the biomass must have been very much less for some while after the advent of the perch disease.

At various times a few exceptionally large perch were caught in the gill-nets set for pike. Estimated L was 463 mm and wet weights were c. 1 kg. Stomach contents showed that these perch were piscivorous and most of the largest had eaten smaller perch (Le Cren 1992).

Principal changes in the population dynamics of pike

Numbers

The first winter's removal by netting in 1945-46 reduced the estimated numbers of pike by about one-third (Fig. 6). The other immediate result of the fishery was an increase in the survival of young pike, and by 1949-50 the
FIG. 6. Estimated numbers (above) and biomass (below) of pike in the North (•) and South (O) basins of Windermere in 1944 to 1981. (Data from Kipling 1983b).
populations had increased to numbers larger than those present in 1994, especially in the South Basin (Fig. 6). During the late 1970s, the numbers of pike in both basins declined, but recovered again in the 1980s. Interpretation of CPUE data (Fig. 7) into real changes in numbers of pike is complicated by (a) the reduction in fishing effort over the years - though it has remained at a steady low level since 1992, (b) the effects of growth rate on the age of recruitment, and (c) some changes in sex ratio (Paxton et al. 1999; Paxton & Winfield 2000). The apparent increase in population numbers since about 1985 should probably await further, more careful, analysis before it becomes clear what has really happened.

**Growth and biomass**

Growth of pike has varied during different periods, but there has been no major increase like that shown by the perch. From 1942 until 1959, growth during the first three years of life was correlated with water temperature during the same three years. From 1960 to 1965, however, growth was much
slower; in the final period for which there are detailed analyses, 1967 to 1982, growth was much faster - in spite of a presumed shortage of perch as prey (Kipling 1983). The largest pike caught in the gill-nets (on 1 February 1960) was a ripening female of 15.9 kg, 110 cm long and in excellent condition; the stomach contained a trout c. ¾ lb (340 g) in weight. The pike's age was 14 years, determined from both scales and opercular bones.

The changes in growth rate, together with the changes in age structure brought about by the fishery, have influenced the biomass of pike in each basin (Fig. 6). In spite of the increase in numbers by 1949-50, the biomass remained below the 1944 level in the North Basin, but increased above it in the South Basin. During the late 1970s the biomasses of pike declined in both basins. Consideration of the changes since 1980 must await further analysis of the data.

**Temperature and growth of perch and pike**

By chance, the summers of 1946 and 1948 were unusually cold, but those of 1947 and 1949 were unusually warm - though that of 1947 followed a very cold spring when the lake was frozen over until April. The effects of these contrasts in water temperature became clearly apparent when I was examining the perch opercular bones from those and the immediately following years; the perch had grown poorly in 1946 and 1948, but particularly well in 1947 and 1949. This stimulated me to look for possible correlations between temperature and growth. Fortunately, FBA staff had recorded the water temperature outside Wray Castle boathouse every morning since the earliest days of the Association, and these were continued at a site near The Ferry House, after the move there in 1950 (Kipling & Roscoe 1977). An eventual analysis of these data (expressed as "degree days >14°C" - the approximate minimum temperature at which perch grow), and those of the growth of the perch at various ages, showed highly significant correlations (Le Cren 1958). Similar correlations with temperature were shown for pike growth (Frost & Kipling 1967; Kipling 1983a).

**Year-class strength and recruitment of perch and pike**

The data from the 1946-1949 year-classes also suggested that warm summers tended to produce stronger year-classes than cool ones, and this was shown to be the case from 1941 to 1973 (Le Cren, Kipling & McCormack 1977; Craig et al. 1979). These, and later data on pike year-classes, were subsequently developed into increasingly more sophisticated models by Craig & Kipling (1983), Mills & Hurley (1990), George & Hewitt (1998) and Winfield et al. (1998). The different authors produce results that vary in detail, but it seems that water temperature is the major abiotic variable determining the survival of both perch and pike in their first year. Young perch survival is also
negatively influenced by the abundance of adult perch, but pike do not seem to show any significant relationship between adult stock and number of recruits - a "stock-recruitment" relationship is not apparent. For pike it seems to be the water temperature in late summer and autumn that is most critical. The abundance of zooplankton also may have some influence on both species, but as the data on zooplankton applies only to that in the open water, and as young perch feed mostly just offshore and young pike feed amongst weeds in shallow water, these correlations have yet to be clarified and the actual biological mechanisms discovered.

**Numbers of Arctic charr**

Because Worthington (1950) envisaged an improvement in the charr fishery as one of the original aims of fisheries for perch and pike, he instituted regular sampling for charr with a gill-net set on one of their spawning grounds each autumn. Until 1973 the net was set in Low Wray Bay, just south of Wray Castle boathouse, but, from 1975, the site was moved to another spawning ground just north of Thompson Holme (Fig. 1). The CPUEs were low for the first five years, but increased from 1945 until 1961, when there was a further substantial increase (Kipling 1984b; Mills & Hurley 1990) (Fig. 8). The initial increase coincided with the first reduction in the numbers of large pike - of a size that feeds on spawning charr in autumn. Charr caught in the gill-net attained lengths of 350-380 mm at 9-14 years of age. 'Chris' (Christopher) Mills and Margaret Hurley (1990) also present data from the records of catches kept by three plumb-line fishermen, and Malcolm Elliott and Ellysar Baroudy (1992, 1995) provide further data from two fishermen and from echo-sounding.

It would appear that the CPUE of this regular annual sampling has tended to decline since about 1986 and this might be associated with some increase in the numbers of larger pike with the reduction in fishing effort. In Windermere there are four races of charr: spring and autumn spawners in each of the two basins (Frost 1963, 1965), and this complicates consideration of their overall abundance. A further complication results from the increasing eutrophication of the South Basin in the 1970s and 1980s which may have affected the survival and recruitment of deep-water spring-spawning charr in that basin. Eutrophication has now been reversed by the adoption of phosphate removal in the Windermere sewage treatment works (Elliott et al. 1996; Reynolds & Irish 2000).

**Brown trout and other species**

Allen (1938) studied the growth and food of the brown trout in Windermere and crudely estimated (from the catches made in seines and some marking experiments) that the total number of trout in the littoral was c. 12,000. Brown
trout have been caught in small numbers in perch traps (from which they have been returned alive) and in the pike gill-nets. The latter trout, being large, have been regarded as piscivorous and have been killed for measurement and to obtain scales for estimating age. These data still have to be fully analysed and published. Allen found that 7-year-old trout were 480 mm in length; 76% of the trout entering the lake from nursery streams were 2 years old. John Craig (1982) studied the juvenile and spawning trout in six becks flowing into Windermere and published growth curves for fish migrating into the lake at different ages, but he did not continue any long-term population studies. Elliott & Baroudy (1992) noted an increase in the catches of trout on charr plumb-lines in the South Basin after 1984. However, the status of the trout in relation to the other species in Windermere, and whether there have been any changes in their populations since 1941, have yet to be ascertained.

Frost (1945a,b) studied the age and growth of eels in Windermere (ranging up to 19 years old, 95 cm length and 2 kg weight), and data were collected in 1942 and other years on the catches in the commercial eel trap at Newby
Bridge, but there has been no recent work on eels. Frost (1943) also studied the basic ecology of the minnow, and Worthington (1950) reported that in a survey of experienced local fishermen in 1945, they expressed the opinion that the numbers of minnows had increased since 1941. However, estimates of their population numbers have not been attempted. 'Bill' (William) Smyly (1957) studied the basic natural history of the bullhead, but no recent work on its populations has been done. The other relatively abundant small species is the three-spined stickleback, but it, too, has been neglected in researches on Windermere. The stickleback and minnow are both eaten by large perch and small pike, so may have a role to play in the interspecific relationships between the various species in the lake.

Early in the perch trapping, a very occasional roach was caught in the shallow waters near the north end of the South Basin. General observations suggest that they have now become quite frequent in this part of the lake, but no attempt has so far been made to estimate their abundance; only a few have appeared in pike stomachs. An occasional bream _Abramis brama_ has been caught in the 1990s and a few young-of-the-year rudd _Scardinius erythrophthalmus_ were once caught in Mitchell Wyke in the late 1950s. Both roach and rudd occur in Esthwaite Water, so could easily reach Windermere via Cunsey Beck; they were also used as live bait (now prohibited) for pike angling.

**Basic research associated with the perch and pike project**

As well as following the changes in population dynamics resulting from the fisheries, the project has provided opportunities, as well as needs, to study several aspects of the basic biology and ecology of the principal species involved. Firstly there was the need to develop the methodologies necessary, and first among these was capture methods (traps, gill-nets and seines). It was necessary to find out their selectivity for size and sex and seasonal variations in this, the variability in their catches, its statistical analysis and techniques for relating CPUE to actual abundance and total population numbers (e.g. Kipling 1963; Bagenal 1972a,b; Craig & Fletcher 1982; Paxton & Winfield 2000). It was also necessary to identify the different stocks of fish in the lake and to consider if they should be regarded as separate populations. This involved taxonomic and genetic studies as well as marking experiments to determine migration patterns (e.g. Frost 1963, 1965; Le Cren & Kipling 1963; Hartley 1966; Kipling & Le Cren 1984; Bodaly et al. 1989; Mills 1989).

**Tagging**

Several tagging experiments have been carried out during the project and have provided valuable data on population numbers and other aspects of population
dynamics as well as information on migrations within the lake (Kipling & Le Cren 1984). While the marking experiments with perch proved disappointing for information on population dynamics, largely because of problems with distinguishing the sex of the fish when they were tagged and some mortality associated with the tagging operation, they did provide one of the earliest discoveries of "homing" in a non-salmonid fish (Le Cren 1945). Tagging the pike on the jaw proved to be very successful and very high rates of recapture (up to 89%) were achieved, so useful estimates of population parameters were obtained. Marking experiments on charr were also carried out that provided data on populations, homing, repeated spawnings at the same site, migrations onto spawning sites, etc. Tagging of all three species aided the verification of age and growth determination (e.g. Frost 1978).

**Food**

Studies of the food of the principal species and rates of food uptake were necessary bases for understanding the predator-prey relationships between the species (e.g. Allen 1935; Frost 1946, 1954, 1957; Johnson 1956a,b; McCormack 1970; Elliott 1975; Craig 1978b). Work on the zooplankton and zoobenthos of Windermere is relevant to assessing the quantities of food needed by the fish. There is some evidence that the availability of zooplankton at critical times of the year may have an influence on the survival of perch and pike in their first year of life (Smyly 1952; George & Harris 1995). Changes in the overall productivity of Windermere, which increased during the 1970s and 1980s (but is now decreasing) also may be relevant to the total biomass production of the fish species. The introduction of new species that may become important links in the food chain also is relevant. Two such species that have appeared in Windermere since 1941 are the macrocrustaceans *Asellus aquaticus* (Moon 1957) and *Crangonyx pseudogracilis* (Garland 1981), and they appeared in the stomachs of perch examined in later food studies (McCormack 1970; Craig 1978b). Kathleen Atkinson & Diane Hewitt (1978) suggested that changes in the numbers of piscivorous birds may also have an effect on the mortality rates of fish.

**Young stages**

The survival of the eggs of fish have been studied by Frost & Kipling (1967), Guma'a (1978c), Baroudy & Elliott (1994b) and Paxton & Willoughby (2000). Smyly (1952) and Said Guma'a (1978a,b) studied the first year of life of the perch with particular reference to their food; both authors found that the perch changed the size of its food as it grew. Smyly suggested that it was an apparent shortage of food in July which led to the largest perch fry becoming cannibalistic on the smallest. Evidence for mortality among young perch from
predation from older perch is conflicting; Allen (1935) and Craig (1978b) quite frequently found small perch in the stomachs of larger ones, but this rarely occurred in samples examined by McCormack (1970). The rare, exceptionally large individual perch (see above) fed predominantly on small fish, including perch; the abundance of prey in years with a strong year-class may have enabled the perch to accelerate their growth and become large (Le Cren 1992). The correlation of higher survival of young perch with warm summers has already been mentioned; the mechanisms that cause this are still obscure.

Frost & Kipling (1967) found where pike spawned in the lake and studied pike fry and the changes in their diet from entomostracans to benthic invertebrates, before they start to adopt an almost entirely fish diet at a length of 30 mm. These authors concluded that water temperature, particularly in late summer, is the dominant factor in determining the survival of pike in their first year. Baroudy & Elliott (1994a,b,c) researched aspects of the biology of young charr.

Estimating the age and growth of fish

The determination of the age and growth of fish from scales or opercular bones was an early topic for detailed consideration. In the case of both the perch and the pike, the development of using the opercular bone, rather than the traditional use of scales, was of major importance in the Windermere project, and some effort was put into verifying its accuracy (Le Cren 1947; Frost & Kipling 1959). This technique estimates past annual growth in body length of each individual fish ("back-calculation"); from these estimates means for the growth of groups of fish can be calculated. Frost (1978) used the scales for age and growth estimation in the charr, but showed that care is needed in the interpretation of annual rings.

Length-weight relationships, condition factors and fecundity

To convert lengths into weight, length-weight relationships were determined for different sexes and ages of fish. Related to the weight-length relationship is the "condition factor", traditionally used by some fish biologists to measure general "well-being" and also seasonal changes in it (Le Cren 1951; Frost & Kipling 1967). Seasonal changes in body composition and gonad development are also part of the seasonal cycles in condition (Craig 1977). The estimation of the fecundity of female fish of different sizes and ages, and possible changes in this correlated with changes in population density and growth rate, have also been considered (Frost & Kipling 1959; Kipling & Frost 1969; Craig 1980).
Mortality

An essential part of the analysis of the population dynamics of fish is the estimation of total mortality and its partitioning into various components, particularly that due to natural causes and that resulting from fishing. Accurate mortality estimation is difficult, and various ingenious methods and statistical devices have had to be used (e.g. Kipling & Frost 1970). Another aspect of mortality is the possible fundamental relationship between growth rate and mortality rate - faster-growing animals have a higher "physiological" death rate. Craig (1978, 1980, 1985) found evidence for this in the perch in Windermere from a comparison between different year-classes.

Other research

Many of the studies briefly mentioned in this section, though carried out primarily in support of the investigation of the long-term changes in population dynamics, have had value in their own right and have been cited in many fish and fishery studies elsewhere. Several important studies on fish, chiefly physiological, that have been carried out at the Windermere Laboratory are not described in this review because they are not directly related to the perch and pike fishery experiment. Nevertheless, many aspects of population dynamics in a project like this one on Windermere depend upon wide-ranging and fundamental studies in basic biology and ecology as well as methodological developments. As examples, the following citations will provide an introduction to the published literature: Swift & Pickford (1965); Pickering & Willoughby (1977); Willoughby (1978); Partington & Mills (1988); Beddington et al. (1989); Pickering (1994); J. A. Elliott (1995); Elliott & Hurley (2000); George et al. (2000).

Possible future developments and conclusions

The project described in this article has now been in progress for over sixty years. Although the intensity of sampling has been reduced in recent years, it is still continuing on a scale that is capable of measuring significant changes in the population dynamics of the three principal species - perch, pike and char. Most of the data are now available in a form (computer disk) that renders them readily usable for further analyses (though care should always be taken in the use and interpretation of data collected in the past by other investigators). Attempts have already been made to model the populations, using the increasingly sophisticated techniques that are now available (e.g. Mills & Hurley 1990; Winfield et al. 1998).

However, the validation and interpretation of these models and the discovery of the biological mechanisms through which they operate will still require further intensive studies in the field and laboratory. For example, the
exact way that water temperature affects the survival of perch in their first year has still to be elucidated. At what time in the summer is temperature important? Does it have its effect directly on the physiology of the perch, or is it mediated through the zooplankton eaten as food? Do faster-growing perch fry suffer a lower mortality rate from predation than slower-growing individuals? What are the causes of mortality among the fry: starvation, cannibalism, predation by other fish or by other animals? Does the major mortality occur in the off-shore pelagic phase or when the perch have returned to the littoral? New techniques, such as the interpretation of daily growth rings on the opercular bones or otoliths, and new apparatus such as echo-sounders that may be able to count perch fry (and perhaps their food organisms), may help in such studies. Similar questions still exist for the survival of young pike. The mechanisms that control year-class strength and recruitment (and their forecasting from abiotic data) are one of the major problems in fishery biology, and the Windermere project can help in solving much wider and practical fishery problems elsewhere.

It is worth emphasising once again the long-term nature of this project and how few of its contributions could have been made by a much shorter investigation. For example, it is now possible to make use of some fifty-five sets of variables, one from each year since 1945. Numbers of this size allow modelling of much greater power and significance than is possible with data from only a decade - let alone from the no more than three years that most research projects are allowed to last nowadays! It also must be borne in mind that individual perch and pike fifteen years or more in age have occurred among the samples; so a study of year-classes throughout the life-spans of these fish is necessarily a long-term process. Moreover, it may be several years before the strength of a particular year-class can be estimated, or the accuracy of a new sampling regime can be tested. This kind of study is very often an "experiment", with nature altering the independent variable year by year, and each year adding only one point to a graph.

In an earlier review of the Windermere perch and pike project (Le Cren 1987), I wrote: "Each period in our studies of fish in Windermere has produced new events, interpretations, and ideas which have caused us to modify previous conclusions. Long-term studies have a special value in fishery research." In my view this conclusion is still pertinent. It is echoed by Elliott (1990), arguing that long-term investigations on a wide variety of biological and environmental phenomena are vital aspects of environmental research.

Acknowledgements

A project such as this, lasting for sixty years, involved many, probably nearly a hundred, people who contributed thought, ideas, and tedious hours reading
opercular bones or operating a calculator or who carried out hard physical labour in inclement conditions on the lake; their work should not be forgotten. Ian Winfield, Charlie Paxton, Janice Fletcher and Malcolm Elliott have been generous with the provision of data from the more recent years and Karen Rouen helped to produce the text-figures. In drafting this review, I have had the benefit of critical advice from several people, particularly Charlie Paxton, Ian Winfield and David Sutcliffe. To all of these I am grateful.

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