Lochs Neldricken, Valley and Round Glenhead with Narroch and Dee behind

The *fall and rise* of Galloway and Carrick trout

Andy Ferguson, Caroline Bradley, Robin Ade, Colin Roberts, Jackie Graham, and Paulo Prodöhl look at the impact of acidification on trout and discuss some results from their current study.

The Galloway and Carrick uplands of South-West Scotland consist of nearly 1,000km^2 of rugged mountain, moorland and bog. It forms the Galloway and Southern Ayrshire UNESCO Biosphere, unique in Scotland. Over 40 lochs of glacial origin are present at altitudes from 200 to 500 metres. These range in size from small lochs such as Twachtan of around one hectare up to Loch Doon at 750ha. Enoch, the highest altitude loch, is the deepest (36m) and most remote requiring a 3-hour strenuous hike from the nearest public road. The lochs are drained by six main river systems, the Cree, Fleet and Ken-Dee flowing south into the Solway Firth, and the Stinchar, Girvan and Doon flowing north into the Firth of Clyde. In addition to natural barriers to trout movement, several of the rivers have artificial dams, partially or completely impassable to trout. Most impacted is the Ken-Dee where, since the 1930s, nine dams have been constructed for hydroelectricity. While conifer afforestation has taken place since the 1950s, much of the central upland zone is unplanted as the last remaining wilderness area in Britain south of the Highlands.

The lochs and rivers have trout populations that date from the end of the last Ice Age, some 12,000 years ago. The region has always been of considerable interest to trout anglers as seen from the many 19th and early 20th century fishing accounts. Indeed Lochs Grannoch and Dee were once regarded as among the best brown trout fishing lochs in Scotland. Similarly the downstream parts of the rivers provided prime sea trout angling. Stocking with farm strains of trout and offspring of native trout, for possible angling enhancement, has been undertaken in some of the lochs and rivers.

Over the past two years we have been carrying out a study of brown trout populations in the area. Because of its diverse ecology, water chemistry and anthropogenic influences, the region is one of the most complex and interesting areas in Britain and Ireland for exploring trout landscape genetics. By combining landscape ecology and demography with population genetics it is possible to investigate how environmental factors impact on colonization, individual movement, population structure, and genetic diversity of trout in the area. Also, in spite of the fact that Scotland has thousands of lakes and rivers with trout, only a few studies of trout genetics have hitherto been undertaken.

Some 3,000 adipose fin clips from 24 lochs and 51 river locations have been collected for DNA analyses, together with morphometric and meristic analyses on some specimens. This makes it the most detailed trout population genetic study hitherto undertaken in Britain and Ireland. During specimen collection, by angling and electrofishing, standard fish biology data were recorded where possible. Details were also kept of catch/angling hour and used to give an indication of the relative abundance of trout in each loch. Before looking at some of the preliminary results of our study it is necessary to consider the recent history of trout in the area.

The upland area consists largely of granitic rocks, often overlain by peat and poorly drained impoverished soils. Thus much of the area is base-poor and this low buffering capacity coupled with high rainfall (around 2,200mm annually), geographical position and prevailing winds resulted in the area being the worst affected in Scotland as a result of acid precipitation. During the 1970s and 80s intensive research on surface water acidification was undertaken on several lochs and monitoring still continues as part of the Acid Waters Monitoring Network. Diatom studies of the loch substrates have shown that acidification started in the early part of the 19th century. The first affected was Loch Enoch where the pH decreased from 5.4 in 1840 to 4.4 in 1982. Late 19th century reports refer to its 'tailless' trout, in which the tail fin rays had become deformed resulting in waviness and clumping of fin rays giving the tail a rounded appearance in extreme cases. While local folklore had it that this was due to abrasion on the very sharp sand, for which Enoch was renowned, it is now known to be due to abnormal development under acidic conditions. Although mid 19th century accounts refer to "baskets of four or five dozen nice trout", Enoch trout were extinct by the 1920s and possibly as early as 1883. In the first part of the 20th century, trout with similar fin deformities were also reported from Lochs Narroch and Fleet. In a survey of acidified lochs in 1984, trout with deformed

Loch Fleet

Loch Grannoch surrounded by extensive afforestation

tails were found at high frequencies in the Round Loch of Glenhead and in Loch Harrow. In our study, a small number of such deformities of tail and other fins were found in Enoch, Narroch and Lochinvar at frequencies <5 per cent (Figure 1).

The increase in acidity reached its peak in the years after 1950 with the pH falling in several lochs to below 4.5 (the same as buttermilk and hundreds of times more acid than pure water pH 7.0). Acid conditions also released high levels of labile aluminium, in some waters to a degree much higher than the normal toxic level (although calcium levels are important in determining this). Coniferous forests exacerbated acidification by intercepting acid deposition in the canopy, this being particularly important in relation to some spawning streams. In 1978-79 and 1984, scientists surveyed 22 lochs and 27 streams in the area; in addition to Enoch, no trout were caught in Lochs Valley, Neldricken, Narroch and Fleet - all known to contain trout in the 1950s. Low numbers were found in many other lochs relative to earlier records. In Loch Grannoch, the most acidified loch, the annual trout catch in 1940 was about 1,000 trout but this declined steadily to <100 trout in the early 1970s, even with greatly increased fishing effort. Studies demonstrated that the extinction and reduction of trout numbers was unquestionably due to acid precipitation. In some lochs, trout from a long-established farm strain were stocked in an attempt to reverse falling catches; in one of these, many were found dead a few days later.

Netting surveys also showed Arctic charr to be absent from two lochs (Grannoch and Dungeon) where they were present in the 1950s, the only surviving population being in Loch Doon. The existence of Arctic charr in these lochs is a very good indication that, although there are current barriers to upstream movement, these lochs must have been available for natural colonisation by trout in the immediate postglacial period. The former presence of another salmonid, the vendace, in lochs of the nearby Annan system and their occurrence in the Derwent system in Cumbria, but nowhere else in Britain or Ireland, suggests that a freshwater glacial refuge existed in the current Solway Firth area.

Peak sulphur emissions were in the 1970s with a sharp decline in the early 1980s followed by relatively consistent levels. In 1987 the UK government began a programme to reduce further the emissions of sulphur and nitrogen. This resulted in improvement in pH and labile aluminium in the Galloway lochs with the most significant improvement occurring during the second half of the 1990s. Catch records showed a rapid improvement in trout numbers over the 90s in spite of the fact that, although acidity had decreased, many lochs still remained chronically acidified. In Lochs Valley and Neldricken, where no trout were caught in the 1984 nettings, trout were found again from the mid 90s onwards. In the Round Loch of Glenhead, where trout survived the peak acid period at low numbers as judged from netting in 1984, catch rates increased 40-fold from 1989 to 2011 (Figure 2), with the greatest increase being from 1995 to 2000, the period of greatest pH increase. This demonstrates how quickly trout populations can respond given only moderate improvement in environmental conditions, just as they declined equally rapidly with deteriorating conditions. Even in these upland trout populations, where size at maturity is relatively low and an average female may produce only 500 eggs, a reduction in egg to spawning adult mortality from 99.7 per cent to 99.5 per cent can change a declining population into an expanding one. In fact, the change required is even less if multiple spawning is taken into account.

Figure 1. Fin deformities

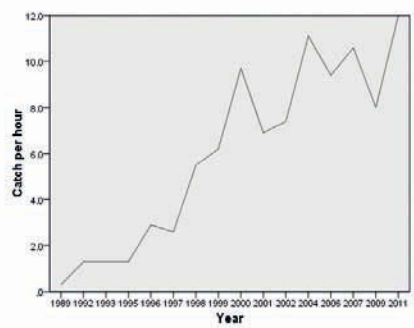

Figure 2. Angler catch rates of trout in Round Loch of Glenhead 1989 – 2011

In Grannoch, the most acidified loch (minimum pH 4.2), trout survived albeit at reduced numbers. Studies have shown that this population has a genetically-based tolerance of acidic conditions. Such tolerance is known to have a higher heritability than that usually found for fitness traits in fishes. Experiments conducted in egg boxes in the Enoch outflow in the 1990s showed that Grannoch eggs and fry, the most sensitive life-stages to acid conditions, survived much better than those from Loch Dee, although both are in the same Ken-Dee tributary 5km apart. The unique adaptation of Grannoch trout to acidic conditions has allowed trout to be re-established in two of the lochs where they had become extinct. Hatchery-reared yearling offspring of Grannoch trout were introduced to Enoch in 1994; similar offspring from successfully established Enoch trout were stocked into Narroch in 1999. Both lochs have good numbers of trout today and DNA analysis indicates that the trout are only of Grannoch parentage, impassable water -falls having prevented natural recolonisation from their catchments. Interestingly, although there is considerable colour variation among trout from different lochs (Figure 3), Enoch and Narroch are remarkably similar in spotting pattern and colouration to their Grannoch ancestors even though these lochs are in two other river catchments. Some stocking of

Grannoch offspring was also undertaken in 1994 into Valley and Neldricken although by that time they had clearly been recolonized by trout from their streams as DNA analysis shows that both lochs largely contain native trout with only small Grannoch contributions.

Grannoch trout provide an excellent illustration of why it is necessary to maintain the genetic diversity that is present among our native populations and not allow this to be lost or diluted by stocking farm strain trout. Since adaptation depends on genetic variation, which is produced by random mutation, it is not possible to predict which population possesses, or will acquire, the ability to deal with future environmental threats, new diseases, etc. Only by ensuring the preservation of as much genetic diversity among populations as possible can we give trout the best chance for the future, given the predicted increase in such challenges. Even if every farm strain of trout was genetically different, which is certainly not the situation given the common ancestry of many, some 50 trout farms could only contain a small proportion of the total genetic diversity present in the many thousands of wild trout populations. Not only is this diversity important for the long-term survival of trout and diversity of life histories, but also for ensuring high fitness, which results in surplus of trout over that required for population sustainability, thus permitting angling exploitation.

Loch Fleet was the focus for many studies on acidification from 1984-94, funded by the UK coal and electricity industries. In the first half of the 20th century, Loch Fleet contained a thriving stock of trout but catches declined markedly after 1950 and no fish were caught after 1975. Diatom records indicated that acidification started c1960 with the pH dropping from 6.6 in 1961 to 4.3 in 1975. During 1984-86, gill-netting, trapping and electrofishing confirmed trout were absent from the loch, its inflowing streams, and the outlet river for a distance of 7km downstream. Trout were present below this point, where the geology resulted in higher pH, but were prevented from passing upstream by a 5m waterfall. Experiments showed that brown trout eggs and fry could not survive in the loch water as a result of low pH, low calcium and high aluminium concentration. The land surrounding the loch was limed in 1986 and 1987 improving conditions and raising pH close to 7.0. Trout were stocked into the loch in 1987 and 1988 from three sources: below the outlet waterfall; Loch Dee; and a long established Leven-based farm strain. From 1988 to 1993 egg survival was monitored in the inlet and the outlet river using eggs from trout trapped in the inlet, except in 1993 when c1,000 eggs from Grannoch trout were substituted. Thus potentially a small number of this type was also introduced. Successful natural spawning occurred from winter 1987 onwards and is still extant today.

Figure 3. Some examples of colour variation in Galloway & Carrick trout

To our surprise, DNA analyses revealed four genetic groups of trout in Loch Fleet where, on the basis of stocking history, we expected to find a single population with an increased level of genetic variability. The existence of separate groups is borne out by the fact that many trout show distinctive colour patterns. Comparisons with samples obtained from the sources used for stocking indicate that one of the groups is of Loch Dee parentage. The other three groups appear to have been formed by initial hybridization of the introduced trout, but subsequently these have diverged from each other. This situation, which has arisen in less than ten generations, illustrates the complexity of 'population structuring' in trout, an aspect discussed further below. Although there is obvious reproductive isolation among the groups it is not clear at present how this is maintained. Loch Fleet is relatively small (17ha) with one small inflowing stream and a short stretch of the outflow suitable for spawning. As with other upland lochs, spawning also likely occurs within the loch where sufficient wave action and water seepage provide suitable hatching conditions (something sometimes forgotten in biological studies of trout). In spite of loch spawning, it is unlikely that isolation is due to spawning in different places. Spawning at different times is also unlikely as all wild progenitor stocks came from within 15km of each other. A possible mechanism is behavioural isolation as a result of mate recognition, something which has recently been shown to be much better developed in trout and other salmonids than previously considered.

In 2011/12, all of the hill lochs that we examined had self-sustaining trout populations. On average, catch/angler/hour was 10 (range 0.5 to 40) reflecting the current abundance of trout in many lochs, even where zero catches were reported in the early 1990s. Although recovery of trout populations has occurred in most lochs, many remain chronically acidified (pH <5.0) and very much on a 'knife-edge'. The recovery of salmonids, including sea trout and salmon, in many headwater streams has been much slower and still remains a significant problem. So what of the future for these populations? Climate change may pose a threat through the projected increase in rainfall and in frequency and intensity of storms, increasing sea-salt deposition which displaces acid particles in the soil increasing acidification. Although sulphur deposition has decreased from its 1970s peak, nitrogen levels have increased, potentially contributing to acidification and nutrient enrichment.

Substantial but highly variable levels of genetic diversity were found within our samples with individual samples showing from 28-63 per cent of the total gene diversity. These differences are accountable for by life history, natural and hydroelectric barriers, population bottlenecks as a result of acidification, and stocking. The populations with highest diversities all have sea trout currently, or had sea trout historically, with inter-population gene flow likely responsible for this high diversity. All of the sea trout samples, whether from the Clyde or Solway catchments, form a distinct group, separate from freshwater ones, reflecting this regular interbreeding.

A very high level of inter-sample genetic diversity was also found, with all samples being significantly genetically different from each other, even adjacent samples within catchments. This, commonly referred to as "population structuring", does not mean that these samples are drawn from separate populations! Rather, these differences arise due to natal homing of trout, barriers to movement within catchments, limited dispersal of trout from their natal areas, genetic drift due to demographic changes, and the continually increasing resolution resulting from improvements in DNA technology. Indeed if enough genes are examined, every individual can be shown to be genetically unique, something which is currently technically feasible! This raises the question presently much discussed among salmonid geneticists: How different is different? In other words, what level of genetic differentiation indicates entities requiring separate management? In many ways this is analogous to the 'what is species' debate and as yet there is no satisfactory answer! For our samples, at one end of the scale, four very distinct genetic groups can be identified, probably representing post-glacial colonising lineages. At the other, many distinct groups are apparent as some samples, such as the Loch Grannoch one, represent more than one genetic group. Thus the number of 'populations' depends on the hierarchical level of genetic resolution chosen.

Samples were indirectly obtained from local fish farms through angling in stocked fisheries with little or no spawning.


Another fin clip in the tube – one of over 300 caught by Margaret

Specimens were also obtained from Loch Leven, the original source of broodstock for many trout farms. A very clear Loch Leven signature persists in local farm strains despite their establishment from Leven broodstock in the late 19th century. This signature provides a valuable method of assessing the genetic impact of stocking such farm strains. Overall of the 75 samples examined only 18 showed farm genes present and seven of these were from the Rivers Girvan and Doon, which are known to have been regularly stocked with farm-reared trout. In these rivers, the overall frequencies of farm genes were 20 per cent and 14 per cent respectively with a maximum of 40 per cent in an individual sample. In the other 11 samples, the maximum frequency of farm genes was 8 per cent, with an average of 3.5 per cent. All but two of these were river samples and both of these have records of historical Leven strain stocking. Thus most of the lochs contain only wild native trout strongly refuting the notion "that as a result of stocking it is almost impossible to find genetically pure native brown trout in the UK"!

While clearly all trout populations are important, given limited conservation resources and increasing threats it is important to identify those most important for conserving trout genetic biodiversity. Several genetically and phenotypically distinct trout populations were identified as high priority populations for conservation action. Interestingly Grannoch, with its heritable tolerance of acidic conditions, is the most unique on DNA analysis. Several populations, thought to represent an early postglacial colonising lineage, were also identified. More detailed results of the genetic analyses will be published over the coming year.

Much of the information on the decline and recovery of Galloway and Carrick native trout populations comes from anglers' records; one fishing club has maintained daily catch records in two wild trout lochs since 1892. Also, 70 per cent of the fin clips used for genetic analysis was obtained by angling. Anglers can play a very valuable role as 'citizen scientists' in monitoring trout populations, especially those in the remoter regions, in the same way as amateurs have done for bird populations over many years. These records can be very valuable in revealing environmental problems. Such monitoring would require anglers to take a leaf out of the birder's notebook and keep detailed records, something which is not always the case. The minimum record for any days fishing should include date, location, time of starting and finishing angling, actual time spent fishing (excluding breaks), fishing method(s) used, weather conditions, number and, where possible, length of all fish caught (tip of snout to fork in tail), and details of any abnormalities or unusual characteristics. We would be very interested to hear from anglers who have such records for the Galloway & Carrick region.

Key references

(References below are available free online, with the exception of Turnpenny et al., which requires purchase. Many other related references can be found by searching on Google SCHOLAR, with keywords such as 'Galloway trout'.)

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Acknowledgements

We are grateful to many organisations and private land-owners for permitting and facilitating our study including Forestry Commission Scotland (Galloway Forest District), Forrest Estate, Scottish Natural Heritage, Ayrshire Rivers Trust, Marine Scotland Freshwater Laboratory, Scottish Environment Protection Agency, J. Curtis and J. Stacey. Also the many anglers and others who assisted with sample collection and background information. Andy Ferguson thanks the Fisheries Society of the British Isles for the award of a Wyn Wheeler Research Grant to cover the travel costs for collecting specimens and preliminary DNA analyses. Dr Bradley is funded by a Beaufort Marine Research Award to Prof Prodöhl.

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