Figure 1: A sea run char from a Northern Icelandic river, likely typical of those which initially colonised rivers of the British Isles after the retreat of the last glaciation

Darwin could have stayed at home

Lessons in salmonid speciation and ecology from Scottish char

Dr. David Fraser provides some insights into the trout's often forgotten cousin, the Arctic char.

As the grip of the last ice age began to recede some 12,000 years ago, one of the first arrivals in our rivers was the Arctic char, *Salvelinus alpinus* which, having resided in waters on the periphery of the great ice sheets, strayed into rivers newly emerged from the retreating ice. These pioneering individuals progressively colonised our freshwaters and form the basis of the approximately 340 British Isles populations of this reclusive but magical cousin of *Salmo trutta*. Those first colonisers were anadromous sea farers, akin to present day sea trout, as can still be encountered in Iceland, Greenland, northern Norway and North America (Figure 1), and essentially anywhere North of 65 degrees latitude, the threshold for sea run char. In the same way that many of our post glacial colonising sea trout populations gave up their wanderlust and became freshwater resident, so too did all our char, which now reside solely in the deeper lochs, loughs, tarns and lakes, primarily in upland regions.

The story from this point forward for char is similar to that of non-migratory trout, with populations being isolated in waters distinctive in their physical, chemical and biological characteristics. Combine this with the fact that the founding fish (original invaders) of each lake population would have differed in their genetic and phenotypic characteristics, and you have all the ingredients for evolutionary diversification amongst char populations. Although both trout and char have been similarly subject to such processes, char differ from trout in the sheer extent to which they have diversified (and before I upset the readership, I speak as one who is fully signed up to the huge value of variability in trout populations!). The result is char which differ from lake to lake, often strikingly in terms of their size, life history, shape, diet, colouration and behaviour. This diversity was recognised (although not fully understood) by the earliest biologists, with fifteen char species being named in the British isles originally. Modern classification now largely regards them as a single species, with extensive intra-species diversity.

But, perhaps the most striking characteristic of Arctic char is their propensity in certain instances to exhibit multiple races or forms within a single water body. Studying and identifying such populations was the basis of my Ph.D., which firmly established my belief in the need to recognise all salmonids (and indeed fish) as not merely individual species, but a group where fish from different catchments, rivers, lakes or even within the same water are likely to be inherently different, and thus need to be managed as such.

My study capitalised on earlier work of Ross Gardiner, Andy Walker, Ron Greer, Colin Adams and others in exploring the multiple forms of Arctic char in Loch Rannoch in Perthshire. Initial studies by these co-workers indicated two forms of char within Rannoch but subsequent work by myself, Colin Adams and Felicity Huntingford using shape, diet and length-at-age analysis indicated three forms: a deep water, bottom-dwelling, piscivorous (fish-eating) form, an open water, planktivorous form (feeding on mid-water invertebrates) and a deep water, benthivorous form (feeding on bottom-dwelling invertebrates). Figure 2 shows three similarly sized individuals of each morph, although the differences are best illustrated by viewing a number of the individuals together (Figure 3).

Figure 2: From top to bottom, piscivorous, benthivorous and planktivorous char forms from Loch Rannoch. These individuals are of identical length and exemplify the head shape differences characteristic of each form. Piscivorous and benthivorous are both superficially similar in terms of pale colouration and markings, but piscivorous individuals have longer heads, larger eyes and gapes and less rounded snouts than benthovores. Planktivores (bottom) are instantly differentiated by their claret colouration, but also have significantly more slender bodies, smaller heads and finer jaws than the other two forms

Figure 3: Three piscivorous char (top) and three planktivourous char (bottom) illustrating the growth potential of the two morphs

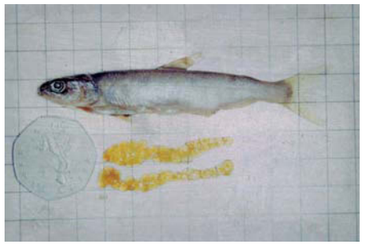

Figure 4: An example of a small sexually mature female char of the piscivorous form

LIFE HISTORY

Planktivores grow rapidly but exhibit a clear limitation in maximum size, never exceeding the sizes illustrated and 7 years of age, whereas piscivores grow slowly but have an indeterminate maximum size. The largest individual in Figure 3 weighed 2.5kg and was 17+ years old. Benthivores (not shown in Figure 3) are similar to planktivores with rapid growth, but a clear limit in maximum size, slightly larger than planktivores. The maximum age recorded for benthivores was 11 years. Another striking feature of the piscivorous form is the maturation of females at a tiny size, the smallest ripe individual recorded being 74mm, and containing 18 eggs; a similar individual is shown in Figure 4.

DIET

The piscivorous form is benthivorous early on in its life, but switches to feeding on fish at 16cm. The benthivores were never found to contain fish, irrespective of size, preferring instead a diet dominated by tiny *Pisidium* pea mussels, chironomid (midge) larvae, and benthic cladocera (water fleas). The planktivorous form consumed predominantly cladocera, but with chironomid larvae also making a significant contribution at certain times of year.

LOCH ERICHT

Having largely figured out the basic biology of the Loch Rannoch char, my attention then turned to Loch Ericht; its similar dimensions to Rannoch and being the next loch upstream in the same catchment made it an obvious comparison site. Field sampling immediately yielded char which visually clearly comprised two different forms (Figure 5). Subsequent quantitative shape analysis confirmed two discrete shape forms, with dietary analysis determining that the pale form was a piscivore, whereas the coloured form was a zooplanktivore. As with Loch Rannoch, the piscivorous form grew relatively slowly but lived longer and attained greater ultimate sizes than the planktivorous form.

HOW DID THESE DIFFERENT CHAR FORMS ARISE?

The question of how such multiple co-occurring forms of a single species arise and persist is one that has generated a great many scientific papers; a key hypothesis is they occur where there is the absence of competition from other fish species, resulting in vacant ecological niches (food sources and habitat). In lakes, the two most discernible niches are the benthic environment where invertebrates living in and on the lake bottom are the key prey item, and the open water or pelagic environment where zooplankton are the main food source. Fish can be considered a third quite different food source. The ability to effectively exploit these requires particular and quite different attributes in the fish, in terms of body and mouth shape and behaviour. Thus, intermediate morphological forms (including the results of hybrids between the different forms) are less efficient at exploiting these discrete food resources and are selected against in evolutionary terms.

RANNOCH VERSUS ERICHT

The next obvious question is why the presence of two bottom dwelling forms in Loch Rannoch but only one in Loch Ericht? A strong hypothesis for explaining this relates to the physical dimensions of Loch Rannoch, which comprises two basins. Catch data indicated that the benthivorous form only occurred in the small shallow west basin, whereas the piscivorous form only occurred in the deep east basin. Although the constriction between these basins is not sufficient to physically prevent movement of the fish, catch data in my study and those of other lakes clearly shows that char are restricted to deeper areas by the competitive dominance of brown trout in the richer shallower habitats. Thus, the two bottom living char forms in Rannoch are effectively isolated within each basin. The west basin is relatively shallow, and thus has a relatively productive lake bottom thus selecting for a benthivorous specialist, whereas the relatively deep west basin has a severely impoverished bottom fauna, meaning that other fish are the main prey opportunity.

These differences are maintained and further reinforced in Loch Rannoch by each form utilising a different spawning habitat. The benthivorous form spawns in the mouth of the River Gaur, the main inflowing river entering the west basin. The planktivorous form (which occurs in both basins) spawns in the shallow stony wave washed zone (1-3m depth), with some evidence existing that the piscivorous form spawns at greater depths.

NURTURE VERSUS NATURE?

Despite the apparently striking differences observed within a single water body, these have been demonstrated to be of environmental rather than genetic origin. In these scenarios individuals from a single gene pool specialise on different habitats

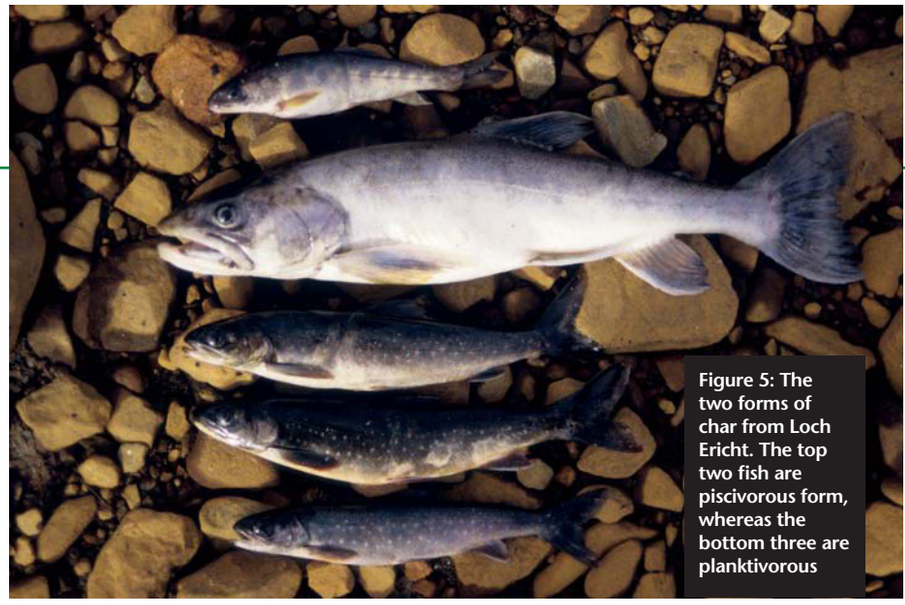

Figure 5: The two forms of char from Loch Ericht. The top two fish are piscivorous form, whereas the bottom three are planktivorous

and prey (typically benthic and pelagic) early on in life, and this specialisation results in two different forms. So, is this the case with the Rannoch char? Common rearing experiments (Adams and Huntingford, 2002) demonstrated that although much of the shape differences between wild planktivorous and benthivorous char disappeared when reared together, indicating a strong environmental component, differences did remain, indicating inherent genetic differences. The authors concluded that this did not undermine the hypothesis that the different Rannoch forms comprised three non-interbreeding gene pools which were at an early stage of the speciation process.

WHAT DO GENETIC STUDIES TELL US?

Although the studies described above provide clear evidence that three reproductively and ecologically discrete forms exist, genetic studies further reinforce this. However, arguably the greatest additional benefit of genetics is in further elucidating hypotheses for how the char arose. Early work on Loch Rannoch char undertaken by Sheila Hartley and developed by Eric Verspoor and colleagues more recently suggests that the two deepwater forms originated from a single post glacial invading race, which diverged into a piscivorous and benthivorous form within Loch Rannoch due to the two basin profile, whereas the planktivorous form derives from a separate post glacial invading race. This two invading race hypothesis may explain why we do not perhaps have more waters with multiple char forms. It may be that a combination of within-lake conditions needs to coincide with two or more invading char races. However, if we consider that invading races were adapted for sea going and might have been broadly similar in shape it is clear that most of the significant divergence in shape, life history and ecology has taken place within Lochs Rannoch and Ericht – and in the last 12,000 years since deglaciation.

THREATS

Despite Loch Rannoch and similar sites being remote and removed from significant development pressure, it would be naive to assume threats don't exist. The introduction of invasive non-native species (and I include here species native to the UK but not to the water body concerned) is surely one of the most acute threats to rare fish communities. During my studies my catches included a crucian carp, which appeared to have been introduced via pike angling live bait. Although this is likely to have been an to be an isolated individual, it highlights that such populations are one discarded or released bucketful of livebait away from potential catastrophe.

Surprisingly, despite the clear value of multiple co-occurring char forms from a scientific, conservation and educational perspective, none of the sites where they exist receives statutory protection; these include not just Lochs Rannoch and Ericht, but also more recent discoveries in Lochs Awe, Tay and Doine. The inadequacy of this situation was thrown into sharp focus in recent years when a planning submission for a multi-million pound golf and leisure development including within lake development was submitted for the south shore of Loch Rannoch. Many parties opposed the development, including Scottish Natural Heritage, although no case was able to be made in terms of the char, due to the loch not being statutorily protected in terms of its char.

One saving grace is the inclusion of Arctic char on the UK Biodiversity Action Plan list which does at least provide an element of recognition of its conservation value at a general level.

PROGNOSIS FOR CHAR

So what of the prospects for a fish whose name indicates that it might not be best able to cope with a warming world? Well, first let me challenge some preconceptions. It is often said that char are an "ice age relic". This is somewhat of a nonsensical term, as all of our current fauna is the result of colonisation of previous glaciated areas and char are no different in this respect from our non-migratory brown trout populations; indeed it may be that the term "Arctic" in the name does the fish disservice by suggesting an exotic origin. Nonetheless, recent analysis of a limited number of UK populations suggests recent decline (Winfield et al., 2009) partly due to climate change. Char populations of the largest, deepest lakes and those at the greatest altitude are likely to be the least affected by climate change, and in this respect Lochs Rannoch and Ericht are well placed. Waters at the other end of the climate sensitivity spectrum may fare less well, particularly when affected by factors such as eutrophication, and the acute and irreversible effects of the introduction of novel fish species.

Compounding these threats, translocation to other waters as a mitigation option does not lend itself to co–occurring forms of char. Remember that these forms are products of the particular environmental conditions of the lake in which they reside, and finding or replicating these in an alternative water body would likely be impossible. In an economic and policy climate where there is often an assumption that any development or impacts can be mitigated by spending money in such ways, it is worth highlighting where this is not the case.

I hope that readers will indulge this deviation from WTT's troutier focus, but in doing so I believe char provide us with an insight to the same processes which take place throughout salmonid fish, including *Salmo trutta*, and which should continue to be the focus of research and conservation efforts. The biodiversity of our salmonids is still far from fully documented, and we can only conserve what we know and understand; there is not one *Salmo trutta*, one *Salmo salar* nor one *Salvelinus alpinus*, there are many, many.

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