SUMMARY

Hybrids between Atlantic salmon and brown trout were detected in two of four watersheds studied in northern Spain. The proportions of hybrids in samples of "salmon" ranged from 0.0% to 7.7% but they were not significantly heterogeneous among locations, resulting in a mean hybridisation rate of 2.3%. This is the highest rate of natural hybridisation so far reported and is significantly greater than rates observed elsewhere in Europe.

INTRODUCTION

Hybridisation between Atlantic salmon (Salmo salar) and brown trout (S. trutta) appears widespread (Solomon & Child, 1978; Beland et al., 1981; Crozier, 1984; Verspoor, 1988) though observed rates vary from region to region. The reasons for this are not clear. Hubbs (1955) predicted that hybridisation will be higher where one species is introduced or where the environment of the species involved has been physically or biologically disturbed. Consistent with this Verspoor (1988) found a significantly higher frequency of hybrids in Newfoundland, where brown trout are introduced, than has been observed in the British Isles and Scandinavia. Reported here are hybridisation rates between Atlantic salmon and brown trout from rivers in northern Spain, where the two species coexist at the southern limit of their endemic distribution in western Europe. The observed hybridisation rates were compared with those reported for North America and other European salmon populations.

METHODS AND MATERIALS

Electrofishing during September and October 1987 was used to collect 169 "salmon" parr from eight locations in four watersheds in northern Spain (Fig. 1) in which both Atlantic salmon and brown trout occur. These watersheds have in recent years accounted for about 30% of the total Spanish salmon catch (Garcia de Leaniz & Martinez, 1988). The fish were then frozen for protein analysis. Six smolts captured by local biologists in 1985 from the River Sella were also examined, giving a total sample of 175 fish.
Hybrids were identified using the diagnostic electrophoretic banding patterns of glucose phosphate isomerase (GPI) and phosphoglucomutase (PGM) as described by Verspoor (1988). All G tests have incorporated William's correction for small expected frequencies (Sokal & Rohlf, 1981).

RESULTS

Atlantic salmon x brown trout hybrids were detected in two of the four watersheds sampled, the Ason and the Pas (Table I). In the Ason watershed, hybrids were present at both sampling locations, a small spawning tributary (Bustablado, site 1, Fig. 1), and the main river (at Valle, site 2, Fig. 1). The hybrids in the Pas were in the sample from Riolangos (site 4, Fig. 1) in the higher reaches of the river; the sample from the lower reaches at Soto de Iruz (site 3, Fig. 1) contained none. In the Ason, Deva, and Sella rivers, significantly more brown trout than salmon were captured during the course of electrofishing, while the reverse was true for the Pas (Table I). The incidence of hybrids ranged from 0 to 7.7% among sampling sites (Table I), but these values were not significantly heterogeneous (2 x 4 contingency table: \( G = 2.16, p >0.5 \)). The overall rate of hybridisation was 4/175 or 2.3%.

The two hybrids found in the river Pas were the smallest of the four hybrids found, and were essentially indistinguishable from salmon parr on the basis of external appearance. The two hybrids from the Ason watershed were larger and visually more intermediate, one more resembling a salmon (Fig. 2, second from top), and the other a brown trout (Fig. 2, bottom).

DISCUSSION

The frequency of hybrids between Atlantic salmon and brown trout detected in the Spanish rivers (2.3%) is over seven times the level reported for the British Isles (0.3% - Solomon & Child, 1978) and over 20 times higher than that observed in Sweden, (~0.1% - Gunnar Stahl, pers. comm. - see Verspoor, 1988). It is also higher than in North America (0.8% - Verspoor, 1988) where because brown trout are an introduced species, hybridisation might be expected to be unnaturally high (Hubbs, 1965). The differences between Spain and Britain is significant (\( G = 6.91, df = 1, p <0.01 \)) respectively, as will be that between Spain and Sweden, though the levels in Spain and North America are not (\( G = 2.20, df = 1, p<0.2 \)).

Verspoor (1988) has pointed out that actual hybridisation rates between Atlantic salmon and brown trout are likely to be much higher than the reported values as the samples collected include only fish resembling one of the two parent species (Payne et al., 1972; Crozier, 1984; Verspoor, 1988; this study). Since hybrids can resemble either salmon or trout (Fig. 2; Piggins, 1965; Solomon & Child, 1978), an unknown proportion of hybrids will be classed as being the "other" species and will not be sampled. The observed incidence of hybrids will also be lower than the true value in rivers where natural populations of salmon and/or trout have been augmented by stocking with hatchery reared fish, and these are included in the sample. While this does not apply to the Newfoundland populations examined by Verspoor (1988), it will to some degree be true for samples from Britain (Payne et al., 1972; Solomon & Child, 1978). In Spanish rivers, the numbers of stocked fish can be quite significant (Garcia de Leaniz & Martinez, 1988), and stocked salmon were present in the samples examined here. Correcting for this is difficult, but based on genetic identification, 29 of the salmon in the samples were introduced salmon (Verspoor & Garcia de Leaniz, unpublished), giving an overall rate of hybridisation closer to 2.8%.
The apparently high frequency of hybrids in the Spanish rivers could be due to several factors. Frequencies observed in Britain were based on samples of adult "salmon" taken in nets along the coast or in estuaries, as well as some migrating smolts (Solomon & Child, 1978) where frequencies may be lower if some hybrids remain resident in the stream. This could also account in part for the observed differences between Britain and North America though not for the difference between Britain and Sweden. It also cannot account for the large difference between Spain and Sweden, and is unlikely to be responsible for most of the difference between Britain and Spain. Even if it is assumed that less than one half of hybrids migrate to sea, the frequencies in the Spanish rivers are still more than four times higher than in Britain.

Several circumstances peculiar to Spanish rivers could potentially promote hybridisation. Catches of adult salmon in Spanish rivers fluctuate greatly between years (Garcia de Leaniz & Martinez, 1988; Martin Ventura, 1988), due in part to the small numbers of year classes represented in the catch. This is because over 95% of Spanish salmon migrate to sea as 1 or 2 year olds, and 75-85% return as two sea winter salmon. As a result, failures in only one year class (either in fresh water or at sea) will have a drastic effect on numbers of adults spawning, and may cause shortages of mates in some years. In 1982, for example, only three adult salmon were caught in the river Ason, whereas the catch levels in the previous and following years were 54 and 70 salmon, respectively (Garcia de Leaniz & Martinez, 1988). Furthermore, in some Spanish rivers, summer droughts coupled with increasing seasonal demand for water abstraction are known to result in isolated pools in which adult salmon and trout are effectively trapped (Garcia de Leaniz & Martinez, 1988), which may favour intercrossing by forcing fish to spawn in reduced areas of the stream.

The mating behaviour of sexually mature male parr (Jones and King, 1952; Myers and Hutchings, 1987) is thought to be less discriminating than that of adult salmon, so intercrossing may be eased in situations where mature parr abound (Crozier, 1984; Verspoor, 1988). Sexual precocity among salmon parr in Spanish rivers has been found to be exceptionally high, 43% of the males maturing as 0+ and almost 100% among the older age classes (Garcia de Leaniz and Hawkins, in prep). Under these conditions, and when the relative density of female adult salmon is low, interspecific crossing between male parr and female brown trout may be expected to increase.

Reproductive isolation may also decrease as a consequence of the introduction of foreign hatchery populations for stocking purposes (Vuorinen & Piironen, 1984). Stocking with foreign salmon ova and fry is widespread in most rivers of northern Spain (Garcia de Leaniz & Martinez, 1988). Indeed, genetic differences between native and introduced salmon, and the genetic make-up of brown trout in Spanish rivers (Verspoor & Garcia de Leaniz, unpublished), allow one of the four hybrids to be unequivocally identified as the progeny of a cross between an introduced salmon and a native brown trout.

Clearly, further research is needed before the factors contributing to hybridisation between Atlantic salmon and brown trout in the wild will be fully understood. However, if as suggested, the disturbance of the populations and their environments is a major cause, then this understanding will be important in the development of management programmes that minimise its occurrence. If this is not done, the implications could be serious as they have been in the case of hybridisation of introduced rainbow trout with native cut-throat trout in North America (Benke, 1972).
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REFERENCES


TABLE I

Observed incidence of Atlantic salmon x brown trout hybrids in samples of "salmon" from rivers in northern Spain. Sampling site numbers correspond to Figure 1

<table>
<thead>
<tr>
<th>Watershed/sampling site</th>
<th>Number of &quot;salmon&quot;</th>
<th>Hybrids</th>
<th>Observed brown trout/salmon ratio(^1) during electrofishing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rio Ason</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Bustablado</td>
<td>29</td>
<td>1</td>
<td>3.4</td>
</tr>
<tr>
<td>2. Valle</td>
<td>28</td>
<td>1</td>
<td>3.6</td>
</tr>
<tr>
<td>Rio Pas</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Soto de Iruz</td>
<td>39</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4. Riolangos</td>
<td>26</td>
<td>2</td>
<td>7.7</td>
</tr>
<tr>
<td>Rio Deva</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Ojedo</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6. Lebena</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rio Sella</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Millares (parr)</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(smolts)</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8. Ponga</td>
<td>31</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>175</td>
<td>4</td>
<td>2.3</td>
</tr>
</tbody>
</table>

\(^1\) Chi-square, ** p<0.01, *** p<0.001
Figure 1. Location of watersheds and sites sampled in northern Spain. Sampling site numbers refer to Table I.
Figure 2. Atlantic salmon, brown trout and natural hybrids from the river Ason. From top to bottom: Atlantic salmon parr, salmon-like hybrid, brown trout, and trout-like hybrid. The abnormal colour pattern of the lower of the two hybrids is an artifact of handling.