



# Wild Trout Trust

## View on Stocking and Rationale

The introduction of farmed trout (stocking) to support anglers' catches is a well-established and widespread practice. Many fisheries rely upon it to remain viable - for example reservoir trout fisheries that lack natural trout production. However, in waters with a natural population of trout, stocking of farmed fish can present risks to the wild population through inter-breeding and competition.

### **Inter-breeding**

A basic concept in conservation is that preserving variety (and the underlying genetic diversity) is crucial, in order to protect the ability of animals and plants to adapt and flourish in the wild (e.g. (Laikre *et al.*, 2008) and (Hindar, Ryman & Utter, 1991).

Salmonid fish possess a particularly extraordinary level of variation in physical characteristics and adaptations (see Fact Box 1). Trout are, consequently, particularly at risk of losing valuable genetic variation from the effects of stocking and that could mean that wild trout populations become less 'fit for life'.

A clue to the phenomenal variation present within wild brown trout *Salmo trutta* is the historic assignation of around fifty separate species to what can be considered to be a single, if unusually adaptable, species (Behnke, 1986). Even today, though, there is not a universal consensus that all this diversity can be adequately assigned to a single species. As an example, twenty eight European species of "*Salmo*" trout are listed in current reference material (Kottelat & Freyhof, 2007). In the British Isles, this tremendous variability is accounted for by at least five distinct groups of trout all derived from a common Atlantic origin – where they had survived the last ice age some twelve to fourteen thousand years ago (Bernatchez, 2001; McKeown *et al.*, 2010). The "Atlantic" lineage of trout that contains these five groups is, itself, one of five major surviving lineages of trout to have evolved over the last 2 million years: the remaining four major lineages being "Danubian", "Adriatic", "Mediterranean" and "*marmoratus*" (Bernatchez, 2001). The post-glacial Atlantic lineage trout that colonised the rivers of the British Isles comprise the "master library" of genetic material from which all modern UK and Irish populations are derived.

Farmed trout were originally obtained from wild brood stock and all of the genes present in farmed strains of brown trout have also been derived from this wild "master library" (the brown trout genome). However, there are very few farmed strains of brown trout compared to the numbers of wild populations. Many farmed strains have been line-bred and selected (deliberately and inadvertently) for characteristics that make them suitable for rearing in a farm environment, i.e. they have been domesticated. These domesticated characteristics are often not compatible with life in the wild and poor survival rates of farmed fish have been observed following their release (e.g. (Bachman, 1984; Clifton-Dey & Walshingham, 1996; Cresswell, 1981).

Because of their limited number, it would not be possible to recreate the full contents of the wild genome by cross-breeding domesticated strains. This also means that domesticated strains do not contain the necessary genetic variation to provide “matches” for the wild populations into which they are stocked. An indication of the potential complexity of wild populations is given by some recent research work undertaken on the River Dart. Tissue sampling work across the Dart catchment has identified genetic structuring of fish populations according to geographic separation (Griffiths *et al.*, 2009). Although five of the groups that were sampled on the Dart owe their distinction to three specific impassable weirs, the rest of the spatial genetic structuring appears to be maintained by fish (predominantly) accurately “homing” to their natal spawning areas in order to breed (Griffiths *et al.*, 2009).

Fact Box 1:

Trout show an amazing variety in their characteristics, both among different populations and between individual fish in the same population. Take body size as an example. The weight of most vertebrate animals varies between individuals by about 15%\* (at a given age, in a single population), but for trout the figure is around 60% (Elliot, 1994).

Of course, there are many, many characteristics (traits) that vary between fish other than just size. Foraging ability, predator avoidance, disease resistance, timing of breeding attempts, temperature range tolerance and selection of breeding sites are just a few more examples. A proportion of the variation in any specific trait is due to genetic variation – with some traits being more strongly influenced by genetic control than others.

\*( measured as the “coefficient of variation” or standard deviation divided by the mean)

Complexity in breeding population structure is also evident through investigation of populations in Europe. Any individual trout population contains only a fraction of the genetic diversity found among different populations in Europe. By studying DNA fragments inherited solely down maternal lines from over 3600 individual fish belonging to more than 70 populations, it is estimated that an average of 15% of the total genetic variation observed was present within individual populations (range 4-28%) across Europe (McKeown *et al.*, 2010). In other words, individuals within a specific population are likely to be more similar to each other than to individuals from more widely separated populations (Fig.1; all populations). However, even though the majority of variation is accounted for by the existence of many different and widely separated populations, **important variety** can still be found *within* populations inhabiting a particular river or lake (e.g. Fig.1; D, (McKeown *et al.*, 2010) and (Ferguson & Taggart, 1991)).

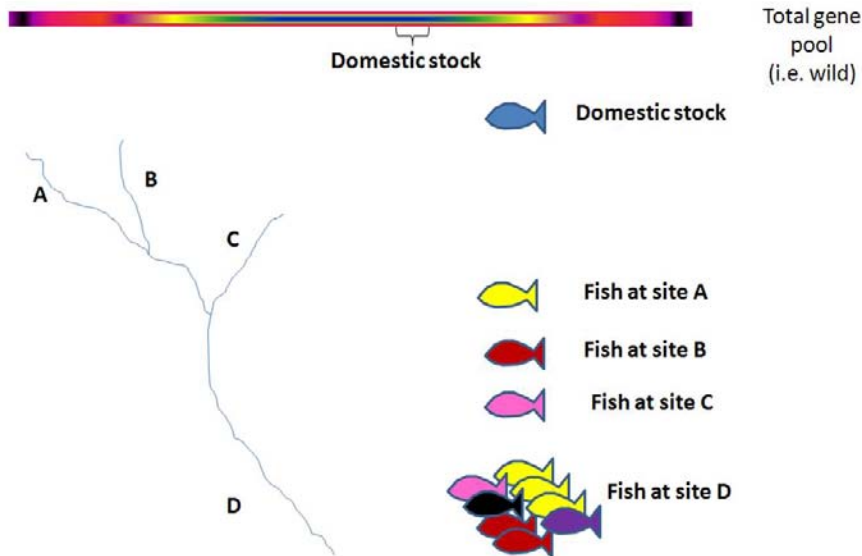


Figure 1: The "master library" of the total brown trout gene pool is represented by a spectrum of all brown trout genes and all of their alternative versions (top). The characteristics of fish from populations that are adapted to thrive in the conditions at sites A, B, C and D are represented by a range of colours. A blue shading represents an example of a domesticated strain derived from the master library and it is very different to the other, locally-adapted fish in this illustration.

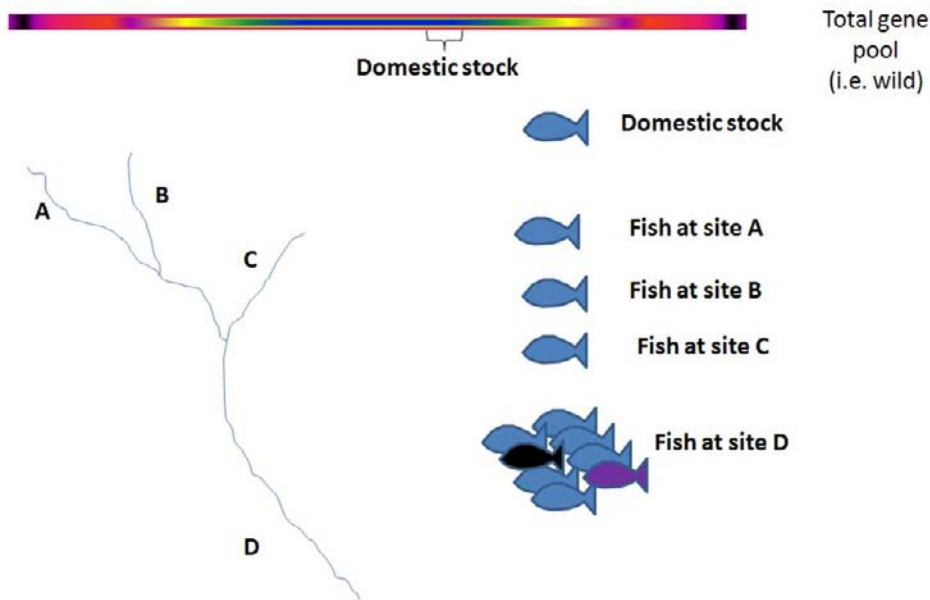


Figure 2: Hybridisation of wild fish with standard domesticated strains tends to make fish populations more similar to each other

The complexity found across all populations – whether in the UK or in a wider European context - makes the outcome of releasing fertile farmed fish into them highly uncertain. The take home message is that anything that makes individuals more genetically similar to each other will certainly reduce the total genetic variation (Fig. 2; all populations). It may also make individuals within specific populations

more similar to each other (Fig.2; D). Such losses of genetic variation equate to a reduction in size of the wild trout's "tool box" in which they are able to find solutions to the demands of life in the wild. With variable pressures arising from human activity, as well as the challenges of a changing global climate, that tool box needs to be as large and adaptable as possible.

### **What is the evidence that stocking with fertile domesticated fish has actually reduced genetic variation in the wild?**

There is an oft-repeated myth that says "There is no scientific evidence that stocking fertile domesticated brown trout can harm wild trout genetic diversity". In fact, there are myriad studies to show that genetic variation has been reduced by introductions of fertile stock fish. European examples of wild brown trout populations being impacted in this precise manner are numerous (Almodovar *et al.*, 2006; Berrebi *et al.*, 2000; Cagigas *et al.*, 1999; Caputo *et al.*, 2004; Garcia-Marin, Sanz & Pla, 1999; Hansen, 2002; Hansen *et al.*, 2009; Krieg & Guyomard, 1985; Machordom *et al.*, 1999; Marzano *et al.*, 2003; Poteaux, Bonhomme & Berrebi, 1999; Sanz *et al.*, 2006; Sonstebo, Borgstrom & Heun, 2008). This is just a small sample of the total number of studies that have reported reduced genetic variation due to stocking with fertile domestic fish. It should come as no surprise that British and Irish brown trout do not escape this general pattern. A study centred around the rivers draining into Lough Erne found that the percentage contribution of hatchery-derived genes in the spawning streams varied from 19% to 91%, with 22% in a sample of lake-caught adult trout (Taggart & Ferguson, 1986). Two unpublished reports undertaken on behalf of the Environment Agency (commissioned by Roy Sedgwick) revealed a comparable situation within the River Dove catchment in England. The average (mean) proportion of genes that originated from farmed fish in stocked areas was 22% - with a maximum value of 51% recorded at a particular stocking location (McMeel & Ferguson, 1997). Developing and using specific genetic markers to distinguish farmed origin from wild origin fish, the "hotspots" for farmed genes were identified (McMeel & Ferguson, 1997). These hotspots coincided with locations that regular stocking took place or where wild trout killed by pollution were replaced using farmed fish (Duguid & Ferguson, 1999).

Even though it only requires a single example of the above studies to refute the hypothesis that "Fertile stock fish never harm wild trout genetic diversity", Fact box 2 shows that the cited examples are not a biased "cherry picking" of the existing literature.

Fact Box 2:

A single (and deliberately broad-scale) search was entered into the academic literature database “ISI Web of Science” (carried out on 09/03/2011). The aim was to obtain an unbiased sample of papers that have considered the effects of stocking fertile hatchery-derived brown trout on native brown trout populations. For this reason, no refinement of the original search term (and hence no particular bias) was applied. Instead every single reference captured by this broad sweep was evaluated. The evaluation allocated each study to one of four categories:

1. Not applicable (species, systems or effects other than brown trout stocking studied)
2. Neutral genetic impact (no effect detected in stream or lake population)
3. Positive genetic impact (increase in genetic variation in stream or lake population)
4. Negative genetic impact (reduction in genetic variation – which is linked to reduced fitness and adaptability)

The search term used was:

***“salmo trutta and (stock\* or supplement\* or support\*) and (effect\* or impact\* or benefit\*)”***

A total of 636 studies were returned and, as would be expected, the majority of studies were not directly applicable to brown trout (586) although many studies were relevant to closely related species and issues. The remaining studies broke down to give Positive impacts (1 study – where the recipient population had almost no genetic variability due to a previous catastrophe wiping out almost all original fish), Neutral impacts (8 studies) and Negative impacts (41 studies); Fig. 3)

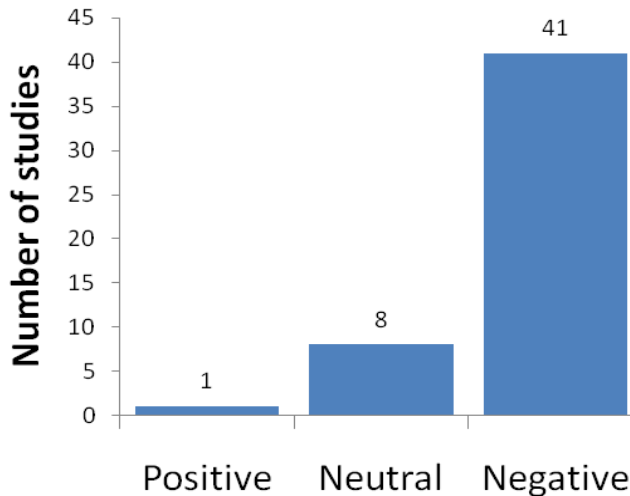


Figure 3: Breakdown of the effects reported in the directly relevant brown trout genetic studies found during a single, unbiased sweep of existing literature

## **What is the evidence that hybridisation between domestic and wild trout actually reduces fish fitness?**

Impacts on fitness have been measured at multiple levels, including the levels of:

- Specific genes
- Individual fish
- Populations of fish

### ***Genes***

Natural selection has been observed to favour different brown trout genes from those favoured in domestication (Hansen, Meier & Mensberg, 2010; Meier et al., 2011). In other words, certain genes and their attendant characteristics that make fish compatible with domestication can cause fish to fare less well in the wild when they carry these genes. This implies that hatchery-derived genes reduce the fitness of hybridised hatchery/wild fish.

### ***Individual Fish***

Although an important role of previous “learning experience” was noted, a study on responses to predators between wild brown trout and both first and second generation hatchery fish reported a genetic component to reduced predator avoidance (Alvarez & Nieceza, 2003). The genetic component of poorer predator avoidance was suggested to arise through artificial selection in domestic fish— where predation is not a relevant selective agent. In other salmonid species (e.g. rainbow trout), hybridised hatchery/wild individuals had reduced fitness (a formal measure of the combination of survival and reproduction) compared to wild fish (e.g. (Araki *et al.*, 2008) and (Miller, Close & Kapuscinski, 2004)). An extensive review article produced in 1991 that cited more than 90 separate, independent studies of salmonid fish, including brown trout in Ireland, Spain and Norway, concluded “*It is noteworthy that wherever there is a detectable effect in comparisons between indigenous and exogenous fish (including hybrids), the performance of the indigenous fish is always better. This one-sidedness of empirical observations in favor [sic] of the local population does not represent a conscious bias in selecting references, but appears to point to a lack of observations in the opposite direction*” (Hindar, Ryman & Utter, 1991).

### ***Populations***

Examining impacts at the level of populations has yielded evidence that hybridised individuals contribute to or persist far less in populations than predicted by numbers of stock fish (Hansen, 2002). In other words, poorer survival and reproduction is conferred onto fish carrying domestic-strain genes and this reduces the effective population size (i.e. the number of fish actively surviving and producing offspring). This effect is also noted through examination of changes in populations through time following differing stocking regimes (stocking ceased 6-years prior to study in one river versus ongoing stocking in another). By mapping the genetic changes before the cessation of stocking and 6-years after, natural selection was found to be acting against the portions of the populations made up of both pure hatchery-bred fish and hybrids between wild and hatchery fish (Poteaux, Beaudou & Berrebi, 1998).

The hybridisation between wild and hatchery fish has been observed to reduce the degree of local adaptation of brown trout populations (Hansen et al., 2009). Scales taken from archived museum specimens (obtained between 1927 and 1956) derived from known populations of brown trout were subjected to extractions of their DNA. In combination with DNA extractions of modern members of these same populations, this enabled the comparison of genetic structures between historic and contemporary populations. These populations had been subjected to around 60 years of artificial stocking with fertile domestic strain brown trout.

Whilst there was no significant difference in the average number of different gene versions (called “alleles”) within each breeding population between historic and contemporary samples, there was a change in the characteristic composition of those genes. Modern populations were much more similar to hatchery strain fish than the equivalent comparison of historic populations to hatchery strain fish (Hansen *et al.*, 2009). Moreover, the historic population structure can be related to adaptation across geographic areas; whereas the contemporary population structure is much more strongly influenced by influxes of hatchery genes than by processes of local adaptation (Hansen *et al.*, 2009). The “over-riding” of natural selection and adaptation results from the continual (artificial) topping up of populations with domesticated stock fish. An assisted advantage of stock fish can, consequently, become too great for natural processes to neutralise over time.

#### **Inter-breeding impacts summary**

In this complicated subject area it is useful to draw out the different types of impact that can occur. Above all, *it is crucial to stress that these impacts have genuine and practical implications to the current and future prospects of brown trout populations; it is not simply an academic exercise in “preserving purity”*. The GENETIC IMPACT CATEGORIES box draws out four separate categories of impact that need to be considered when decisions are taken on the best way to manage trout stocks:

## GENETIC IMPACT CATEGORIES

### **Loss of genetic diversity among wild populations**

Although variation within a single farm strain may be greater than a single wild population; there are only a few tens of farm strains versus many thousands of wild populations. Replacement of wild population genetic variation with genes from farmed strains causes a loss of overall genetic variation among wild populations and increases the risk of extinction through an inability to adapt to future conditions.

### **Reduction in fitness due to loss of local adaptations as a result of interbreeding with farm-reared trout**

Wild brown trout populations show many adaptations to local conditions such as tolerance of environmental conditions, resistance to diseases and parasites, time of spawning (e.g. to match water temperature to ensure that food is available when fry emerge) and many other factors. As farm-reared trout are in almost all cases non-native to where they are stocked they do not possess the appropriate adaptations for the local conditions. Hybrids between farmed and wild fish consequently have reduced adaptation to their current local environment.

### **Reduction in fitness as a result of interbreeding with farm-reared trout, which are mal-adapted for life in the wild**

When any animal is kept in captivity domestication inevitably occurs as a result of choosing the founder individuals, deliberate & accidentally selective matings as well as purely random processes. This domestication results in reduced fitness for life in the wild. Hybrids between domesticated and wild fish are less able to survive and reproduce in the wild than purely wild fish NOTE THAT THIS EFFECT IS SEPARATE FROM THE PREVIOUS CATEGORY - IT WOULD OCCUR EVEN IF ALL WILD POPULATIONS WERE GENETICALLY IDENTICAL TO EACH OTHER AND LOCAL ADAPTATION OF WILD POPULATIONS DID NOT EXIST.

### **Loss of key life history types, and consequent reduction in diversity of angling opportunity and experience**

Life history types - such as migration to the sea or delayed maturation leading to trophy sized individuals - have a significant genetic component. These distinct characteristics are maintained by the breeding behaviour and physical attributes "programmed" by particular genes. Introducing farmed fish that go on to breed with wild fish can "dilute" those characteristics - possibly to the point that they disappear.

**Does this mean that the damage is already done and there is no value in halting the loss of genetic diversity?**

No. Some of the studies that detect extensive hybridisation in specific populations also record other populations that are unaffected e.g. (Almodovar *et al.*, 2006; Caputo *et al.*, 2004; Hansen *et al.*, 1993;



Hansen *et al.*, 2001; Heggenes *et al.*, 2006). Even in a population containing over 70% farmed fish genes, around 14% of sampled individuals (7 out of 53 fish) contained no farmed genes at all; most likely as a result of differences in breeding time between the remaining wild component of stocks and farmed fish (Hansen & Mensberg, 2009). In fact, whilst a general trend has been identified in terms of where there could be higher risk of more extensive hybridisation, such as fertile rivers with stable flow/similarity to hatchery conditions and higher intensity of stocking (Almodovar *et al.*, 2006), populations are known to buck this trend (e.g. (Almodovar *et al.*, 2006; Hansen *et al.*, 1993; Machordom *et al.*, 1999). This means that it is not possible to make good predictions of which populations will be either affected or unaffected based on stocking history or nature of the watercourse. An unexpected source of some of this uncertainty could be from management options for taking fish for the table. Slightly less genetic impact has been observed in “catch and kill” sections of some Mediterranean rivers due to stock fish apparently being more susceptible to angler capture than wild fish e.g. (Garcia-Marin, Sanz & Pla, 1999). Unfortunately, in other cases, angling has no protective impact (Almodovar *et al.*, 2006) – so blanket catch and kill of stocked fish is not a reliable method to adopt (but past fishery management may, in some cases, have accidentally offered a little protection against extensive hybridisation).

It is encouraging to learn that local adaptation of native populations and natural selection against hatchery genes can override stocking inputs (Hansen, 2002). Similarly, Swiss populations still retain enough of their original genetic population structure to be identifiable in spite of massive stocking (Keller, Taverna & Seehausen, 2011). Clearly it is not sensible to continue to erode this variation, particularly when there is even more encouraging evidence for recovery of genetic identity following the cessation of stocking (Poteaux, Bonhomme & Berrebi, 1999).

### **WTT advice for what to do for the best?**

Stocking with fertile farmed fish has potential for serious impacts to native trout populations. Supportive breeding (i.e. using wild brood stock to produce fish for stocking) is not a universal panacea for three main reasons:

- A good understanding of the existing native population genetic structures is required to avoid causing more harm than good (for example by inadvertently mixing co-existing but distinct wild populations). The investigations to gain such understanding are too expensive and challenging to be routinely achievable;
- Large numbers of broodstock are required to prevent “swamping” with the offspring of a small number of parents. This means a net loss of in-stream breeding by removing wild broodstock from donor populations, plus a risk of loss of production through human error;
- Inevitable domestication via artificial breeding from wild broodstock resulting in offspring that differ significantly from the wild populations; this has been demonstrated to occur over just a single generation (Griffiths, Bright & Stevens, 2009) – see also Fact Box 3.



## Competition

Even though some studies struggle to find obvious competitive impacts of stocked trout on native populations (e.g. (Huusko & Vehanen, 2011), problems of competition for food or space as well as direct predation still potentially exist with any stock fish introduction. Bachman (1984) observed the foraging behaviour of wild brown trout in a stream over a three-year period and described how the fish largely stayed in stationary positions within a home range, feeding on drifting food items brought by the current (net energy maximisation); he described the social structure as a cost-minimising, size-dependent linear dominance hierarchy of individuals having overlapping home ranges. The trout had aggressive encounters with each other that determined the hierarchy. Hatchery brown trout introduced to the study site were much less efficient in their feeding and use of energy cost-minimising habitat, resulting in poor annual survival rates. However, aggressive encounters between wild and hatchery fish occurred (mostly started by wild fish), were much longer-lasting than encounters solely between wild fish, were sometimes observed to leave wild fish in a state of stress not previously observed, and overall the outcome of each encounter did not favour wild or hatchery fish (although larger, dominant wild fish tended to “win”).

The lack of effects cited in (Huusko & Vehanen, 2011) could be related to the additions of stock fish being matched to produce relatively low “natural” population densities. By contrast, a definite reduction in growth rate with increased population numbers through stocking is reported in an example where higher population densities were examined (Bohlin *et al.*, 2002). It is notable in this latter study that the density-dependent reduction in growth rate occurred irrespective of the nature of the added fish (i.e. whether numbers of wild or domesticated fish were increased; (Bohlin *et al.*, 2002)). Consequently, it appears that the precise nature of the introduced fish may be less important than the overall number or biomass of fish added during stocking. This observation is potentially significant, given the lack of specific investigations to test whether fertile (diploid) or sterilised (triploid) stock fish differ in their competitive impacts on wild trout. Based on current information (e.g. inherent differences in optimal temperature ranges/metabolic rate between diploid and triploid salmonid fish (Atkins & Benfey, 2008)), any discrepancies between impacts of diploid and triploid stock fish, are likely to be only differences of degree. The large numbers of stock fish routinely added to many UK river systems is likely to make such differences of degree largely irrelevant. In other words - *as far as purely competitive impacts are concerned* - the number and size added is likely to be much more important than whether stocked fish are diploid or triploid.

## Summary

**Given that some fisheries operate as catch and kill (or otherwise do not produce sufficient wild fish to make the fishery viable) there may be a requirement to stock fish for anglers. Taking all the preceding information into account the Wild Trout Trust recommends that, where there is a perceived requirement to stock a fishery, it is better to stock sterile (triploid) fish rather than fertile (diploid) stock fish. The number and size of fish stocked should be consistent with the density and size-range of the natural trout population.**

Of course, **the option with the greatest benefit to river ecosystems is to operate as a catch-and-release fishery in the absence of stocking whilst promoting healthy habitat, water quality and quantity.** This option avoids the risks to wild trout stocks discussed above but also avoids the need to harvest marine protein to manufacture the commercial feeds required in the production of farmed stock fish.

### Simple “Dos” and “Don’ts”

- **DO** consider whether you need to stock your fishery (or whether it could operate on a wild catch and release basis)
- If you stock, **DO** try to assess the density of adult trout that your fishery can realistically support and match your stocking densities appropriately. This will minimise any negative competitive impacts (as well as reducing wastage of stock fish and money). The WTT can advise on broad “upper realistic limits” in terms of density of adult fish per m<sup>2</sup>
- **DO** add fish in small batches on frequent occasions throughout the season (rather than as one or two bulk stocking events). This will help to avoid damaging “peaks” in competitive/predation impacts from stock fish and should maximise your catch returns on your costly stock fish
- **DO** try to get the majority of stock fish out of the river by the end of the fishing season. They are unlikely to over-winter successfully, may well compete with wild fish whilst they struggle to survive the lean winter months and could also attract cormorants and saw-bill ducks.
- **DO** use only infertile stock fish
- **DO** ensure that the habitat, water quality and quantity in your fishery are all as good as they can be; both wild fish and stock fish need a good home in order to survive (WTT can advise here too)
- **DON’T** kill wild fish for the table – for every wild adult fish that exists; many hundreds of its brethren will have perished as eggs and particularly during juvenile stages. Wild populations are consequently very sensitive to over-exploitation. Fish suppliers can mark your stock fish so that anglers can quickly tell them apart.

*This document was produced by Dr Paul Gaskell in conjunction with the Wild Trout Trust conservation team and knowledge network.*

### Cited References

- Almodovar, A., Nicola, G.G., Elvira, B. & Garcia-Marin, J.L. (2006) Introgression variability among Iberian brown trout Evolutionary Significant Units: the influence of local management and environmental features. *Freshwater Biology*, **51**(6), 1175-87.
- Alvarez, D. & Nieceza, A.G. (2003) Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *Journal of Fish Biology*, **63**(6), 1565-77.

- Araki, H., Berejikian, B.A., Ford, M.J. & Blouin, M.S. (2008) Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, **1**(2), 342-55.
- Atkins, M.E. & Benfey, T.J. (2008) Effect of acclimation temperature on routine metabolic rate in triploid salmonids. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, **149**(2), 157-61.
- Bachman, R.A. (1984) Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society*, **113**, 1-32.
- Bernatchez, L. (2001) The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. *Evolution*, **55**(2), 351-79.
- Berrebi, P., Poteaux, C., Fissier, M. & Cattaneo-Berrebi, G. (2000) Stocking impact and allozyme diversity in brown trout from Mediterranean southern France. *Journal of Fish Biology*, **56**(4), 949-60.
- Bohlin, T., Sundstrom, L.F., Johnsson, J.I., Hojesjo, J. & Pettersson, J. (2002) Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. *Journal of Animal Ecology*, **71**(4), 683-92.
- Cagigas, M.E., Vazquez, E., Blanco, G. & Sanchez, J.A. (1999) Genetic effects of introduced hatchery stocks on indigenous brown trout (*Salmo trutta* L.) populations in Spain. *Ecology of Freshwater Fish*, **8**(3), 141-50.
- Caputo, V., Giovannotti, M., Cerioni, P.N., Caniglia, M.L. & Splendiani, A. (2004) Genetic diversity of brown trout in central Italy. *Journal of Fish Biology*, **65**(2), 403-18.
- Clifton-Dey, D. & Walshingham, M. (1996) An investigation of the recapture rates for tagged brown trout stocked into the River Ribble. *Environment Agency North West Region Technical Report No. EA/NW/FTR/96/8*.
- Cresswell, R.C. (1981) Post-stocking movements and recapture of hatchery-reared trout released into flowing waters – a review. *Journal of Fish Biology*, **18**, 429-42.
- Duguid, A. & Ferguson, A. (1999). The genetics of brown trout in the River Dove catchment: assessment of the geographical distribution of farmed fish genes. . In. Unpublished report to the Environment Agency.
- Ferguson, A. & Taggart, J.B. (1991) Genetic Differentiation among the Sympatric Brown Trout (*Salmo Trutta*) Populations of Lough Melvin, Ireland. *Biological Journal of the Linnean Society*, **43**(3), 221-37.
- Forsberg, L.A., Dannewitz, J., Petersson, E. & Grahn, M. (2007) Influence of genetic dissimilarity in the reproductive success and mate choice of brown trout - females fishing for optimal MHC dissimilarity. *Journal of Evolutionary Biology*, **20**(5), 1859-69.
- Garcia-Marin, J.L., Sanz, N. & Pla, C. (1999) Erosion of the native genetic resources of brown trout in Spain. *Ecology of Freshwater Fish*, **8**(3), 151-58.
- Griffiths, A.M., Bright, D. & Stevens, J.R. (2009) Comparison of patterns of genetic variability in wild and supportively bred stocks of brown trout, *Salmo trutta*. *Fisheries Management and Ecology*, **16**(6), 514-19.
- Griffiths, A.M., Koizumi, I., Bright, D. & Stevens, J.R. (2009) A case of isolation by distance and short-term temporal stability of population structure in brown trout (*Salmo trutta*) within the River Dart, southwest England. *Evolutionary Applications*, **2**(4), 537-54.
- Hansen, M.M. (2002) Estimating the long-term effects of stocking domesticated trout into wild brown trout (*Salmo trutta*) populations: an approach using microsatellite DNA analysis of historical and contemporary samples. *Molecular Ecology*, **11**(6), 1003-15.
- Hansen, M.M., Fraser, D.J., Meier, K. & Mensberg, K.-L.D. (2009) Sixty years of anthropogenic pressure: a spatio-temporal genetic analysis of brown trout populations subject to stocking and population declines. *Molecular Ecology*, **18**(12), 2549-62.

- Hansen, M.M., Loeschcke, V., Rasmussen, G. & Simonsen, V. (1993) Genetic Differentiation among Danish Brown Trout (*Salmo-Trutta*) Populations. *Hereditas*, **118**(2), 177-85.
- Hansen, M.M., Meier, K. & Mensberg, K.-L.D. (2010) Identifying footprints of selection in stocked brown trout populations: a spatio-temporal approach. *Molecular Ecology*, **19**(9), 1787-800.
- Hansen, M.M. & Mensberg, K.L.D. (2009) Admixture analysis of stocked brown trout populations using mapped microsatellite DNA markers: indigenous trout persist in introgressed populations. *Biology Letters*, **5**(5), 656-59.
- Hansen, M.M., Ruzzante, D.E., Nielsen, E.E. & Mensberg, K.L.D. (2001) Brown trout (*Salmo trutta*) stocking impact assessment using microsatellite DNA markers. *Ecological Applications*, **11**(1), 148-60.
- Heggenes, J., Skaala, O., Borgstrom, R. & Igland, O.T. (2006) Minimal gene flow from introduced brown trout (*Salmo trutta* L.) after 30 years of stocking. *Journal of Applied Ichthyology*, **22**(2), 119-24.
- Hindar, K., Ryman, N. & Utter, F. (1991) Genetic-Effects of Cultured Fish on Natural Fish Populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**(5), 945-57.
- Huusko, A. & Vehanen, T. (2011) Do hatchery-reared brown trout affect the growth and habitat use of wild congeners? *Fisheries Management and Ecology*, **18**(3), 258-61.
- Keller, I., Taverna, A. & Seehausen, O. (2011) Evidence of neutral and adaptive genetic divergence between European trout populations sampled along altitudinal gradients. *Molecular Ecology*, **20**(9), 1888-904.
- Kottelat, M. & Freyhof, J. (2007) *Handbook of European Freshwater Fishes* Kottelat Publications, Cornol, Switzerland.
- Krieg, F. & Guyomard, R. (1985) Population-Genetics of French Brown Trout (*Salmo-Trutta-L*) - Large Geographical Differentiation of Wild Populations and High Similarity of Domesticated Stocks. *Genetics Selection Evolution*, **17**(2), 225-42.
- Laikre, L., Larsson, L.C., Palme, A., Charlier, J., Josefsson, M. & Ryman, N. (2008) Potentials for monitoring gene level biodiversity: using Sweden as an example. *Biodiversity and Conservation*, **17**(4), 893-910.
- Machordom, A., Garcia-Marin, J.L., Sanz, N., Almodovar, A. & Pla, C. (1999) Allozyme diversity in brown trout (*Salmo trutta*) from Central Spain: Genetic consequences of restocking. *Freshwater Biology*, **41**(4), 707-17.
- Marzano, F.N., Corradi, N., Papa, R., Tagliavini, J., Marzano, F.N. & Gandolfi, G. (2003) Molecular evidence for introgression and loss of genetic variability in *Salmo (trutta) macrostigma* as a result of massive restocking of Apennine populations (Northern and Central Italy). *Environmental Biology of Fishes*, **68**(4), 349-56.
- McKeown, N.J., Hynes, R.A., Duguid, R.A., Ferguson, A. & Prodoehl, P.A. (2010) Phylogeographic structure of brown trout *Salmo trutta* in Britain and Ireland: glacial refugia, postglacial colonization and origins of sympatric populations. *Journal of Fish Biology*, **76**(2), 319-47.
- McLean, J.E., Bentzen, P. & Quinn, T.P. (2005) Nonrandom, size- and timing-biased breeding in a hatchery population of steelhead trout. *Conservation Biology*, **19**(2), 446-54.
- McMeel, O. & Ferguson, A. (1997). The genetic diversity of brown trout in the River Dove. In. Unpublished report to the Environment Agency.
- Meier, K., Hansen, M.M., Bekkevold, D., Skaala, O. & Mensberg, K.L.D. (2011) An assessment of the spatial scale of local adaptation in brown trout (*Salmo trutta* L.): footprints of selection at microsatellite DNA loci. *Heredity*, **106**(3), 488-99.
- Miller, L.M., Close, T. & Kapuscinski, A.R. (2004) Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. *Molecular Ecology*, **13**(11), 3379-88.
- Poteaux, C., Beaudou, D. & Berrebi, P. (1998) Temporal variations of genetic introgression in stocked brown trout populations. *Journal of Fish Biology*, **53**(4), 701-13.

- Poteaux, C., Bonhomme, F. & Berrebi, P. (1999) Microsatellite polymorphism and genetic impact of restocking in Mediterranean brown trout (*Salmo trutta* L.). *Heredity*, **82**, 645-53.
- Sanz, N., Cortey, M., Pla, C. & Garcia-Marin, J.L. (2006) Hatchery introgression blurs ancient hybridization between brown trout (*Salmo trutta*) lineages as indicated by complementary allozymes and mtDNA markers. *Biological Conservation*, **130**(2), 278-89.
- Sonstebo, J.H., Borgstrom, R. & Heun, M. (2008) High genetic introgression in alpine brown trout (*Salmo trutta* L.) populations from Hardangervidda, Norway. *Ecology of Freshwater Fish*, **17**(1), 174-83.
- Taggart, J.B. & Ferguson, A. (1986) Electrophoretic Evaluation of a Supplemental Stocking Program for Brown Trout *Salmo-Trutta*. *Aquaculture and Fisheries Management*, **17**(2), 155-62.
- Wedekind, C., Jacob, A., Evanno, G., Nussle, S. & Mueller, R. (2008) Viability of brown trout embryos positively linked to melanin-based but negatively to carotenoid-based colours of their fathers. *Proceedings of the Royal Society B-Biological Sciences*, **275**(1644), 1737-44.