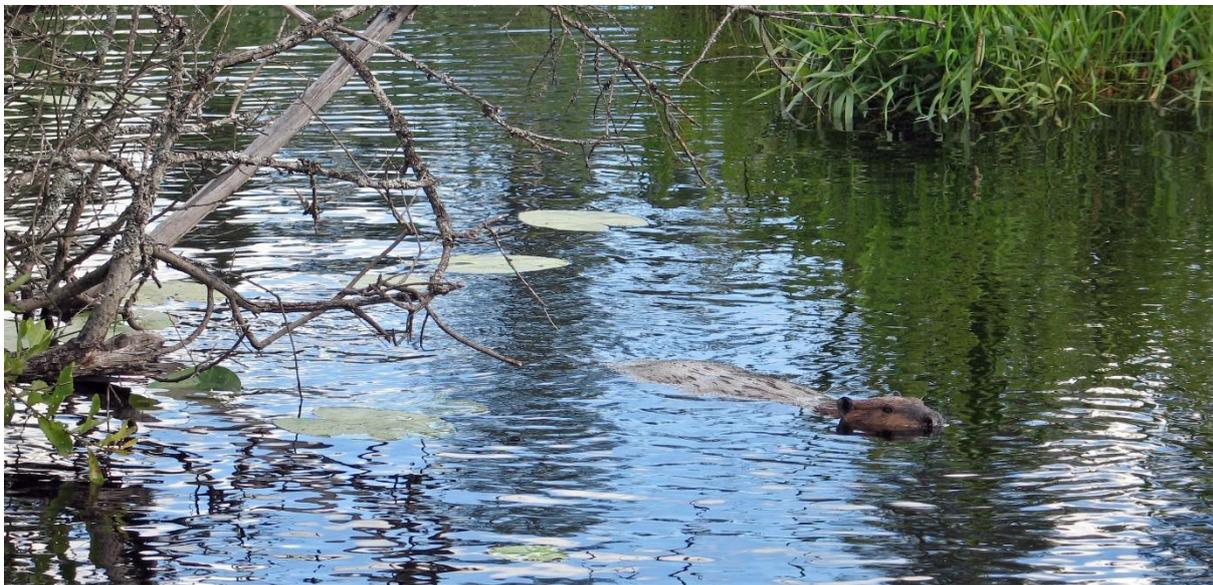




Wild Trout Trust View on Beaver – Trout Interactions

In June 2015, arguably the most comprehensive synthesis to date regarding a species reintroduction, *Beavers in Scotland*, was submitted to Scottish Ministers. The report draws on 20 years of work on beavers, including information from the Scottish Beaver Trial (SBT), the Tayside Beaver Study Group, the Beaver-Salmonid Working Group (BSWG), other projects organised by Scottish Natural Heritage (SNH), as well as a broad range of international studies primarily from North America and Fenno-scandia. The latter studies are essential for speculating on the potential impacts (both positive and negative) of beaver reintroductions, since baseline data pre beaver extirpation are lacking.



The European beaver (*Castor fiber*) photographed in a dammed section of river, Finland: J.Grey

All the SNH publications and commissioned reports that fed into the synthesis document are available to download at: www.snh.gov.uk/beavers-in-scotland. *Beavers in Scotland* covers a wide range of topics from beaver interactions with natural and human environments, to legal issues and management considerations. A more focussed report by the BSWG considers the potential impacts of beaver activity on salmonids (Atlantic salmon and brown trout).

Despite the fact that the Eurasian beaver (*Castor fiber*) co-evolved and still co-exists with fish throughout its geographical range, and in areas such as Fenno-Scandia, France, and some Baltic states where beavers co-exist with high economic value species such as Atlantic salmon, there is surprisingly little published information relating to beaver–salmonid interactions. The following is a précis of the SNH beaver reports and incorporating a wider scan of the current, available literature with particular regard to implications for the brown trout. Much of the information compiled in the SNH reports focuses on the creation of dams by beavers and how that affects the Atlantic salmon because of its migratory (anadromous) life strategy and its socio-economic importance. Sea trout are assumed to be affected in much the same manner as salmon except for some variation in timing of migration. However, it should be

remembered that *all* brown trout are migratory within rivers (potadromous) at different spatial and temporal scales and for a variety of reasons (see Forty et al., 2016).

It is important to understand the fundamental behavioural ecology and environmental requirements of beavers to fully assess their likely interactions with salmonids (and other fish / fisheries); See Box 1.

Box 1: Beaver ecology

Eurasian beavers are semi-aquatic, herbivorous, highly territorial mammals, and crepuscular in activity (i.e. at dawn and dusk). They occupy territories ranging from 1-7 km dependent upon food availability ((Kramer et al., 2012); (Polvi and Wohl, 2012)), and typically living in small colonies comprising 3-5 individuals.

Beavers are '*ecosystem engineers*' (Butler and Malanson, 2005); (Rosell et al., 2005); they can modify the structure of the surrounding ecosystem and induce a diverse array of effects caused by the construction of dams and side-channels along small to medium-sized rivers. They tend to build dams (although colonies can exist without them) on low-gradient small streams to create impoundments which provide secure access to food and building resources across the resultant 'floodplain' and may also serve to conceal the entrances to their lodges or burrows (Naiman et al., 1986).

As a consequence, they exert a strong influence on riparian landscapes, effectively converting terrestrial habitats into wetlands; the inundation will kill most woody species if flooded for multiple years. By felling trees, beavers create open areas in riparian woodlands and allow greater light penetration which may, over time, change the species composition of riparian woodland. Hence, beavers might also be described as '*keystone*' riparian species (Collen and Gibson 2001); their presence and activities increase local biodiversity and modifies the surrounding river bank habitats beyond that expected relative to their biomass.

Depending on where beavers build dams within a drainage network, they impact lateral and longitudinal connectivity by introducing roughness elements that fundamentally change the timing, delivery, and storage of water, sediment, nutrients, and organic matter (Macfarlane et al. 2016). As such, and elsewhere across Europe where currently present, beavers are considered an important component and indicator of healthy, functioning rivers and wetlands.

The range of physical conditions under which beavers can construct dams has been described using a variety of metrics: stream gradient, stream order, stream power, depth, width and valley shape in North America (e.g. Naiman et al., 1986; Pollock et al., 2003; Green and Westbrook, 2009) and Sweden (Hartman and Törnlov, 2006). In the latter survey of 74 dams in Sweden, Eurasian beavers maintained dams on small, shallow streams of less than 2.5% gradient, with a mean water depth (downstream of dams) of 0.36m (range 0.10-0.85 m) and stream width of 2.5m (range 0.5-6.0m). The proportions of the dam structure are related to the physical characteristics of the channel; hence, given the above, most are small but can measure >100m in length and >2m in height. Beaver dams are generally ephemeral; they can

be reduced in size and structural integrity or removed completely during periods of high flow (Taylor et al., 2010).

The density of functional dams within the river corridor is expected to vary with season and flow regime, food supply and beaver population dynamics (Gurnell, 1998; Pollock et al., 2014; Kemp et al., 2012; Macfarlane et al. 2016), and consequently is known to vary considerably. For example, one dam for every 14.3 km of stream reported in a Norwegian study (Parker and Rønning, 2007) as compared to 24 dams in a 1.3km reach of a Polish mountain stream (Zurowski, 1989).

MacFarlane et al. (2016) have developed a model to predict where American beavers (*C. canadensis*) may build dams, and validate their model using the observed locations of 3000 dams in Utah. The presence of suitable riparian vegetation (mostly tree species) near to the river bank is fundamental to whether dams are built or not. Other drivers of lower importance are: flow regime - base flows are sufficiently low to enable construction of dams, and spate flows are not so large to destroy dams; channel gradient - neither so low that dam density is limited, but not so high that stream power prevents construction and/or persistence in floods; and width - the beaver is able to construct a dam to span the channel.

Widespread habitat modifications due to ecosystem engineering by Eurasian beaver is predicted to occur at peak population density, most likely 11-34 years after initial colonisation (Hartman, 1994; Vissing *et al.*, 2012). In light of such timescales, any evidence on the ecological impacts of beavers accruing from the 'trial introductions' that have occurred in the UK should be treated with a degree of caution, and only emphasises the need to draw careful inference from studies of well-established populations in comparable habitats elsewhere.

Beaver – trout interactions

It is important to reiterate that beavers co-evolved and naturally co-exist with salmonids and other freshwater fish species throughout their range but of course their level of ecological interaction and how that has affected the population size of either species over that timeframe is unknown. While it is widely accepted that the Eurasian beaver is a natural component of UK's wildlife heritage and that it was lost as a result of human activities, primarily over-hunting, it should be noted that (except for the isolated trials and illegal introductions / escapees) beavers have been absent from the English landscape since the 12th Century (Macdonald et al., 1995) and from Scotland since the 16th Century (Gaywood, 2001). There have been significant changes to the composition of the UK landscape in that period, as well as to some of the flora and fauna which may have provided food/refuge or may have preyed upon beavers, respectively, and thus potentially reduced the suitability for beaver occupation and/or cause a behavioural shift (for example to burrow dwelling rather than dam building; Parker and Rønning (2007).



IN LIGHT OF SUCH TIMESCALES, ANY EVIDENCE ON THE ECOLOGICAL IMPACTS OF BEAVERS ACCRUING FROM THE 'TRIAL INTRODUCTIONS' THAT HAVE OCCURRED IN THE UK SHOULD BE TREATED WITH A DEGREE OF CAUTION

Current pressures on the UK landscape from human activities are more likely to result in conflict now with beavers as they become (re)established. These in turn have altered the

context for possible beaver-salmonid interactions within the UK; the BSWG highlighted pressures on river habitat, such as land use (for forestry, agriculture and urban development), water impoundment and abstraction for domestic and industrial use, riparian habitat degradation (through, for example, overgrazing and encroachment by invasive non-native plants), climate change, and diffuse pollution. These pressures may have been entirely absent or certainly less prevalent when salmonids previously co-existed with beavers, and historically there may have been fewer or greater numbers of salmonids produced in the presence of beavers, regardless of these other factors.

IN THEIR RELATIVELY RECENT REVIEW, KEMP ET AL. (2012) CONSIDERED 35 SPECIES OF FISH AND FOUND THERE WAS GENERALLY MORE EVIDENCE FOR POSITIVE EFFECTS OF BEAVERS ON FISH, THAN NEGATIVES.

Beaver-fish interactions have been the subject of extensive reviews including Collen & Gibson, (2001) and Kemp *et al.* (2012); neither of these exclusively consider salmonids and much of the research relates to North American beavers. All potential ecological interactions are complex and may

be expected to vary between catchments and over time, so extrapolation from, for example, American ecosystems to the UK context should proceed with caution. Nevertheless, the research contained within such reviews is valuable and forms the basis of a mechanistic understanding of the interaction between beavers and salmonids. In their relatively recent review, Kemp *et al.* (2012) considered 35 species of fish and found there was generally more evidence for positive effects of beavers on fish, than negatives. However, the balance of potential positive and negative interactions is difficult to judge, especially for a particular species like the brown trout which has many different environmental requirements throughout ontogeny (at different life-stages), yet is rather adaptable to change.

Movement & connectivity

Hindrance to adult spawning migration was the most commonly cited negative effect of beavers on fish (including salmonids) in 46 of 108 studies reviewed by Kemp *et al.*, (2012). However, it should be noted that 78% of those studies citing a negative impact actually had no empirical data to support the claim. Whether beaver dams act as barriers to fish and the extent to which they impede the movement of different species are questions in need of clarification, although there is mounting evidence that suggests the parochial view of beaver dams being impassable for potadromous species is now untenable (see below and Box 2). Trout need to move through rivers at different points of their life cycle, including upstream spawning migration and return seaward movements after spawning, within-river juvenile movement between habitats, and for some populations, downstream (smolt) emigration to the sea. Mature trout can also undertake considerable within-river migrations driven by feeding requirements, to avoid adverse conditions or to recover from displacement following on from disturbance events, or seasonal distribution shifts (Baras and Lucas, 2001). A recent count identified ~25,000 fish migration barriers on UK rivers (Gough *et al.*, 2012) and a considerable effort is currently underway to improve fish passage on these man-made structures. Yet there is a paucity in knowledge of the true effectiveness of different fish-pass designs for each species of migratory fish on man-made obstructions (Bunt *et al.*, 2012), so it is very difficult to assess such issues on structurally variable and temporally transient beaver dams.

Adult spawning migration

Sea trout tend to migrate into rivers predominantly in summer months, and together with resident trout, undertake spawning migrations predominantly during the autumn and winter months. They typically remain in wide, deep reaches, such as main stems, or adjoining rivers (Stewart et al., 2006) and where beaver activity is relatively unlikely, before migrating to smaller streams and tributaries with more appropriate spawning habitat in autumn. Accessibility is dependent upon the characteristics of water flow and degree of physical obstruction (reviewed by (Thorstad et al., 2008) and hence, it is in these smaller systems that beaver-trout interactions may be extensive because beavers can better maintain dams on these small streams.

Fish access to spawning sites upstream of beaver dams depends strongly upon the integrity of the structure and the magnitude and occurrence of high water flows relative to the specific structure; while North American beaver dams completely prevented upstream passage in some years, they had *no detectable effect* in others (Mitchell and Cunjak, 2007; Taylor *et al.*, 2010). Cunjak and Therrien (1998) have reported that one particular beaver dam (*but only in one year*) in Catamaran Brook, New Brunswick, severely limited spawning distribution, and may have resulted in a subsequent reduction in survival, and an increase in emigration of salmon fry hatched below this dam in the following year. Four dams (ranging between 0.5 to 1.6m height) on a small Norwegian stream appeared to have *little restrictive effect* on spawning success as juvenile trout and salmon parr were found above, although the authors could not differentiate whether these were the progeny of adult salmonids that spawned upstream of the dams, or whether the juveniles actually negotiated the dams from below (Halley & Lamberg, 2001). Indeed, other studies have demonstrated that juvenile salmonids *are more than capable* of negotiating passage over or through dams (Bryant, 1984; Swanston, 1991; Schlosser 1995; Alexander, 1998; Virbickas et al., 2015) as the diversity of flow pathways directly through, or over, under, and around (e.g. side channels of diverted flow that act as fish ladders) such dams provides a number of plausible pathways. These flow paths change regularly with ongoing beaver maintenance and construction activities, and further, with fluctuations in discharge.

Hagglund and Sjoberg (1999) and Kesminas et al. (2013) have conducted trout density comparisons between beaver impacted *versus* unimpacted reference streams in Sweden and Lithuania, respectively, and both suggested that the trout population size structure differed with larger fish found in beaver ponds. On the basis of electrofishing data and redd counting it was suggested that beaver dams impeded trout movement but only in some instances. (Parker and Rønning, 2007) hypothesised the impact of beaver dams on up- and downstream migration of salmonids was negligible, and should not impact upon long-term salmonid reproductive success due to the low frequency, generally small size, and ephemeral nature of beaver dams on spawning tributaries in Norway. This is supported by North American research on Pacific and Atlantic salmon reviewed in Collen and Gibson (2001), and the very fact that beavers and salmonids have co-existed for millennia where habitats are suitable.

It should be noted that even if fish are able to negotiate beaver dams, they may cause delays and an increase in energy expenditure associated with multiple attempts, both of which increase the risk of predation (see **Predation** section), and both of which are difficult to assess.

Box 2: Experimental approaches

To assess the extent to which beaver dams act as movement barriers to salmonids and whether successful dam passage (either up- or downstream) differs among species, requires experimentation.

Lokteff et al. (2013) used passive integrated transponder (PIT) tags inserted into individual fish in two Utah streams containing 21 beaver dams, and from three species: native Bonneville cutthroat trout (*Oncorhynchus clarkii*), non-native brook charr (*Salvelinus fontinalis*), and non-native brown trout. While some of their results were confirmatory, in that the physical characteristics of dams, such as height and upstream location, affected the passage of each species, others revealed that there might be species-specific interactions. Beaver dams did not impede Bonneville cutthroat trout or brook trout but appeared to restrict the movements of invasive brown trout as passage attempts were much lower than expected.

Visual implant elastomer (VIE) tags have also been used to detect limited dam passage by juvenile salmonids in Alaska (chinook *O. tshawytscha* and coho *O. kisutch*; Malison et al. (2014), but there are currently few comparable tagging data for salmonids available in a European context. Virbickas et al. (2015) conducted a study using sea trout parr marked with PIT tags and demonstrated that individuals passed through several successive beaver dams in an upstream direction, but no tagged fish were detected above the uppermost dam in their study system.

At the time of compilation, [Marine Science Scotland](#) are analysing data from a brown trout PIT-tagging study in Tayside; only a small number of fish were recaptured (27/100) but of those, 13 had negotiated dams (fish size: 132-215mm).

Juvenile / mature parr / smolt movement

Movement soon after hatching in juvenile salmonids is predominantly downstream and generally at a scale of a few hundreds of metres (e.g. Einum et al., 2011). Parr may also migrate during spawning to find females (precocious males; Garcia-Vazquez et al., 2001), in relocating to find overwintering habitat, and in migrating out of tributary streams in autumn (Baras & Lucas, 2001; Forty et al., 2016). These small fish are adept at finding routes through structurally complex habitats (Bryant, 1984; Swanston, 1991; Schlosser 1995; Alexander, 1998). Trout smolts migrate from rivers during spring and the majority of smolts running in any given year typically reach salt water between March and June. This should mean that there is ample flow in the majority of rivers during the transit period, i.e. beaver dams *could* be less passable in low-flow periods (Cunjak and Therrien, 1998). But it is the question of impedance and any associated impacts that remains unclear.

Using a man-made analogue (and far from perfect one as beaver dams are far more porous and ephemeral than concrete weirs), a recent study in the Tweed Catchment concluded that sea trout smolts can be impeded by small, over-flowing concrete weirs, and that impedance increases during low flow periods (Gauld et al., 2013). Additionally, losses assumed to predation were higher in a year of low flows (19% survival rate) compared to a year with no extremely low flows (45% survival rate), demonstrating that it is not simply the 'direct'

impedance aspect that affects salmonid populations. The UK riverine landscape has changed considerably since beavers and trout last interacted freely, and so the balance of interactions between the two will be heavily influenced by anthropogenic modifications to the environment such as weirs and flow regulation, channel incision and floodplain connectivity, removal of natural predators, and riparian vegetation community composition (Kemp et al. 2012; MacFarlane et al. 2016).

THE UK RIVERINE LANDSCAPE HAS CHANGED CONSIDERABLY ... SO THE BALANCE OF INTERACTIONS BETWEEN (BEAVERS & TROUT) WILL BE HEAVILY INFLUENCED BY ANTHROPOGENIC MODIFICATIONS TO THE ENVIRONMENT...

Impacts on spawning habitat

Trout require well oxygenated gravel substrates and typically spawn at the tail of pools where there is low intrusion of fine organic sediments (Armstrong et al., 2003). The impact of beaver dams on spawning habitat quality is both positive and negative and will depend upon location. As flow energy is dissipated in pools behind beaver dams, sediments will drop out of suspension and accumulate, therefore locally reducing the availability of suitable substrate in the impounded section (Collen & Gibson, 2001; Kemp *et al.* 2012). However, sedimentation in the pool means that the load of suspended solids supplied further down the system is reduced. Furthermore, accelerated flow immediately downstream of dams will help to maintain gravels free from fine sediments (Macdonald *et al.*, 1995).

Competition and predation

In changing the physical habitat, beavers may alter the balance of both competition (between trout and other fish species, notably salmon) and predation pressures. Competitive interaction between trout and salmon means that these species tend to occupy different microhabitats within the same river or stream (Hearn, 1987; Heggenes and Saltveit, 1990; Heggenes, 2002). Even subtle changes to the composition of in-stream habitat induced by beaver dams may shift the balance in favour of one species over the other, especially during population bottlenecks, when the standing stock approaches the carrying capacity of the environment (Armstrong et al. 2003). Juvenile trout have a strong affinity with pool environments, as do larger resident trout because pools offer important refugia (Cunjak and Power, 1986; Cunjak, 1996; Collen and Gibson, 2001).

An increase in the number of pooled environments may promote populations of other fish species too, if they are already present in the system (Schlosser, 1998; Snodgrass and Meffe, 1998, Snodgrass and Meffe, 1999). Minnows (*Phoxinus phoxinus*) have been shown to increase in density in beaver ponds (Bylak et al., 2014) and may exert resource competition on trout of similar size ranges (Museth et al., 2007), but conversely may constitute a prey resource for larger individual trout. Pike (*Esox lucius*) also favour pool habitats; their predatory nature will have a negative effect on trout populations and particularly on smolt stages if the results of a study on pike predation of hatchery-reared Atlantic salmon smolts by (Kekäläinen et al., 2008) can be extended to trout.

Trout are preyed upon by a range of species in the UK: otter (*Lutra lutra*), heron (*Ardea cinerea*), goosander (*Mergus merganser*), red-breasted merganser (*Mergus serrator*) and

cormorant (*Phalacrocorax carbo*) amongst others (see Gowans et al., 2003). The risk of increased fish predation in more open beaver pools has been cited as a concern in the review by Collen & Gibson (2001), particularly in relation to the increased time it may take fish to successfully complete passage of dams (see above). However, Kemp *et al.* (2012) noted that increased cover from introduced woody debris and increased water depth in impounded sections may mitigate losses to some predators.

Dam duration and ramifications to ecosystem productivity

Greater diversity of instream and floodplain habitats associated with beavers diversifies the production base which promotes a greater biomass and biodiversity than in river segments not inhabited by beavers (McDowell and Naiman, 1986; Wright, 2009). For example, Hering et al. (2001) reviewed the effects of beaver activity on macroinvertebrate community assemblages in Central European mountain streams, and concluded that key trout prey items such as mayfly, blackfly and midge abundance tended to increase, whereas stonefly and caddisfly abundance decreased, reflecting habitat preferences.

Furthermore, the age and integrity of a beaver dam is key in governing the productivity of the local system and the wider aquatic community composition as studies from North America (Malison *et al.* 2014), Poland (Bylak *et al.* 2014), and Scotland (Law et al., 2014) have revealed. With reference to an initial pulse of production (as noted earlier under **Beaver Ecology**), salmonid productivity reflects this temporal trend, peaking within 2-4 years of dam construction and declining thereafter (Snodgrass and Meffe, 1998, Sigourney et al., 2006); dam age also influences habitat use by juveniles (Malison *et al.* 2014). Hence, while newly created impoundments may be beneficial for trout production in terms of richer feeding opportunities, this may be offset by any long-standing ponds or abandoned sites which are more likely to be detrimental.

Wider impacts

While there are considerable uncertainties in forecasting the specifics of climate change, there are expected to be increases in air temperature across the UK with associated impacts on dissolved oxygen carrying capacity of waters, and increases in the seasonal amplitude of river flow regimes (as winter precipitation increases and there is greater potential for extended periods of drought; Bates et al., 2008).

Any predicted increases in water temperature are of concern for salmonids (Elliott, 1991; Todd et al., 2008). The typical temperature span for trout growth is 3.5-19.5°C and optimal at 13°C (Solomon & Lightfoot, 2008); production of trout would be curtailed if water temperatures exceeded the thermal optimum (Kemp et al. 2012). The ecosystem engineering activities of beavers could increase water temperatures by altering the surface area exposed to direct sunlight (via impounding), and by clearing the tree canopy. As the planting of riparian trees is a common strategy in river habitat restoration and for increasing ecosystem resilience to climate change (Thomas et al., 2015), there is clearly a conflict in the making.

Beaver dams obstruct and impound flows, increase water residence via raising the water table and extent of wetlands, and hence mitigate against extremes of flow, both high and low (Gurnell 1998; Hood and Bayley, 2008; Westbrook et al., 2011; Wohl, 2013). Under extended

drought conditions, the activities of beavers may actually benefit trout populations via the maintenance of pool refugia and prolonged flows (Duncan, 1984; Kemp et al. 2012).

Box 3: A note on beaver management

A management plan for both beavers and dams is required, to be drawn up in discussion with all potential stakeholders, prior to any concerted effort for reintroduction.

In Europe, beaver populations will tend to grow until the availability of habitat and/or food supply is limiting, as their natural predators have already been extirpated or are at low density. Man must fulfil this role. To mitigate impacts on agriculture and infrastructure, a range of general beaver management techniques have been used (Nolet and Rosell, 1998). These range from simple notches created in dams to improve fish passage (Taylor et al., 2010), to translocation or culling (undertaken under licence where applicable) of problem beavers, although culling (or translocation) is often a temporary solution to human-beaver conflicts, as other beavers can re-occupy vacant territories (Nolet and Rosell, 1998). In the UK, culling of beavers is likely to meet significant resistance from the public:

<http://www.bbc.co.uk/news/uk-scotland-tayside-central-35568593>

It should be noted that removal of dams has implications for release of stored sediments, nutrients and pollutants that might have accumulated. Management options all incur cost; from monitoring to determine perceived impacts through to physical removal of dams or problem animals. More is made of potential management implications in the SNH reports. Campbell-Parker et al. (2016) provides the most comprehensive and recent overview of potential management issues.

This document was produced by Prof Jonathan Grey & Dr Paul Gaskell in conjunction with the Wild Trout Trust conservation team and knowledge network; particular thanks are owed to Dr Gary Mantle.

Cited References

- Alexander, M.D. (1998). Effects of beaver (*Castor canadensis*) impoundments on stream temperature and fish community species composition and growth in selected tributaries of Miramichi River, New Brunswick. Canadian Technical Report of Fisheries Aquatic Science 2227: 1-53.
- Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M. and Milner, N. J. (2003) 'Habitat requirements of Atlantic salmon and brown trout in rivers and streams', *Fisheries research*, 62(2), pp. 143-170.
- Baras, E., Lucas, M.C. (2001) Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *Ecohydrology and Hydrobiology* 1, 291-304.
- Bates, B., Kundzewicz, Z. W., Wu, S. and Palutikof, J. (2008) *Climate change and water: Technical paper vi*. Intergovernmental Panel on Climate Change (IPCC).

- Bryant, M.D. (1984) The role of beaver dams as coho salmon habitat in southeast Alaska streams. In: Proceedings of the Olympic Wild Fish Conference. Fisheries Technology Programme (eds J.M. Walton and D.B. Houston). Peninsula College, Port Angeles, Washington, pp. 183–192.
- Bunt, C.M., Castro-Santos, T. & Haro, A. (2012) Performance of fish passage structures at upstream barriers to migration. *River Research and Applications* 28, 457-478.
- Butler, D. R. and Malanson, G. P. (2005) 'The geomorphic influences of beaver dams and failures of beaver dams', *Geomorphology*, 71(1–2), pp. 48-60.
- Bylak, A., Kukula, K. and Mitka, J. (2014) 'Beaver impact on stream fish life histories: the role of landscape and local attributes', *Canadian Journal of Fisheries and Aquatic Sciences*, 71(11), pp. 1603-1615.
- Campbell-Parker, R., Gow, D., Schwab, G., Halley, D., Gurnell, J., Girling, S.J., Lisle, S., Jones, S., Rosell, F. and Dickinson, H. (2016) 'The Eurasian Beaver Handbook : ecology and management of *Castor fiber*', *Pelagic Publishing*.
- Collen, P. and Gibson, R. J. 'The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review', *Reviews in Fish Biology and Fisheries*, 10(4), pp. 439-461.
- Cunjak, R. A. (1996) 'Winter habitat of selected stream fishes and potential impacts from land-use activity', *Canadian Journal of Fisheries and Aquatic Sciences*, 53(S1), pp. 267-282.
- Cunjak, R. A. and Power, G. (1986) 'Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*)', *Canadian Journal of Fisheries and Aquatic Sciences*, 43(10), pp. 1970-1981.
- Cunjak, R. A. and Therrien, J. (1998) 'Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L', *Fisheries Management and Ecology*, 5(3), pp. 209-223.
- Duncan, S. L. (1984) 'Ecology: Leaving it to Beaver', *Environment: Science and Policy for Sustainable Development*, 26(3), pp. 41-45.
- Einum, S., Robertsen, G., Nislow, K. H., McKelvey, S. and Armstrong, J. D. (2011) 'The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon', *Oecologia*, 165(4), pp. 959-969.
- Elliott, J. M. (1991) 'Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*', *Freshwater Biology*, 25(1), pp. 61-70.
- Forty, M., Spees, J. and Lucas, M.C. (2016) 'Not just for adults! Evaluating the performance of multiple fish passage designs at low-head barriers for the upstream movement of juvenile and adult trout *Salmo trutta*', *Ecological Engineering*, 94, pp. 214–224.
- Garcia-Vazquez, E., Moran, P., Martinez, J., Perez, J., de Gaudemar, B., Beall, E. (2001) Alternative mating strategies in Atlantic salmon and brown trout. *Journal of Heredity* 92, 146-149.
- Gauld, N. R., Campbell, R. N. B. and Lucas, M. C. (2013) 'Reduced flow impacts salmonid smolt emigration in a river with low-head weirs', *Science of the total environment*, 458, pp. 435-443.
- Gaywood, M (2001). A trial re-introduction of the European beaver to Scotland. In: Czech, A, & Schwab, G (eds) The European Beaver in a New Millennium. Proceedings of second European Beaver Symposium, 27-30 September 2000, Bialowieza, Poland. Carpathian Heritage Society, Krakow, Poland.
- Gough, P., Philipsen, P., Schollema, P.P., Wanningen, H. (2012) From Sea to Source: International Guidance for the Restoration of Fish Migration Highways. Regional Water Authority Hunze en Aas, AD Veendam, The Netherlands.

- Gowans, A. R. D., Armstrong, J. D., Priede, I. G. and McKelvey, S. (2003) 'Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland', *Ecology of Freshwater Fish*, 12(3), pp. 177-189.
- Green, K. C. and Westbrook, C. J. (2009) 'Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams', *Journal of Ecosystems and Management*, 10(1).
- Hagglund, A. and Sjöberg, G. (1999) 'Effects of beaver dams on the fish fauna of forest streams', *Forest Ecology and Management*, 115(2), pp. 259-266.
- Halley, D. J. & Lamberg, A. (2001). Populations of juvenile salmon and trout in relation to beaver damming of a spawning stream. 2nd European Beaver Symposium, Bialowieza, Krakow, Poland. Carpathian Heritage Society, 122-127.
- Hartman, G. (1994) 'Long-Term Population Development of a Reintroduced Beaver (*Castor fiber*) Population in Sweden', *Conservation Biology*, 8(3), pp. 713-717.
- Hartman, G. and Törnlov, S. (2006) 'Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*)', *Journal of Zoology*, 268(2), pp. 127-131.
- Hearn, W. E. (1987) 'Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review', *Fisheries*, 12(5), pp. 24-31.
- Heggenes, J. (2002) 'Flexible summer habitat selection by wild, allopatric brown trout in lotic environments', *Transactions of the American Fisheries Society*, 131(2), pp. 287-298.
- Heggenes, J. and Saltveit, S. J. (1990) 'Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river', *Journal of Fish Biology*, 36(5), pp. 707-720.
- Hering, D., Gerhard, M., Kiel, E., Ehler, T. and Pottgiesser, T. (2001) 'Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: Results of the "REG meeting" 2000', *Limnologica-Ecology and Management of Inland Waters*, 31(2), pp. 81-92.
- Hood, G. A. and Bayley, S. E. (2008) 'Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada', *Biological Conservation*, 141(2), pp. 556-567.
- Kekäläinen, J., Niva, T. and Huuskonen, H. (2008) 'Pike predation on hatchery-reared Atlantic salmon smolts in a northern Baltic river', *Ecology of Freshwater Fish*, 17(1), pp. 100-109.
- Kemp, P. S., Worthington, T. A., Langford, T. E. L., Tree, A. R. J. and Gaywood, M. J. (2012) 'Qualitative and quantitative effects of reintroduced beavers on stream fish', *Fish and Fisheries*, 13(2), pp. 158-181.
- Kesminas, V., Steponėnas, A., Pliūraitė, V., Virbickas, T. (2013). Ecological impact of Eurasian beaver (*Castor fiber*) activity on fish communities in Lithuanian trout streams. *Rocznik Ochrona Środowiska* 15, 59-80
- Kramer, N., Wohl, E. E. and Harry, D. L. (2012) 'Using ground penetrating radar to 'unearth' buried beaver dams', *Geology*, 40(1), pp. 43-46.
- Law, A., Jones, K. C. and Willby, N. J. (2014) 'Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation', *Aquatic Botany*, 116, pp. 27-34.
- Lokteff, R. L., Roper, B. B. and Wheaton, J. M. (2013) 'Do Beaver Dams Impede the Movement of Trout?', *Transactions of the American Fisheries Society*, 142(4), pp. 1114-1125.
- Macdonald, D. W., Tattersall, F. H., Brown, E. D. and Balharry, D. (1995) 'Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity?', *Mammal Review*, 25(4), pp. 161-200.

- Macfarlane, W. W., Wheaton, J. M., Bouwes, N., Jensen, M. L., Gilbert, J. T., Hough-Snee, N. and Shivik, J. A. 'Modeling the capacity of riverscapes to support beaver dams', *Geomorphology*.
- Malison, R. L., Lorang, M. S., Whited, D. C. and Stanford, J. A. (2014) 'Beavers (*Castor canadensis*) influence habitat for juvenile salmon in a large Alaskan river floodplain', *Freshwater Biology*, 59(6), pp. 1229-1246.
- McDowell, D. M. and Naiman, R. J. (1986) 'Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*)', *Oecologia*, 68(4), pp. 481-489.
- Mitchell, S. C. and Cunjak, R. A. (2007) 'Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream', *Journal of Animal Ecology*, 76(6), pp. 1062-1074.
- Museth, J., Hesthagen, T., Sandlund, O. T., Thorstad, E. B. and Ugedal, O. (2007) 'The history of the minnow *Phoxinus phoxinus* (L.) in Norway: from harmless species to pest', *Journal of Fish Biology*, 71(sd), pp. 184-195.
- Naiman, R. J., Melillo, J. M. and Hobbie, J. E. (1986) 'Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*)', *Ecology*, 67(5), pp. 1254-1269.
- Nolet, B. A. and Rosell, F. (1998) 'Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems', *Biological Conservation*, 83(2), pp. 165-173.
- Parker, H. and Rønning, Ø. C. (2007) 'Low potential for restraint of anadromous salmonid reproduction by beaver *Castor fiber* in the Numedalslågen River catchment, Norway', *River Research and Applications*, 23(7), pp. 752-762.
- Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N. and Volk, C. (2014) 'Using Beaver Dams to Restore Incised Stream Ecosystems', *BioScience*.
- Pollock, M. M., Heim, M. and Werner, D. (2003) 'Hydrologic and geomorphic effects of beaver dams and their influence on fishes', *American Fisheries Society Symposium*, 2003(37), pp. 213-233.
- Polvi, L. E. and Wohl, E. (2012) 'The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development', *Earth Surface Processes and Landforms*, 37(3), pp. 332-346.
- Rosell, F., Bozser, O., Collen, P. and Parker, H. (2005) 'Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems', *Mammal review*, 35(3-4), pp. 248-276.
- Schlosser, I. J. (1998) 'Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment', *Oecologia*, 113(2), pp. 260-268.
- Sigourney, D. B., Letcher, B. H. and Cunjak, R. A. (2006) 'Influence of beaver activity on summer growth and condition of age-2 Atlantic salmon parr', *Transactions of the American Fisheries Society*, 135(4), pp. 1068-1075.
- Solomon, D. & Lightfoot, G.W. (2008). The thermal biology of brown trout and Atlantic salmon. Science Report SCHO0808BOLV-E-P Environment Agency, Bristol. 48pp.
- Snodgrass, J. W. and Meffe, G. K. (1998) 'Influence of beavers on stream fish assemblages: effects of pond age and watershed position', *Ecology*, 79(3), pp. 928-942.
- Snodgrass, J. W. and Meffe, G. K. (1999) 'Habitat use and temporal dynamics of blackwater stream fishes in and adjacent to beaver ponds', *Copeia*, pp. 628-639.
- Stewart, D. C., Middlemas, S. J. and Youngson, A. F. (2006) 'Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks', *Ecology of Freshwater Fish*, 15(4), pp. 552-558.

- Swanston, D.N. (1991) Natural processes. In: Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats (ed W.R. Meehan). American Fisheries Society Special Publication 19, Bethesda, Maryland, pp. 139–179.
- Taylor, B. R., MacInnis, C. and Floyd, T. A. (2010) 'Influence of rainfall and beaver dams on upstream movement of spawning Atlantic salmon in a restored brook in Nova scotia, Canada', *River Research and Applications*, 26(2), pp. 183-193.
- Thomas, S. M., Griffiths, S. W. and Ormerod, S. J. (2015) 'Adapting streams for climate change using riparian broadleaf trees and its consequences for stream salmonids', *Freshwater Biology*, 60(1), pp. 64-77.
- Thorstad, E. B., Økland, F., Aarestrup, K. and Heggberget, T. G. (2008) 'Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts', *Reviews in Fish Biology and Fisheries*, 18(4), pp. 345-371.
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E. and Biuw, E. M. (2008) 'Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon', *Global Change Biology*, 14(5), pp. 958-970.
- Virbickas, T., Stakenas, S. and Steponenas, A. (2015) 'Impact of Beaver Dams on Abundance and Distribution of Anadromous Salmonids in Two Lowland Streams in Lithuania', *Plos One*, 10(4).
- Vissing, M. S., Rasmussen, N. K., Fehrmann, S. & Sunde, P. (2012). Development and dispersal in a population of European beaver (*Castor fiber*) the first eleven years after reintroduction at Klosterheden in Denmark. *Flora og Fauna*, 118, 15-24.
- Westbrook, C. J., Cooper, D. J. and Baker, B. W. (2011) 'Beaver assisted river valley formation', *River Research and Applications*, 27(2), pp. 247-256.
- Wohl, E. (2013) 'Landscape-scale carbon storage associated with beaver dams', *Geophysical Research Letters*, 40(14), pp. 3631-3636.
- Wright, J. P. (2009) 'Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer', *Ecology*, 90(12), pp. 3418-3429.
- Zurowski, W. (1989). Dam building activity of beaver on the mountainous streams. In Abstracts. Fifth international theriological congress: 316–317. Rome: Nage Snc.

Appendix 1: Table summarising potential beaver-trout interactions relating to specific activities (adapted from SNH report)

Activity	Mechanism	Positive effects	Negative effects
Felling	Changes to riparian woodland: Opening of the canopy and increased canopy patchiness	<ul style="list-style-type: none"> • Increased light penetration may lead to increased production within rivers and ponds. Increased primary productivity and temperature may increase production of macroinvertebrate prey items for fish. This could lead to increased fish productivity and improved individual growth rates. • Increased temperatures may favour the establishment of non-salmonid species which have a higher tolerance to lower dissolved oxygen concentrations (such as cyprinids and sticklebacks). • Increased light may lead to the establishment of macrophyte communities creating complex habitats that offer shelter to some fish species (e.g. pike, perch, roach & sticklebacks) and their Prey. • Penetration of light to the riparian zone may result in the development of plant communities that will stabilise banks, reduce erosion and provide increased opportunities for greater terrestrial input of food items for fish. 	<ul style="list-style-type: none"> • Reduction in shading has the potential to increase water temperature and result in increased thermal stress upon some fish species, particularly salmonids. • Increased temperatures may favour the establishment of fish species which may compete with, or prey upon, salmonids. • Increased temperatures can contribute to reduced dissolved oxygen in some circumstances. This may be unfavourable for some fish species (such as salmonids). <p>NOTE: Tree-felling may also impact upon the extensive tree-planting restoration work that has taken place in some catchments, particularly where there is little natural tree cover remaining.</p>
	Changes to riparian woodland: Change in the relative abundance of different tree species.	<ul style="list-style-type: none"> • Possible increases in the supply and/or quality of terrestrial material derived from different sources (principally leaf litter), which may benefit some macroinvertebrate species and, hence, the fish which prey on them. 	<ul style="list-style-type: none"> • Possible reduction in quantity and/or quality of terrestrial material (principally leaf litter) may lead to a reduction in macroinvertebrate diversity and production. This may negatively affect fish which prey on them. • Possible reduction in the quantity of terrestrial (invertebrate) prey items that enter the aquatic environment.
	Changes to riparian woodland: Change in age classes of trees,	<ul style="list-style-type: none"> • Possible changes to tree age class in riparian or littoral areas may result in 	<ul style="list-style-type: none"> • Loss of mature woodland may result in reduced quantities of terrestrial material entering

	contributing to canopy structure change / patchiness.	a more open canopy and increased light penetration, with consequent benefits for some species (see above).	<p>waterbodies. This can affect macroinvertebrate production and therefore the production of fish.</p> <ul style="list-style-type: none"> • Possible reduction in the size and quantity of large woody material entering the watercourse in the longer term may affect in-stream habitat structure, and this may adversely affect some fish species. • Possible changes to tree age class in riparian or littoral areas may result in a more open canopy and increased light penetration, with consequent negative effects for some species (see above). <p>NOTE: Effects will depend on the nature of changes, and the extent to which trees affected by beavers regrow.</p>
	Changes to riparian woodland: Amount/diversity of fallen dead wood on woodland floor.		
Felling and constructions	Changes in the amount/diversity of woody material in watercourses	<ul style="list-style-type: none"> • Greater quantities of large woody material in rivers and ponds can result in increased habitat diversity, availability of prey items, and fish cover. • Where large woody material occurs, it may reduce the transport of sediment downstream. 	<ul style="list-style-type: none"> • The establishment of large log jams could temporarily hinder the in-stream movement of some fish species if they act as barriers. • Depending on where woody items aggregate, such material can act as a barrier to movement or result in the loss of habitat. • Where the quantity of large and small woody items is too great, this may result in blockages which may affect the transport of important gravels.
Feeding	Feeding on specific terrestrial herbaceous & aquatic plant species.	<ul style="list-style-type: none"> • Changes to macrophyte community structure may favour some species of (non-salmonid) fish and their prey. 	<ul style="list-style-type: none"> • Decrease in macrophyte species in some lochs may have a negative impact on species that depend on them for food or shelter. E.g. Pike are often associated with macrophytes because they use these as cover when ambushing prey. Roach & perch may use macrophytes as refugia from pike. Salmonids are rarely associated with macrophytes.

Dams / pond creation	Change from flowing to stillwater habitat.	<ul style="list-style-type: none"> • Increase in habitat diversity, which may favour some fish species or fish life-history stages. In some situations this may also result in an increase in species richness – of both fish and invertebrate prey items. • Increased temperatures, changes in habitat availability and feeding opportunities in stillwater habitats may result in increased individual growth rates, fish condition and overall production. • Depending on depth and location, impoundments may offer a high-temperature refuge for some fish. 	<ul style="list-style-type: none"> • Increase in habitat diversity for fish may favour some species over others, or benefit only some life-history stages (e.g. juvenile or adult fish). • Depending on location, the creation of lentic habitats may result in habitat loss for species which favour or dominate flowing habitats. • Accumulation and smothering of bed sediment upstream of dams, and a reduction in habitat quality for some species (principally salmonids). • Reduction in turbulence may occur upstream of dams, resulting in a reduction in dissolved oxygen. • Possibility of increased opportunities for fish predators (e.g. goosander, cormorant, otter, mink) and poachers.
	Change in hydrological processes on riparian & downstream habitat	<ul style="list-style-type: none"> • Reduction in the transport of fine material may improve the quality of spawning and rearing habitats downstream of any impoundment. • Impoundments may create low- and high-flow refuges for fish. • Flooding of riparian and wetland habitats can provide spawning opportunities for species such as pike and additional habitat for species such as eel. 	<ul style="list-style-type: none"> • Changes in flow may result in sediment starvation in gravel spawning areas. This can affect both salmonids and spawning lamprey. • A reduction in flow downstream of the structure may result in a reduced wetted width and a loss of juvenile fish habitat.
	Changes in water quality downstream	<ul style="list-style-type: none"> • Reduction in the amount of fine material deposited on the stream or riverbed downstream of the impoundment. This may result in an improvement in the quality of gravel spawning areas (downstream) for salmonids and lamprey. • Accumulation of fine sediments may increase the volume of available habitat for lamprey ammocoetes. 	

	Change in standing dead wood resulting from inundation of trees.	<ul style="list-style-type: none"> • Possible increase in terrestrial invertebrate prey entering the aquatic environment. 	
	Longer term successional changes after dam abandonment e.g. beaver meadows.		
	Impacts on movement of species.		<ul style="list-style-type: none"> • Prevention of the free movement of fish to all habitats required during their life cycle. This is particularly relevant to key migration periods (such as spawning migrations), but also at other times. • The scale of impact may be greater for species which have a limited ability to overcome in-stream obstacles (such as lamprey).
Other constructions	Creation of lodges, burrows, canals etc.		
Other	Fisheries.		<ul style="list-style-type: none"> • Beaver habitats (impoundments and flooded wetlands) may benefit Invasive Non-Native Species such as skunk cabbage or signal crayfish, if these are present within the catchment.
Indirect habitat creation/ restoration initiatives as result of beaver presence.	Beaver used to promote opportunities for riparian and freshwater habitat creation/ restoration.	<ul style="list-style-type: none"> • Presence of beaver may act as an incentive for greater investment, management and monitoring. This could include those related to the restoration and management of riparian woodland. 	<ul style="list-style-type: none"> • Beaver presence may impact on fish-related riparian woodland restoration activities.