Scottish Natural Heritage

Commissioned Report 349

A critical review of the effects of beavers upon fish and fish stocks

COMMISSIONED REPORT

Commissioned Report No. 349

A critical review of the effects of beavers upon fish and fish stocks

(*iBids No. 8770*)

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COMMISSIONED REPORT

Summary

A critical review of the effects of beavers upon fish and fish stocks

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Background

Scottish Natural Heritage (SNH), in collaboration with specialists based across Europe and the UK and with full national consultation, has conducted an extensive assessment of the feasibility and desirability of reintroducing the European beaver (*Castor fiber*) to Scotland. This accords with UK Government obligations to consider the desirability of reintroducing certain extinct species under Article 22 of the European Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna (the 'Habitats Directive'). The European beaver became extinct in Scotland as a result of over-hunting around the 16th Century. Further, the European beaver is one of 32 species included in Scotland's "Species Action Framework" as a focus of new management action for five years from 2007 for SNH and a range of partners. The Species Action Framework, launched in 2007 by Ministers, sets out a strategic approach to species management in Scotland.

As a result of the findings of the feasibility and desirability studies, a trial reintroduction of up to four families of European beaver to Knapdale Forest, Argyll, by the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS) on behalf of the 'Scottish Beaver Trial' partnership was sanctioned by the Minister of the Environment in 2008. The trial aims to conduct a five year robustly monitored reintroduction which will facilitate decision makers tasked with considering the feasibility and desirability of reintroducing European beaver to the whole of Scotland. Once the trial has been completed, SNH will provide a final report to the Scottish Government.

The aim of this report is to provide an independent critical review, based on scientific literature and expert opinion, of the impacts of beaver on fish and fish stocks and to collate new, updated information which can be used in the wider consideration of beaver reintroduction to Scotland.

Main findings

- The results of meta-analysis highlight a bias towards studies of beaver/ fish interactions in North America (90) compared to Europe (8).
- The meta-analysis indicated the main positive impacts of beaver activity on fish cited were increased habitat heterogeneity, greater area for rearing and overwintering, higher invertebrate production, and the provision of refuge from both high and low flows.

- The main negative impacts of beaver activity cited were barriers to fish movement due to the construction of dams, loss of spawning habitat due to siltation, and reductions in oxygen levels in beaver ponds leading to fish kills.

- Overall, positive impacts (157) were cited more frequently than negative impacts (102).

- The impact of beaver on fish populations is spatially and temporally variable, and differs inter- and intraspecifically.

- The results of an Expert Opinion Survey (EOS) that involved 45 North American and European experts (70% return) revealed that the majority of fisheries scientists and managers tended to suggest that the overall impact of beavers on fish populations was positive (58% of items).

- The impact of beavers on the abundance and productivity of migratory salmonids was considered positive.

- The impact of beaver dams on the movement of aquatic organisms in tributary streams, including upstream and downstream migrating salmonids, and on the availability of suitable salmonid spawning habitat was generally considered negative.

- A high level of agreement (≥50%) was achieved for half of all items responded to.

For further information on beaver issues in Scotland see:
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Table of Contents **Page**

List of Figures Page

List of Tables Page

1 INTRODUCTION

There are many benefits of species reintroduction; released animals might increase natural biodiversity, fulfil a role as keystone components of an ecosystem, and/or create the public and political support necessary to undertake habitat restoration or to implement species protection measures (Seddon, 1999; Hodder and Bullock, 1997; Seddon *et al.,* 2007; Maunder, 1992). Reintroduced species may also provide significant economic benefits, such as ecotourism (Rees, 2001, Maunder, 1992), to regions where other types of activity may be limited. However, obligations under international agreements (e.g. Article 9 of the Convention on Biological Diversity, 1992) may be one of the most significant drivers for elevated interest in species reintroduction, providing an increasingly popular tool for conservation managers tasked with restoring lost biodiversity. The use of reintroduction as a conservation tool is based on the simplistic assumption that by releasing individuals of a species into a suitable habitat within their former range, it is possible to restore natural biodiversity (Seddon, 1999). The Convention on the Conservation of European Wildlife and Natural Habitats (1979), the 'Berne Convention', was the first wildlife treaty to encourage its parties to reintroduce native species as a method of conservation. While a legal framework for considering the reintroduction of species exists in some regions, the encouragement to reintroduce species created by the Berne Convention is not reflected in European law and has been replaced by an obligation only to study the desirability of reintroduction (Rees, 2001). Article 22(a) of the Habitats Directive provides for the assessment of the desirability of reintroducing species listed on Annex IV (including, the European beaver *Castor fiber*) to areas where they were once native, to contribute to the re-establishment of these species at favourable conservation status.

As with most other wildlife management processes, species reintroduction has many inherent risks and challenges that should be addressed to maximize the probability of success. Most importantly, the causal factors responsible for extinction should be identified and shown to no longer persist; *C. fiber* is thought to have become extinct in Scotland due to over-hunting in the 16th century. Further, when done correctly, reintroduction represents a high-cost activity that commits personnel to long-term monitoring and management (Maunder, 1992). The potential for reintroductions to fail represents a significant financial (and political) risk. Therefore, even if the benefits of reintroduction are considered to be substantial, a project may not be deemed desirable. The benefits must outweigh the costs, including risk.

The consideration of sociological factors, in addition to ecological implications, is an essential element in enhancing the probability of success of any reintroduction project (Reading and Kellert, 1993). Rees (2001) contends that successful reintroductions will be achieved only with public support, and this is more likely where clear objectives have been established after public consultation. Key to this is quantifying and responding to public attitudes and opinion, especially those of key stakeholders most likely to be affected by any reintroduction programme. Negative perceptions among key stakeholders can prove detrimental to success; reintroductions rarely succeed if values, attitudes, behaviours and desires are not actively considered and incorporated into assessments of programme feasibility (Reading and Kellert, 1993). One of the most famous examples relates to the reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park, Wyoming (USA). This project was forestalled for two decades by strong opposition from stakeholders within the region (Fritts *et al.*, 1997). The future reintroduction of wolves to the Olympic Peninsula (USA), while feasible on ecological grounds, was not thought to be prudent as substantial political, social, and financial consequences are associated with range expansion outside the National Park (Leaper *et al.,* 1999). Conversely, acceptance by local people was crucial to the success of reintroducing brown bears (*Ursus arctos*) to the Pyrenees (Arquilliere, 1998). Even if a reintroduction project goes ahead, without support for conservation from the local population and stakeholders, the species is likely to become threatened. In both the United

States and Europe, reintroduced animals continue to act as a source of conflict, and in some cases are killed by opposing factions (Breitenmoser cited in Breitenmoser, 1998; Fritts *et al.,* 1997). Understanding public/stakeholder perception is also important in project implementation, e.g. the selection of suitable reintroduction sites.

Plans to conduct a trial reintroduction of European beaver to Scotland have been the subject of much debate (see Gaywood *et al.*, 2008). Article 22(a) of the EU Habitats Directive requires that any reintroduction should take place only after proper consultation with the public concerned. National and local public consultation exercises conducted since 1998 indicate that the majority support the plans, but some individuals and key stakeholder groups (e.g. some of those representing fisheries interests) maintain reservations and continue to raise concerns. The aim of this report is to provide a thorough review of the available literature on the interactions between beaver[1] and fish populations so that the nature and magnitude of any impacts on fish populations can be ascertained. SNH previously commissioned a review (Collen, 1997) of potential impacts of beaver on the ecology and movement of fish in Scotland over a decade ago. It is timely to reassess the current state of understanding.

Previous reviews have consistently recognised that the ecological (and socio-economic) impacts of beaver can be considered as either positive or negative depending on the viewpoint of the stakeholder; the "winners and losers" paradigm. It is important to recognise that what might be considered positive by some, e.g. enhanced physical habitat heterogeneity (geomorphologist), may be considered negative by others, e.g. increased risk of flooding (riparian landowner). To date, there has been a disagreement over whether the impact of beaver reintroduction could be considered beneficial or detrimental when viewed from the more holisitic perspective. Unlike other reviews, this report endeavours to provide weighting for arguments posed in relation to the impact of beaver activity on fish and fisheries. By necessity, impacts are categorised as either positive or negative when viewed from a fisheries management perspective. A meta-analysis of the literature provides quantitative information to support the review. Further, an Expert Opinion Survey (EOS) illustrating "impressions" of an appropriate scientific community is presented to supplement information provided by the literature analysis and the results of previous public perception surveys. It is the intention that this report will: provide valuable information for decision makers; enable SNH to respond to concerns raised by groups representing fisheries interests; and provide fisheries groups with the information required to better understand and appreciate the implications of a European beaver reintroduction.

1.1 Aims and objectives

The principal aims of the report are:

A1) Provide a critical and comprehensive review of the literature pertaining to the impacts of beavers on fish and fish stocks; and

A2) Provide a critical review of expert opinions on the effects of beavers on fish and fish stocks.

The following objectives were set to enable the aims to be achieved:

[1] Note that where the term 'beaver' is used it refers to both the North American and European species.

O1) Undertake a critical and comprehensive literature review conducted by a team of experts in fisheries, reintroduction and the impacts of debris dams on fish populations at the International Centre for Ecohydraulic Research, University of Southampton;

O2) Perform a meta-analysis to provide quantitative information that describes the extent of understanding of specific components of available literature; highlights gaps in knowledge; and identifies trends and biases; and

O3) Conduct an EOS based on the experience of fisheries scientists, terrestrial ecologists/beaver experts, geomorphologists, and representatives from other relevant disciplines in North America and Europe providing additional information not easily obtained from traditional literature reviews.

2 BEAVERS AND THEIR IMPACTS ON FISH: A LITERATURE REVIEW AND META-ANALYSIS

2.1 Abstract

This section examines the impact of both North American (*Castor canadensis*) and European beaver on fish populations to identify potential threats posed by the proposed European beaver reintroduction to Scotland's freshwater fisheries. A meta-analysis was conducted to highlight biases within the literature, gaps in understanding, and positive and negative aspects of beaver/fish interactions. A distinct regional bias exists, with 90 literature sources considering North American beaver compared with 8 for the European species. This probably relates to the fact that, until relatively recently, the European beaver was extirpated from many countries. Due to the regional bias in research, the species of fish considered also tended to be North American, especially the Pacific salmonids, although Atlantic salmon (*Salmo salar*) and brown/sea trout (*S. trutta*), i.e. species of considerable interest from the Scottish perspective, were the subject of 13 and 11 studies respectively. In general, the literature review indicates that overall effects of beavers on fish populations can be positive, with 157 positive impacts recorded compared to 102 negative ones. However, the impact of beaver on fish populations is spatially and temporally variable, and differs between (interspecifically) and within (intraspecifically) species.

2.2 Introduction

With the exception of humans, no creature modifies the environment to the same degree as the beaver. Both the North American and European species have suffered a major reduction in numbers and a contraction in range due to their overexploitation by humans. However, both species has seen a dramatic revival since the 1920s as a result of increased legislation and reintroduction programmes (Rosell *et al.,* 2005).

The European beaver was reduced to about 1,200 animals in eight isolated populations by the beginning of the 20th century (Halley and Rosell, 2003). By 2003 populations had been established in all countries within their former natural range in Europe except for Britain, Portugal, Italy and the south Balkans, with an estimated population of 639,000 (Halley and Rosell, 2003).

Given its ability to modify the surrounding environment the re-establishment and reintroduction of both beaver species has not always been regarded favourably. In some instances, the fisheries lobby have been particularly vocal in their opposition. This concern is illustrated by the considerable literature describing beaver/fish interaction, the majority of which originated in North America, with numerous studies on the impact on trout species (Sayler, 1935; Bradt, 1935; Cook, 1940). More recently the subject has come to prevalence in Europe where the species has been reintroduced, or reintroduction is planned, in a number of countries. Such projects frequently face opposition from fisheries groups. In Denmark, anglers were concerned that European beaver dams would create ponds and thereby destroy spawning areas of salmonid species (Bau, 2001). There is also opposition to the proposed reintroduction of European beaver to Scotland, where fisheries groups fear beaver dams will block salmonid spawning runs and cause siltation of spawning gravels (Cramb, 1998).

Beaver influence freshwater ecosystems (Naiman *et al.,* 1988; Pollock *et al.,* 1995). A number of studies have reviewed the effect of beavers on the abiotic environment in terms of hydrology, geomorphology, water chemistry and temperature (see Collen and Gibson, 2001; Rosell *et al.,* 2005).

The aim of this literature review is to synthesise knowledge on the effects of beaver activity on fish populations by building on previous reviews by Collen (1997), Collen and Gibson (2001), Pollock *et al.,* (2003), Rosell *et al., (*2005), and Venturini (2006), and performing a meta-analysis to highlight bias and gaps in understanding. The information obtained is supplemented by an EOS (Section 5).

2.3 Methods

Both peer reviewed and "grey" literature relating to the impact of beavers on fish and fish populations was collected via two routes. First, the bibliographic search engines 'Google Scholar' and 'Web of Science', were interrogated using ten combinations of search terms:
(i) "European beaver" + "Atlantic salmon";
(ii) "European beaver" + "salmon";
(iii) "European beaver" + "trout";
(iv) "European beaver" + "salmonid";
(v) "European beaver" + "fish";
(vi) "beaver reintroduction" + "fish";
(vii) "beaver" + "reintroduction" + "fish";
(viii) "beaver" + "reintroduction" + "salmon";
(ix) "beaver" + "impact on fish"; and
(x) "beaver" +"impact on salmon".
The search results were then assessed for their relevance and any suitable records were added to the bibliography. Second, additional references from the review papers by Avery (1983), Collen (1997), Collen and Gibson (2001); Pollock *et al.,* (2003), Rosell *et al.* (2005), and Venturini (2006) were added to the bibliography.

Full articles were sourced, either online, or from the British Library, London or the Natural History Museum's Zoology Library, London. The articles were searched for sections of relevance to the impacts of beaver on fish populations. These sections were added to the meta-analysis database. The database consisted of fields containing: the journal title; the year of publication; the location of the study area or region described; and the beaver and fish species observed. The impacts of beaver on fish species were classified as either positive or negative and added to the database accordingly. Impacts were categorised (Table 1), 15 of which were positive and 11 negative.

Any new articles found while evaluating the original reference were then sourced and added to the bibliography.

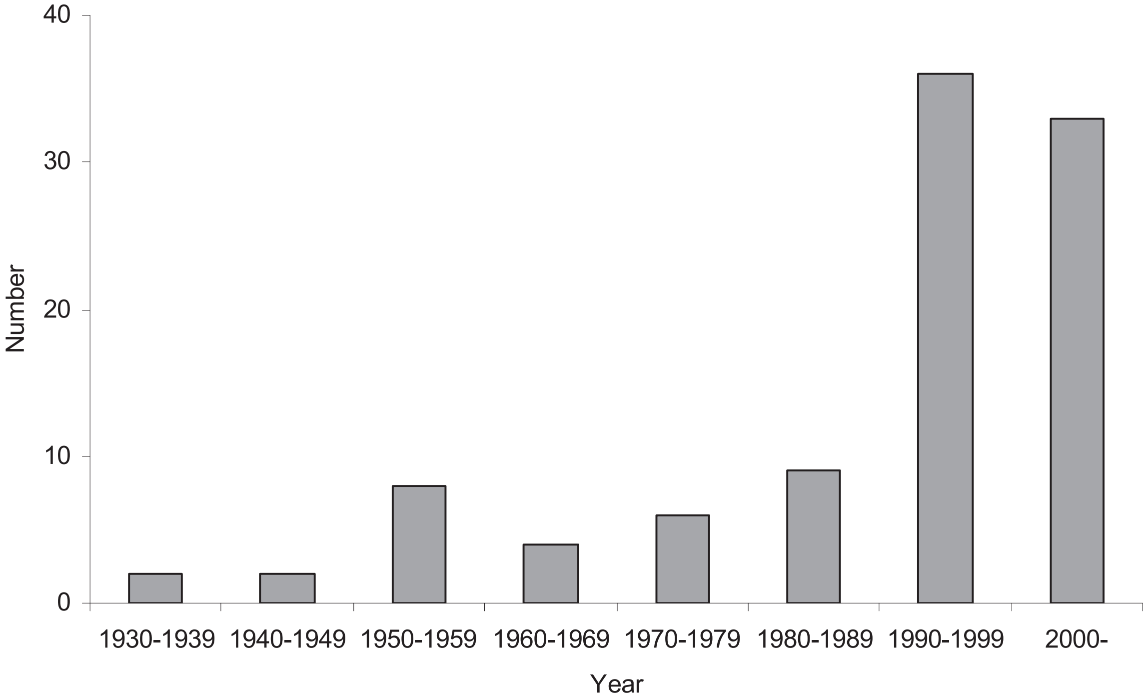
Table 1 The categories of perceived positive and negative impacts of beavers

Positive impacts	**Negative impacts**
Enhanced habitat availability / complexity	Barriers to fish movement
Enhanced overwintering habitat	Reduced spawning habitat
Enhanced rearing habitat	Altered temperature regime
Provision of cover	Reduced oxygen levels
Enhanced diversity / species richness	Reduced habitat quality
Enhanced abundance / productivity	Altered flow regimes
Provision of habitat under low flows	Loss of cover
Provision of high flow refuge	Reduced productivity
Provision of temperature refuge	Reduced growth
Enhanced water quality	Abandonment of beaver settlements
Sediment trap	Reduced water quality
Enhanced invertebrate productivity	
Enhanced growth rates	
Enhanced fish condition	
Provision of fishing areas	

2.4 Results

The literature search produced 100 references containing information on the interactions between beavers and fish. Of these, the majority (69%) were published after 1989 (Figure 1), with the remaining records relatively evenly spread over the preceding six decades. The earliest studies found were published in 1935.

Figure 1 The number of studies considering beaver/ fish interaction published since 1935



Publications were regionally biased. Ninety (90%) were based on North American research, the majority of which (68) were from the United States. Eight studies were based on European experience (three in Norway, and one each in Germany, Estonia, Latvia, Sweden, and Denmark). Two studies took a global perspective. Clearly, as the majority of research was conducted in North American, then there is a corresponding bias to consideration of the North American beaver. None of the studies reviewed considered the impact of the introduced North American beaver on fish populations in Europe.

Forty-seven fish species and sub-species were recorded in the literature on beaver/fish interactions reviewed (some papers examined the effects on the river's entire fish assemblage, therefore, the total number of individual species is likely to be higher). The most numerously cited species were brook trout (including eastern brook trout) (N.B. this species is a charr, *Salvelinus fontinalis*) (23 records), coho salmon (*Oncorhynchus kisutch*) (14), cutthroat trout (*O. clarki*, composed of several sub-species) (13), brown trout (including sea trout) (11), Atlantic salmon (13), rainbow trout (*O. mykiss*, including the golden trout sub-species) (8), and the anadromous form, steelhead trout (*O. mykiss*) (6). A number of studies, rather than stipulating specific species, considered the impact of beavers on trout species in general (10 records), salmonids (5), all anadromous species (1), or all species in the study location (14). For the purposes of this report, the species were categorized into groups. If more than one trout species was cited in a record, then all were considered as being part of the "trout" group. The results show that trout species were recorded in 29 records (29% of the total), charr in 24 records (24%), and salmon in 29 records (29%) of which 11 (11%) considered Pacific salmon.

Figure 2 The number of studies recording positive (solid bars) and negative (grey bars) impacts of beavers on fish

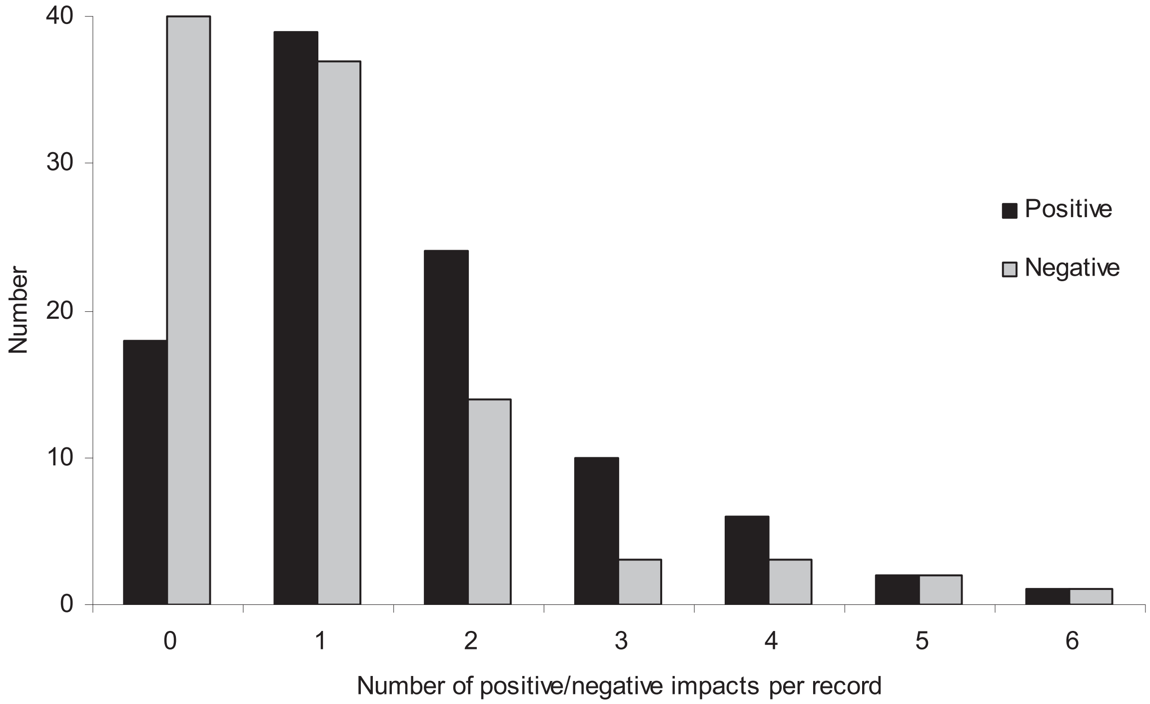


Table 2 Citation of positive impacts of beaver activity on fish populations. Different impacts are expressed as the number of times they are cited in 100 literature sources and as a percentage of the total number of citations.

Positive impacts	**Number**	**% of total citations**
Enhanced habitat availability / complexity	13	8.3
Enhanced overwintering habitat	15	9.6
Enhanced rearing habitat	16	10.2
Provision of cover	5	3.2
Enhanced diversity / species richness	7	4.5
Enhanced abundance / productivity	41	26.1
Provision of habitat under low flows	11	7
Provision of high flow refuge	3	1.9
Provision of temperature refuge	9	5.7
Enhanced water quality	2	1.3
Sediment trap	3	1.9
Enhanced invertebrate productivity	15	9.6
Enhanced growth rates	13	8.3
Enhanced fish condition	1	0.6
Provision of fishing areas	3	1.9
Total	**157**	**100**

Table 3 Citation of negative impacts of beaver activity on fish populations. Different impacts are expressed as the number of times they are cited in 100 literature sources and as a percentage of the total number of citations.

Negative impacts	**Number**	**% of total citations**
Barriers to fish movement	44	43.1
Reduced spawning habitat	16	15.7
Altered temperature regime	9	8.8
Reduced oxygen levels	12	11.8
Reduced habitat quality	2	2.0
Altered flow regimes	2	2.0
Loss of cover	5	4.9
Reduced productivity	9	8.8
Retarded growth	1	1.0
Abandonment of beaver settlements	1	1.0
Reduced water quality	1	1.0
Total	**102**	**100**

Positive impacts of beavers on fish populations were cited more frequently than negative impacts (Figure 2). A total of 157 positive interactions were recorded compared to 102 negative impacts. Eighteen of the records contained only negative impacts of beaver on fish populations whereas 40 references provided descriptions of positive impacts only.

The most frequently recorded positive impact was an increase in fish productivity or abundance, followed by an increase in fish habitat or habitat complexity, the provision of overwintering habitat, and an increase in rearing habitat (Table 2). 'Barriers to fish movement' was the most frequently cited negative impact, followed by 'reduced spawning habitat', and 'altered temperature regime' (towards the upper range of a species thermal tolerance) (Table 3).

2.5 Literature review

The following section is a review of the literature on which the meta-analysis was constructed. It is divided into two main components. First, the positive and negative impacts of beaver on fish populations as highlighted by the meta-analysis are discussed, primarily in relation to studies conducted in North America. Second, a more detailed review of the few papers that examine interactions between fish and European beaver is provided.

2.5.1 Positive impacts of beaver on fish populations

2.5.1.1 Habitat

Beaver activity creates a varied riverine habitat mosaic (Hanson and Campbell*,* 1963) by creating patches of lentic habitat within a corridor of lotic habitat (Snodgrass and Meffe, 1999). This heterogeneous habitat, which is characterised by the presence of tree roots and large woody debris (Kauffman *et al.,* 1993), can be beneficial for many organisms, including several fish species. The majority of the research has focused on beaver created habitat for salmonid species due to their economic importance (Bryant, 1984; Lichatowich, 1999). Andonaegui (2000) suggested that areas and opportunities for North American beaver reintroduction and management should be investigated as a low-cost (and sustainable) strategy for improving Pacific salmon habitat. Indeed, current research conducted by the United States National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service in Oregon is attempting to manipulate North American beaver behaviour by providing Beaver Dam Support (BDS) structures (Figure 3) to attract North American beaver activity in specific predesignated areas (M. Pollock, pers. comm.). The Lower Bridge Creek, a tributary of the John Day River, has been incised by anthropogenic activity. Incision of the river channel has lessened juvenile steelhead overwintering habitat. In this case study, North American beaver dams are intended to enhance streambed aggradation and elevate the floodplain water table resulting in an increase in summer flows, decreased stream temperatures, a narrower and more sinuous stream channel, and expanded riparian forest (Pollock *et al.*, 2003). A series of BDS structures, designed to assist North American beaver in construction of dams that will create pool habitat for juvenile steelhead in the short term, and trap sediment, aggrade the streambed and create gravel bedded reaches in the long term, have been installed. Each BDS consists of a series of 0.1 m diameter posts inserted approximately 1 m into the substrate, with equal height above the ground, and between 1 and 2 m spacing between the posts. Early results indicate that the BDS can be employed successfully to generate dam construction in areas not previously used, resulting in beneficial physical response from the perspective of river management/restoration. Despite the focus on salmonids, the benefit of improved habitat created as a result of beaver activity will also be realised by many non-salmonid species (Ray *et al.,* 2004).

A number of species actively select North American beaver created habitats including brown trout (Young, 1995), Oregon chub (*Oregonichthys crameri*) (Scheerer *et al.,* 2004) and brook trout (Winkle *et al.,* 1990). Ray *et al.* (2004) observed that fish species quickly colonized new peatland pool habitat in Minnesota (USA) created by North American beaver activity, and concluded that beaver-flooded peatlands, like streams, support multi-species fish assemblages.

Figure 3 Beaver Dams Support (BDS) structure designed to assist North American beaver dam construction in the incised Bridge Creek, Oregon, United States (photograph provided by M. Pollock).

Cunjak (1996) suggests that in shallow, ice-covered streams, North American beaver ponds may represent one of the few available overwintering sites for fish. Chisolm *et al.* (1987) and Lindstrom and Hubert (2004) observed that North American beaver ponds with low current velocities reduced ice cover and the stable temperature regimes provided important refuge for fish in mountain streams during the winter. North American beaver ponds are a key winter habitat for bull trout (*Salvelinus confluentus*) and cutthroat trout (Jakober *et al.,* 1998; Rasmussen, 1941), coho salmon (Nickelson *et al.,* 1992; Swales and Levings, 1989) and Dolly Varden (*S. malma malma*) (Gregory, 1988 in Reynolds, 1997). Survival of overwintering coho salmon in North American beaver ponds was approximately twice that observed for the rest of the river system on Vancouver Island, Canada. Jakober *et al.* (2000) observed a positive preference exhibited by bull trout and cutthroat trout for North American beaver ponds, as more than 70% of fish congregated in five beaver ponds that represented 30% of the area sampled.

North American beaver ponds, with their relatively slow waters and high invertebrate productivity, provide important rearing habitat for andromous fish species (Johnson and Weiss 2006; Swanston, 1991; Taylor, 1999), such as coho salmon (Lang *et al.,* 2006; Leidholt-Bruner *et al.,* 1992; Rosenau and Angelo, 1999; Swales and Levings, 1989; Beechie *et al.,* 2001 in Collins *et al.,* 2003), Chinook salmon (*Oncorhynchus tshawytscha*) (Rosenau and Angelo, 1999), steelhead trout (Lichatowich, 1999), Atlantic salmon, and brook trout (Scruton *et al.,* 1998). Grasse (1979) even proposed that North American beaver ponds should be stocked with trout species to increase productivity via the provision of rearing habitat. Brook trout successfully spawned on a 0.3 m thick aggregation of waterlogged sticks in a small lake in Algonquin Park, Ontario (Canada) (Fraser, 1982).

Many of the sticks were old 'cuttings' that are commonly found in North American beaver dams and lodges.

Beaver activity can provide cover for fish (Rasmussen, 1941; Rutherford, 1955; Sayler, 1935). Beedle (1991) suggests presence of wood used during lodge and dam construction within pools may provide large quantities of escape and hiding cover for fish.

While often cited as a negative impact due to the siltation of important spawning gravels (section 3.5.2.2), the impact of beaver dams on sediment budgets may prove beneficial (Halley, 1995). Storage of sediment behind dams (Beedle, 1991) may be detrimental locally due to impacts on salmonid spawning gravels, but reduces sediment load downstream (Grasse, 1951; Halley, 1995). Beedle (1991) argues that sediment storage, particularly in low order tributaries, may prevent damage to important spawning and rearing sites.

2.5.1.2 Species richness

A number of studies have found increased species richness/diversity in the presence of North American beaver activity (France, 1997; Hanson and Campbell, 1963). Keast and Fox (1990) argue that while species richness in North American beaver ponds in Ontario was lower than surrounding lakes, it was higher than expected based on the species-area curve. North American beaver created peatland ponds in Minnesota, when considered at the landscape scale, offered considerable habitat for fish, increased complexity of biological food webs, and contributed to biological diversity (Ray *et al.,* 2004). Snodgrass and Meffe (1998, 1999) found 31 fish species in active and abandoned North American beaver ponds in South Carolina (USA) and estimated that the removal of this habitat would reduce species richness by over half, while Schlosser and Kallenmeyn (2000) suggest that collapsed North American beaver ponds with their combination of stream and pool habitats had the highest species richness. Mitchell and Cunjak (2007) showed that in New Brunswick (Canada), North American beaver dams cause disturbance without which a lower diversity throughout the length of the stream would be expected, as Atlantic salmon would dominate the entire length of stream.

2.5.1.3 Species productivity and abundance

The long-term impact of beaver activity on abundance and productivity is often the main interest of fisheries managers. The effect of beaver activity on fish abundance and productivity varies interspecifically (Table 4) and intraspecifically (via spatial differences), as highlighted by studies concerning Atlantic salmon (Scruton *et al.,* 1998; Cunjak and Therrien, 1998; Mitchell and Cunjak, 2007).

Table 4 Studies showing positive (+) and/ or negative (-) impacts of beaver on species abundance or productivity

Species	Impact	References
Atlantic salmon	+/-	Scruton *et al.,* 1998; Cunjak *et al.,* 1998; Cunjak and Therrien 1998; Mitchell and Cunjak, 2007; Guignion, 2009
Bonneville cutthroat trout	+	White and Rahel, 2008
Brook stickleback	+	France, 1997
Brook trout	+/-	Hale, 1966; Scruton *et al.,* 1998; Rabe, 1970; Rutherford, 1955; Gard, 1961; Collins, 1993; Balon and Chadwick, 1979; Mitchell and Cunjak, 2007
Brown trout	+	Hale, 1966; Müller-Schwarze, 2003; Gard and Seegrist 1972; Gard, 1961
Bull trout	+	Andonaegui, 2000
Chinook salmon	+	Andonaegui, 2000
Coho salmon	+	Bustard *et al.,* 1975; Pollock *et al.,* 2004; Lang *et al.,* 2006; Leidholt-Bruner *et al.,* 1992; Nickelson, 1992; Bryant, 1984; Murphy *et al.,* 1989; Riley and Lemieux ,1998 in Gottesfeld *et al.,* 2002
Colorado River cutthroat trout	+	Horan *et al.,*, 2000
Creek chub	+	Schlosser, 1998; Rupp, 1954
Cutthroat trout	+	Grasse, 1951
Dolly Varden	+	Gregory, 1988 in Reynolds, 1997
Eastern brook trout	+	Rupp, 1954; Grasse, 1951
Fallfish	+	Rupp, 1954
Fathead minnow	+	France, 1997
Finescale dace	+	France, 1997
Golden trout	-	Müller-Schwarze, 2003
Lahontan cutthroat trout	+	Talabere, 2002
Lake whitefish	-	Bertolo and Magnan, 2006
Minnow	+	Hale, 1966
Mudminnow	+	Knudsen, 1962
Muskellunge	+	Frohnauer *et al.,* 2007
Ninespine stickleback	+	Rupp, 1954
Northern pike	+	Bertolo and Magnan, 2006; Knudsen, 1962
Northern redbelly dace	+	Rupp, 1954; France, 1997
Pinewoods darter	-	Rohde and Arndt, 1991
Rainbow trout	+	Muller-Schwarze, 2003; Grasse, 1951; Andonaegui, 2000; Gard, 1961
Sandhills chub	-	Rohde and Arndt, 1991
Slimy sculpin	+	Mitchell and Cunjak, 2007; France, 1997
Sockeye salmon	+	Murphy *et al.,* 1989
Steelhead salmon	+	Andonaegui, 2000
Walleye	-	Bertolo and Magnan, 2006
White sucker	+	Rupp, 1954; France, 1997
Yellow Perch	+	Balon and Chadwick, 1979

The meta-analysis indicated that for a greater number of species, beaver presence was associated with an increase rather than a decrease in productivity. Prior to European settlement in the Pacific Northwest of the United States, fluvial systems would have exhibited a mosaic of North American beaver created wetland complexes, active side channels, and riparian forests that provided highly productive habitat for Pacific salmonids (Andonaegui, 2000). Lichatowich (1999) argues that extensive North American beaver activity in wetlands provides stable Pacific salmon habitat and buffers variability in abundance. Collins (1993) suggests that the presence of North American beaver ponds in Wyoming is critical to the continued survival of sensitive species such as the Colorado River and Bear River cutthroat trout.

Based on aerial photography, Pollock *et al.,* (2004) estimated the current summer coho salmon smolt production potential of the Stillaguamish River Basin, Washington (USA) to be 965,000 smolts; this was compared with a historic summer production level of 2.5 million. The authors argue this decline is due to a reduction in summer habitat capacity by 61% of historic levels, primarily as a result of the loss of North American beaver ponds. The primary physical limitation to coho salmon production in the Stillaguamish basin is the lack of North American beaver ponds or similar slow-water habitats (Pollock *et al.,* 2004).

In Minnesota, North American beaver ponds have been described as reproductive 'source' habitats for fish at the landscape scale, while adjacent stream environments act as potential 'sinks' (Schlosser, 1993; 1995a, 1995b). However, full functioning of the entire spatial and temporal mosaic of successional habitats associated with North American beaver activity, including those due to the creation and abandonment of North American beaver ponds, is required for fish populations to maximize potential benefits (Schlosser and Kallenmeyn, 2000).

2.5.1.4 Flow

Beaver dams, while forming barriers to fish movement (section 3.5.2.1), can provide benefits by stabilising river flow (Halley, 1995; Grasse and Putnam, 1955). Beaver impoundments stabilize stream flows in two ways. First, they act as reservoirs, increasing the water-holding capacity of the watershed, and reducing peaks in the hydrograph (Finnegan and Marshall, 1997). Second, the flooding of land in the vicinity of beaver colonies raises the level of the water table, while stored groundwater is slowly released back into the stream to maintain flow during periods of drought (Finnegan and Marshall, 1997).

The ponds created by beavers can be utilised as a refuge during periods of low flow (Bruner, 1990; Cook, 1940). This is particularly important in the arid regions of North America. Knudsen (1962) suggested that during severe drought North American beaver ponds may function as sanctuaries for brook trout. In Wyoming, White and Rahel (2008) found that North American beaver activity and less intensive livestock grazing reduced negative impacts of drought acting on fish populations, facilitating production of Bonneville cutthroat trout (*O. clarki utah*) in years when other nearby tributaries failed. Conversely, North American beaver activity also creates areas of slack water which can provide velocity refuges, especially for juveniles, at times of peak discharge (Taylor, 1999; NRC, 1995).

2.5.1.5 Temperature

Beaver activity alters water temperature by opening the river to sunlight and creating broad shallow pools (Cook, 1940). The influence of beaver ponds on fish populations via their effects on water temperature varies spatially. By raising water temperatures, North American beaver ponds may benefit species in areas where fish distribution or productivity is limited by low water temperatures (Baker and Hill, 2003; Gard, 1961; Grasse and Putnam, 1955; Rasmussen, 1941; Swales and Levings, 1989). Data from Oregon (USA) suggests that, for temperature limited populations, the presence of North American beaver ponds may increase survival of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) (Talabere, 2002).

In Wisconsin (USA), a study of thermal characteristics of a North American beaver impacted stream found no consistent relationship between size or number of beaver impoundments and the degree of downstream warming (McRae and Edwards, 1994). While a slight warming downstream was detected, the presence of North American beaver structures reduced fluctuations in river temperature. The removal of dams did not generally influence upstream/downstream temperature differences (McRae and Edwards, 1994). The authors argue that the direct thermal benefits of dam removal in headwater streams may be outweighed by the potentially disruptive effects on the composition of fish and invertebrate communities downstream.

2.5.1.6 Water quality

While reduced oxygen levels is frequently cited as a problem in beaver ponds (section 3.5.2.4), Halley (1995) argues that through its activities, the European beaver reduces acidity which benefits all species downstream, including salmonids.

2.5.1.7 Invertebrates

The presence of beaver dams has implications for benthic invertebrate communities (see Naiman *et al.,* 1988). A number of studies on beaver-fish interactions highlight the importance to fish of increased invertebrate production as a result of North American beaver activity (Gard, 1961; Rutherford, 1955). North American beaver activity enhances biological production (Swanston, 1991; Duncan, 1984; Sayler, 1935), resulting in a high standing crop of aquatic invertebrates (Rasmussen, 1941; Call, 1966), and increased food-web complexity (Ray *et al.,* 2004). North American beaver ponds can reduce the abundance of some invertebrate species selectively taken by brown and brook trout, although overall invertebrate productivity is often greater (Cook, 1940).

A study in Colorado (USA) estimated that unit-area production of benthic invertebrates was low in North American beaver ponds, but due to greater area of substrate, total production was more than doubled, resulting in higher fish abundance compared with non-impounded reaches (Rupp, 1954).

2.5.1.8 Growth rates

The combination of increased invertebrate productivity and elevated water temperatures within European beaver ponds is thought to enhance fish growth compared to neighbouring stream sections (Rosell and Parker, 1996). This has been validated for sockeye (*O. nerka*) and coho salmon (Murphy *et al.,* 1989; Swales and Levings, 1989), and various trout species (Cook, 1940; Hale, 1966; Knudsen, 1962; Rutherford, 1955; Shetter and Whalls, 1955; Patterson, 1951).

A study in New Brunswick found that Atlantic salmon parr recaptured from a North American beaver pond had higher growth rates than individuals sampled from above or below the pond (Sigourney *et al.,* 2006). The Atlantic salmon parr in the North American beaver pond also better maintained condition than those above and below during the summer period (Sigourney *et al.,* 2006).

2.5.1.9 Impacts on angling

A number of early papers on beaver/fish interactions concentrate on how beaver activity, especially the construction of dams and subsequent ponding, affects angling, especially for trout species. Several studies suggest that trout (eastern brook trout and cutthroat trout) fishing was improved by the presence of North American beaver (Neff, 1957; Grasse 1951). In the Colorado Rockies, Neff (1957) showed that fishing for eastern brook trout and cutthroat trout was significantly better on North American beaver occupied streams compared to those which beaver had abandoned. Further, systematic planting of aspen, a preferred food for North American beaver, was suggested to reduce the risk of beaver abandonment of a site. A small percentage of landowners in Arkansas cited the provision of fishing ponds due to North American beaver activity as a positive result of their presence in the local area (Wigley and Garner, 1987).

2.5.2 Negative impacts of beaver on fish populations

2.5.2.1 Barriers to movement

The most frequently cited negative impact of beaver activity was the creation of barriers to fish migration due to the construction of dams (Figure 4). Barriers can have a number of effects on fish populations (Table 5), including impeding spawning migrations, inhibiting colonisation of new areas, and isolating populations. The magnitude of impacts is dependent on the fish species concerned and varies with prevailing stream conditions. The magnitude of delay is not predictable; fish can be delayed at barriers that appear easily passable, or they may quickly pass barriers that appear difficult (Thorstad *et al.,* 2008). Dams, which consist of wood partially sealed with mud and vegetation, create semi-permeable barriers to both the upstream and downstream movement of fish, and permeability varies with flow (Schlosser, 1995a). Snodgrass and Meffe (1998) suggest that as dam height and the transition zone between the stream and pond increase, boundary permeability reduces.

In Brierly Brook, Nova Scotia, Canada, Taylor *et al.,* (2009) found that some North American beaver dams posed serious obstacles to upstream migrating Atlantic salmon, especially under low flows, during which salmon were seen to congregate below the dams. However, the majority of North American beaver dams in most years had no detectable effect on the distribution of spawning redds and in years of normal rainfall Atlantic salmon passed the dams easily. The impact of North American beaver dams on Atlantic salmon migration is temporally variable and as beaver dams are built, expanded and abandoned over time, the relationship between stream discharge and the success of salmon migration continually adjusts (Taylor *et al.,* 2009)

On Prince Edward Island, Canada the re-establishment and expansion of the North American beaver population has been blamed for the loss of Atlantic salmon from several river systems and the reduced abundance in other systems (Guignion, 2009). The author states alongside sedimentation that the island's Atlantic salmon population is limited by North American beaver blockages which prevent adults from reaching their spawning grounds and can also impinge on the downstream smolt movement. However the study provides little quantitative evidence to support these claims.

While the information in Table 5 paints a bleak picture of the effect of beaver dams on fish movement, many studies qualify this by pointing to the temporal and spatial variability of theses structures (Mitchell and Cunjak, 2007; Schlosser and Kallemeyn, 2000). Taylor (1999) argues that North American beaver dams are not permanent and, in the North-western United States, are usually washed out during the same freshets that Pacific salmon use to reach their spawning grounds. For some fish species the presence of North

American beaver dams appears not to hinder their movement e.g. steelhead trout (Lowry, 1993), or dams can be overcome with sufficient water levels e.g. cutthroat trout and rainbow trout (Grasse 1951). In the Numedalslågen catchment, Norway, Parker and Ronning (2007) suggest due to the low frequency, small size and apparent short lifetime that European beaver dams will have a negligible effect on the upstream and downstream migrations of Atlantic salmon and sea trout.

Table 5 The impacts of beaver dams on fish

Species	Effect of beaver dams	Reference
Atlantic salmon	Limit spawning distribution	Cunjak and Therrein, 1998; Cunjak *et al.*, 1998; Mitchell and Cunjak, 2007
Atlantic salmon	Some North American beaver dams pose serious obstacles to migrating salmon, especially when discharge is low	Taylor *et al.,* 2009
Atlantic salmon, brook trout	Partial to complete blockage	Scruton *et al.,* 1998
Atlantic salmon, brook trout, alewife	Prevent both upstream migrants from reaching spawning grounds also impacts seaward movements for some species	Guignion, 2009
Atlantic salmon, sea trout	Obstruct upstream and downstream migration	Parker and Ronning, 2007
Bull trout	Blocked or delayed downstream movements	Dupont *et al.,* 2007
Brook trout	Dam removal leads to range expansion but not abundance increase	Avery, 1991
Brook trout	Fall spawners blocked from reaching spawning grounds	Hale, 1966; Patterson, 1951; Doucett *et al.,* 1999; Grasse, 1951
Brook trout	Dam impede upstream and downstream migration, but not totally impassable.	Rupp, 1954
Brown trout	Impact ability to colonize new areas	Bertolo *et al.,* 2008
Brown trout	Block downstream movement	Tambets *et al.,* 2005
Brown trout, minnow, bullhead, burbot, pike	Barriers to colonisation and migration, especially for slow dispersing species	Hägglund and Sjöberg, 1999
Coho salmon	Dams (one = 2 m height), did not block migration. Movement facilitated by fall freshets.	Bryant, 1984
Coho salmon, steelhead trout	Impact ability to colonize new areas	Murphy *et al.,* 1989
Cutthroat trout, rainbow trout	Fish usually pass due to high spring flows	Grasse, 1951
Lahontan cutthroat trout	Seasonal blockage of at least upstream movement	Talabere, 2002
Lake whitefish, walleye	Reduce access to spawning grounds	Bertolo and Magnan, 2006
Northern pike, walleye	Block spawning runs	Knudsen, 1962; Patterson, 1951
Oregon chub	Population isolation	Scheerer *et al.,* 2004
Roach, sticklebacks, brook lamprey	Total barrier to movement	Elmeros *et al.,* 2003
Salish suckers	Species rarely crossed North American beaver dams	Pearson and Healey, 2003
Sea trout	Partially block spawning run	Elmeros *et al.,* 2003
Steelhead trout	Fish appeared able to cross barriers	Lowry, 1993
Steelhead trout, rainbow trout	Upper extent of distribution fluctuates with occurrence of dams	Andonaegui, 2000
Trout sp.	Adults unable to return downstream after spawning	Rasmussen, 1941
Trout sp.	Block spawning runs or upstream migration	Grasse, 1979; Cook, 1940; Knudsen, 1962; Bradt, 1935; Sayler, 1935

Figure 4 Beaver dams can impede the movement of fish due to the physical impediment created (a) and/or dewatering of the downstream channel (b) (photograph a and b provided by P. Kemp; photograph c provided by M. Gaywood).

(a) North American beaver dam in Glacier National Park (USA)

(b) North American beaver dam on backwater channel of the Columbia River (USA)

(c) European beaver dam, Telemark (Norway)

2.5.2.2 Loss of spawning habitat

After barriers to migration/movement, the loss of spawning habitat due to the siltation of spawning gravels is the most commonly cited negative impact of beaver activity. Behind North American beaver dams, spawning areas are covered with deep, slow flowing water where fine sediment is deposited (Swanston, 1991). The impact of siltation is particularly problematic for salmonids due to their need for clean spawning gravels (Cook, 1940; Gard, 1961; Knudsen, 1962; Rasmussen, 1941; Sayler, 1935; Patterson, 1951). In the Californian Sierras, North American beaver dams led to the deposition of silt on native golden trout (*Salmo irideus*) spawning gravels. It is suggested that as a result, brown and rainbow trout displaced the species (Müller-Schwarze and Sun, 2003). In Brierly Brook (Nova Scotia), redds were typically not found between 100 – 300m upstream of North American beaver dams because spawning habitat quality tends to be poor in the impounded reach (Taylor, 2009).

2.5.2.3 Temperature

An increase in water temperature due to the reduction of canopy can prove detrimental to fish in areas where temperatures reach values close to the upper limit of thermal tolerance for the species (Swanston, 1991). The problem is particularly acute during summer months (NRC, 1995; Guignion, 2009), and can affect fish downstream of dams in addition to those frequenting North American beaver impoundments (Shetter and Whalls, 1955). Baker and Hill (2003) suggest that populations of trout species in eastern United States are limited by high water temperature, and that North American beaver activity may increase temperatures beyond tolerable limits. Conversely, it has been suggested that spawning of brown and brook trout in Michigan was negatively affected by North American beaver activity as temperatures were lowered below the spawning threshold of the two species, due to greater exposure to the air (Sayler, 1935).

2.5.2.4 Water quality

North American beaver activity can have a detrimental effect on water quality within and below impoundments (Rupp, 1954), with reduction in dissolved oxygen most often cited (Bryant, 1984; Call, 1966; Cook, 1940; Dolloff, 1987; NRC, 1995; Guignion, 2009). Bertolo *et al.* (2008) suggest that the impact of North American beaver in Ontario might create transient anoxic conditions for brook trout. Schlosser and Kallenmeyn (2000) sampled upland and lowland, and partially rebuilt North American beaver ponds in Minnesota during the winter. Their results indicated virtually all were hypoxic, with oxygen concentrations throughout the water column being <0.4 mg l^{-1}. In addition to affecting the oxygen budget of the stream, Sayler (1935) suggests that acidity of the water increases with age of North American beaver dams to the extent that pH can be reduced to below the tolerance of brown and brook trout. In two North American beaver ponds in Ontario, pumpkinseed (*Lepomis gibbosus*) populations fluctuated drastically as a result of winter mortality (winter kills) from hypoxia and a decline in water level (Fox and Keast, 1990). These winter kills eliminated as many as 96% of the older pumpkinseeds and resulted in populations consisting mainly of individuals aged 0–2 (Fox and Keast, 1990).

2.5.2.5 Habitat quality

Rutherford (1955) argued that recently constructed North American beaver impoundments provide food and cover conducive to greater numbers of brook trout than neighboring streams sections, but older ponds tend to produce poor conditions due to habitat deterioration over time. Rohde and Arndt, (1991) cited habitat deterioration due to the activities of humans and the successful reintroduction of North American beavers to North and South Carolina as one of the main reasons behind the contraction in range of the sandhills chub (*Semotilus lumbee*) and pinewoods darter (*Etheostoma mariae*).

2.5.2.6 Flow regime

Beaver dams create pool habitat that provide refuge for fish during periods of low flow (Section 3.5.1.4). However, dewatering of the stream section downstream of dams has been suggested to pose a problem for juvenile salmonids (Bryant, 1984). The change in flow regime from a lotic to a more lentic system has proved negative for certain species such as the sandhills chub and pinewoods darter (Rohde and Arndt, 1991).

2.5.2.7 Loss of cover

While beaver activity can enhance the density of instream cover, there is likely a corresponding negative effect in terms of loss of riparian shade. As discussed, a loss of canopy can cause an increase in temperature that negatively affects brown and brook trout (Knudsen, 1962; Sayler, 1935; Guignion, 2009). Parker and Ronning (2007) suggest that while barriers may only affect a minor length of stream within a catchment, a reduction in shade due to tree felling may occur over much longer reaches.

2.5.2.8 Growth

Although beaver ponds often provide conditions for enhanced fish growth (high temperatures and density of prey) compared with non-impounded reaches, Rabe (1970) found that brook trout in North American beaver ponds in Colorado were present at such a high density that individuals tended to be stunted.

2.5.2.9 Abandonment of beaver settlements

As a component of a dynamic fluvial system, beaver ponds create a temporally successional habitat pattern. The effects of the collapse of a North American beaver dam on the surrounding ecology was studied by Stock and Schlosser (1991). They found that distance from a North American beaver pond has a profound effect on the riverine community. Following the collapse, there was a short term influx of lentic fish species raising species richness. This was followed by a reduction in species richness and abundance to levels lower than prior to the collapse. The collapse also severely impacted benthic invertebrates with a dramatic (>90%) decrease in density (Stock and Schlosser, 1991).

2.5.3 European beaver studies

The meta-analysis highlighted eight studies that specifically examined the effect of European beaver on fish populations, three of which provided limited information. The first, a study of two brooks in the Spessart mountains in Hesse, Germany, suggested that higher invertebrate abundance as a result of a European beaver reintroduction would benefit fish by providing more food (Harthun, 1999). The second involved a study of habitat availability for pearl mussels (*Margaritifera margaritifera*) in Latvia (Rudzite, 1995). It was claimed that European beavers had destroyed the habitat for pearl mussels (and Atlantic salmon) by creating impounded reaches of still, warm water, with elevated nitrogen concentrations. In the third, Halley (1995) responded to concerns raised by Lever (1994) regarding the effect of European beaver reintroduction on Atlantic salmon fisheries in Britain. Halley (1995) suggests that the European beaver population in Norway, which has expanded from c. 100 individuals in 1900 to over 50,000 in 1995, has had a mildly beneficial effect on Norwegian Atlantic salmon stocks as European beaver help stabilise flow regimes, and reduce silt loads and acidity.

The remaining five studies consider the effects of a reintroduction or range expansion of European beaver in much greater detail. The results of these studies are summarized below.

2.5.3.1 Klosterheden State Forest District, Denmark (Elmeros et al., 2003)

In 1999, 18 European beavers were released to the Klosterheden State Forest District as a trial reintroduction (note that trial reintroductions are less common than “full” reintroductions). By 2003 the number had risen to 51 individuals and European beaver inhabited the entire release catchment and had dispersed to a neighbouring river catchment 25-30 km away. Studies of the effect of the reintroduced European beaver on fish populations, spawning grounds, and the ability of fish to negotiate beaver dams were conducted between 1999 and 2003. European beaver presence was not considered to have had a negative impact on the spawning habitat of brown and sea trout. However, restriction of the spawning migration of the sea trout was considered to be an issue. Most dams constructed were on streams less than 2 m in width. Dams were thought to be complete barriers to roach (*Rutilus rutilus*), stickleback (*Gasterosteus aculeatus*) and brook lamprey (*Lampetra planeri*), with sea trout only able to pass them during periods of high flow. Only eels (*Anguilla anguilla*) were thought to be unaffected. It was suggested however, that small bypasses, formed around some dams, may have enabled small fish to move upstream. The authors suggested that European beaver will not have a negative effect on eel or brook lamprey, and will benefit roach and stickleback populations when new ponds develop.

2.5.3.2 Boreal Forest, central Sweden (Hägglund and Sjöberg, 1999)

In Sweden, reintroduced European beaver populations have reached high densities. Studies of the fish fauna in seven small to moderate sized streams showed brown trout were more numerous in the unaffected reference section, compared to sections with European beaver activity, while for minnow (*Phoxinus phoxinus*) the pattern was reversed. However, brown trout caught in European beaver ponds were larger than those from riffle sections. The authors argue that European beaver ponds provided important spawning and rearing habitat for minnow fry, leading to increased density in the nearby riffles. Ponds also provided refuge for large brown trout during low flow periods. The only negative impact discussed was that dams act as barriers to colonisation and migration, especially for slow dispersing species such as bullhead (*Cottus gobio*).

2.5.3.3 Litlelva stream, North Trondelag, Norway (Halley and Lamberg, 2001)

The impact of European beaver dam construction on Atlantic salmon, sea trout and brown trout on the Litlelva River was assessed. European beaver had recolonised the area in the 1990s and over a stretch of c.600 m had constructed four dams ranging from 0.5 m to 1.6 m in height. The authors estimate that dam construction had led to the loss of approximately 1600 m² of spawning habitat due to the siltation of gravels. Juvenile 0+ and 1+ Atlantic salmon and trout were found above the dams, confirming that salmon at least are capable of upstream passage through the dams (juvenile trout may be from the resident population). The authors suggest that while the hypothesis that European beaver dams have had no impact on Atlantic salmon and brown/sea trout cannot be supported, neither can the view that anadromous fish are unable to negotiate beaver dams.

2.5.3.4 Numedalslågen river catchment, Norway (Parker and Ronning, 2007)

European beaver recolonised the Numedalslågen catchment in 1957, a river that maintains populations of Atlantic salmon and sea trout. Within the Numedalslågen catchment most salmon spawn in the main river, while sea trout tend to spawn in tributary streams. European beaver and Atlantic salmon habitat was found to overlap for 15% of the tributary stream length. European beavers constructed five dams (all less than 0.5 m high) on the tributary streams which had the potential to stop Atlantic salmon and sea trout from reaching 3% and 18% of their spawning habitat respectively. While barriers affected only a minor length of stream within the catchment, reduction of shade due to tree felling occurred over much longer reaches. The increase in lentic habitat is thought to be of greatest benefit to sea trout due to their reliance on pools. The authors argue that while the presence of European beavers can obstruct both the upstream and downstream migration of Atlantic salmon and sea trout, negative impacts will be negligible due to the low frequency, small size, and short lifetime of dams. Atlantic salmon reproduction in the catchment appeared to be unconstrained by European beaver. In Norway, there has been a simultaneous increase in European beaver population size and sea trout and Atlantic salmon catches over a 40 year period.

2.5.3.5 Esna River, Estonia (Tambets et al., 2005)

A study assessing the effects of drought during the period 2002–2003 on the River Esna indicated that European beaver dams provided a major impediment to downstream fish migration. With the exception of nine-spined stickleback (*Pungitius pungitius*), fish stranded in the small ponds upstream of the European beaver dams did not survive. In 2004, flows were higher and the restoration of fish fauna occurred up to the first downstream large European beaver dam. The dam proved to be a major obstacle to species recolonising the river. In sections upstream of the European beaver dams, no brown trout or other species except nine-spined stickleback were caught.

2.6 Discussion

The meta-analysis indicates a regional bias in research on beaver-fish interactions. A greater number of studies (90%) have examined the effects of North American beaver on fish populations than for European beaver (8%). While the two species exhibit many ecological and biological similarities, certain aspects of their life history diverge and consequently the effects on stream ecology and fish communities may differ (Parker and Ronning, 2007). For example, evidence provided by the EOS indicates European beaver dams tend to be smaller than those constructed by North American beaver (see Appendix 2).

The relative paucity of studies relating to European beaver was expected as this species was extirpated from many countries, and has only been reintroduced to some relatively recently. Thus, opportunities to investigate the impact of beavers on fish from a European perspective have been available in many countries only over recent years. Further, as is common to reintroductions in general, robust monitoring post release is often lacking. Any information that is available on the effects of the re-established species on the recipient ecosystem tend to be found in the grey literature, and not published in peer reviewed articles and is thus often unavailable to a wider audience. Historically, there has been a tendency for reintroduction research to be fragmented and *ad hoc*, rather than an organized attempt to gain the knowledge needed to improve probability of success (Seddon *et al*., 2007).

The majority of the studies focus on salmonids, which is unsurprising due to their economic importance. A number of these consider Atlantic salmon and brown/sea trout, the two salmonids of particular interest from the perspective of a reintroduction of European beaver to Scotland.

The majority of studies consider both positive and negative impacts. European beaver dams have been demonstrated to impede the movement of brown and sea trout in Estonia (Tambets *et al.,* 2005), Sweden (Hägglund and Sjöberg, 1999), and Denmark (Elmerous *et al.,* 2003). These barriers do not totally block fish movement, and dams tend to be temporary, small in size, and unlikely to have significant impacts on the Atlantic salmon and sea trout populations (Parker and Ronning, 2007). Indeed, a number of studies suggest beaver activity corresponds with an increase in brown trout productivity (Hale, 1966; Müller-Schwarze and Sun, 2003; Gard and Seegrist 1972; Gard, 1961). Parker and Ronning (2007) suggest that sea trout will benefit from the increase in lentic habitat associated with European beaver activity, while Young (1995) suggests brown trout may select habitat created by North American beavers.

As is the case in the absence of beaver, Atlantic salmon productivity in beaver affected landscapes varies spatially. Beaver activity can reduce fish productivity by limiting access to spawning areas; the impediment to migration is considered the most significant negative impact (Cunjak and Therrein, 1998; Cunjak *et al.,* 1998; Mitchell and Cunjak, 2007; Scruton *et al.,* 1998; Parker and Ronning, 2007). Conversely, Scruton *et al.* (1998) suggest that in Newfoundland (Canada), increased rearing habitat as a result of North American beaver activity has led to a dramatic increase in biomass of larger juvenile Atlantic salmon. Sigourney *et al.* (2006) found fish recaptured in North American beaver ponds exhibited greater summer growth rates and displayed higher condition than fish recaptured immediately above or below.

The creation of a heterogeneous fluvial habitat is frequently cited as a positive impact of beaver activity. This will, however, benefit some species more than others. In the Pacific Northwest of the United States, the importance of North American beaver ponds as salmonid rearing and overwintering areas has been highlighted; impounded reaches often provide greater cover than neighbouring stream sections.

A number of fish species respond positively to the presence of beaver, resulting in increased growth, and ultimately productivity. The results of the meta-analysis indicated that for 34 species productivity increased in 28 cases due to beaver activity (Table 5), while it decreased for four species and showed both increases and decreases in the other two. The increase in abundance and size has been attributed to increased invertebrate productivity in beaver ponds coupled with raised water temperatures. However, several authors caution that this relationship applies only to cold water areas; in arid environments the temperature can increase above the thermal tolerance limit of some species (Hale, 1966; Collen and Gibson, 2001).

A key benefit to fish of beaver presence is the influence on flow regime. Under both high and low flows, beaver activity can create habitat to the benefit of fish. During low flows beaver created habitat may provide some of the only remaining wetted areas in a channel. During high discharge, beaver structures can create areas of slack water that provide flow refuge for aquatic biota, including fish; this is particularly important in heavily engineered rivers where suitable shelter is often lacking.

Despite positive aspects, critics of a European beaver reintroduction to Scotland highlight several negative impacts of beaver on fish populations. The impact of beaver dams on fish passage is the most frequently cited of these (Table 5). The second most commonly cited impact is the beaver's effect on river habitat, primarily the loss of important spawning areas due to siltation. Further, the change from a lotic to a lentic habitat, while favouring some species, can be detrimental to others. The meta-analysis highlights nine instances when productivity was reduced in the presence of beaver dams. Beaver activity can also reduce shading of the channel as trees are cut down for the construction of lodges and dams. In some cases this can lead to a warming of the water to above the thermal tolerance of some species.

The meta-analysis suggests that overall the impacts of beavers on fish populations can be positive, but locally variable. The number of positive impacts within the literature assessed was 157 compared to 102 that were negative. It is important to understand that the effects of beavers vary both temporally and spatially. The impact on habitat, temperature, flow regime, and water quality has been found to be both positive and negative. The effect of beavers on specific species also varies greatly, with some studies illustrating negative and others positive consequences for Atlantic salmon.

It is important, however, to take account of the regional bias to North America for information related to the impacts of beaver on fish species. It is unclear to what extent the conclusions of these studies can be translated to a Scottish context. European beavers have smaller litters and construct fewer dams than the North American species (Danilov and Kan'shiev, 1982 in Collen and Gibson, 2001), therefore, the impact on fish migration may be lower.

European studies illustrate both positive and negative effects of expanding/reintroduced European beaver populations. Tambets *et al.* (2005) credits the loss of many species and the subsequent inability to recolonise areas following a drought to the presence of European beaver. In Norway, Parker and Ronning (2007) argue that from a fisheries management perspective, European beaver activity might improve salmonid productivity and that the benefits may outweigh the costs. Elmeros *et al.* (2003) highlight the restriction of the sea trout population as the major impact of reintroduced European beaver to Denmark, but suggest other species may benefit from their presence.

Overall, it appears that the activities of both species of beaver can enhance or negatively impact fish populations. The literature gathered for this review provided more information about positive effects than negative effects. The reintroduction of European beaver to Scotland should be considered in the light of the full suite of ecological, social, and economic factors against which objectives have been set.

3 THE IMPACT OF IN-CHANNEL WOODY STRUCTURE ON FISH

3.1 Introduction

The result of beaver activity can be thought of as an extension of the range of woody structure that occurs widely and naturally in freshwater ecosystems (Gurnell *et al.*, 2009). The physical and biological effects of naturally occurring debris dams can be considered to have many similarities and relevant data might therefore be translated to predict the effects of beaver dams.

There are several comprehensive reviews dealing with wood in rivers (e.g. Bisson *et al.,* 1987; Maser and Sedell, 1994; Bryant and Sedell, 1995; Gurnell *et al.,* 1995; Gregory *et al.,* 2003) most of which refer to aquatic ecology or aquatic habitats either in the title or in the text. Despite this, the number of publications in the open literature which include biological data of direct relevance to the role of wood in streams and rivers is relatively small (Gurnell *et al.,* 1995; Gregory *et al.,* 2003). Coarse woody debris (CWD) has, however, been recorded or measured as a habitat variable in many studies particularly in relation to salmonids (Gorman and Karr, 1978; Binns and Eiserman, 1979; Heggenes, 1988; Martin-Smith 1998).

The following section discusses the generic influence that woody structure and debris dams have on populations of fish in an attempt to gain further insight on potential impacts of beaver dams.

3.2 Woody debris

A physically diverse habitat is necessary for the maintenance of community diversity. The management of species diversity or populations will depend on the localised variability in hydraulic conditions and consequent sedimentation, in addition to the structural diversity of the channel. In streams and small rivers, this can be determined by channel configuration and structure, which in turn is determined by flow and in-channel physical structures such as boulders, rocks, tree-root matrices and large pieces of timber debris (such as CWD) (e.g. Hawkins *et al.,* 1993)

There is a general perception that, prior to human interference, natural streams and rivers would have contained large amounts of natural woody debris, from leaves and twigs to whole uprooted trees. Clearance of this wood for drainage, navigation, log-transport and hydro-electric power clearly changes the hydrology, geomorphology and ecology of the affected watercourses (see Gregory *et al.,* 2003). Further, streams undisturbed by human influence would also contain beaver dams in many regions of the world. The palaeoecology of these undisturbed streams is not well known and it is impossible to determine if they contained the same densities of salmonids and other fishes as at present. Indeed, if natural wood accumulation was considerably greater than it is in today's managed systems, it is possible that natural salmonid populations in some systems may have been smaller because of limitations on the extent of spawning riffles.

The process of clearing wood in European rivers is not as well documented as it is for the United States. Bryant and Sedell (1995) and Harmon *et al.* (1986) cite examples of the use of European and Middle Eastern rivers which led to the clearance of timber debris from the channels. In Europe, the navigation of major and minor river channels increased with the dawn of the industrial revolution and rivers such as the Rhine, Danube, Volga, and their tributaries would have experienced the clearance of timber debris, as seen more recently in the rivers of North America. Today, ancient riparian forests are rare in Europe, and almost entirely absent from the lowlands. The remains of lignicolous aquatic invertebrates in ancient timber unearthed from the River Rhine (Amoros and Van Urk, 1989) are some indication of the long-term occurrence of woody debris in the river prior to clearance. Lignicolous Diptera still forms an important component of stream faunas in other less managed parts of the world (Armitage *et al.,* 1995).

In the UK, the clearance of forests in the major river catchments occurred mainly between 5000 BC and 1000 AD (Wiltshire and Moore, 1983). However, even though rivers and small streams had been used for navigation and fishing for many centuries, it is unlikely that much clearance of wood debris occurred until more commercial navigation began and water mills increased the need for clear channels and the channelization of anastomosed streams. Most of the rivers in the UK are today relatively free of woody debris accumulations, particularly where drainage or navigational operations are a priority. Riparian vegetation is also scarce along many river channels, such as those in the Fenlands and drained marshes where access for machinery is needed. The few stream systems with significant amounts of timber debris are mostly in upland areas, or the few remaining lowland forests such as the New Forest (Langford, 1996) and the Forest of Dean. In the past decade, wooden structures, simulating CWD matrices have been used as components of river channel modifications ostensibly to enhance both invertebrate and fish populations (e.g. de Jalon, 1995; Cowx and Welcomme, 1998).

In the UK, timber debris accumulates in many reaches of New Forest rivers, forming as debris dams of various sizes and configurations (Gurnell and Gregory, 1984; Gregory and Davis, 1992). These dams, usually composed of tree trunks and large branches augmented by smaller sections of wood, can have significant effects on channel processes including sedimentation, the travel times of flood peaks, and channel migration (Gurnell and Gregory, 1984; Gregory *et al.,* 1985; Gregory *et al.*, 1994). The impoundment of water by such dams is also reputed to have adverse effects on the drainage of forest lawns and plantations, and hence on the grazing of livestock and the survival of trees. Furthermore, anglers believe that the migration of sea trout to their spawning reaches is impeded by the dams (Anon, 1992) though there are no scientific data to support or refute these suggestions.

It can be expected that the physical, chemical, and biological effects of beaver dams will parallel those of both natural and introduced woody debris dams.

3.3 Effects of woody debris

Apart from its role in river and floodplain processes, CWD provides a physical resource at various levels and scales in aquatic ecosystems including surface structures for colonisation by bacteria and fungi (see Langford, 1983, 1990), algae (e.g. Shamsudin and Sleigh, 1994), and invertebrates (Cudney and Wallace, 1980; Smock *et al.,* 1985; Chergui and Pattee, 1991; Langford, 1996), physical refugia for invertebrates and fish (e.g. Angermeier and Karr, 1984; Fausch and Northcote, 1992; Harvey *et al.,* 1999), direct food resources for micro-organisms and invertebrates (e.g. Triska and Cromack, 1980; Dudley and Anderson, 1987; Shearer and Webster, 1991; Armitage *et al.,* 1995), and an indirect food resource for fish, preying on colonising or sheltering invertebrates or other fish (e.g. Benke *et al.,* 1985; Smock *et al.,* 1989). Woody debris dams can also be a major influence on the temporary inundation of the by promoting overbank flow (Gurnell *et al.,* 1995). These wet margins of streams harbour both plants and animals that are dependent on regular and frequent inundation and the deposition of dead plant material and sediment.

3.3.1 Organic sediment and micro-organisms

Reach and sub-reach scale studies show considerable variation in the relative density (in proportion to area of stream bed) of CWD and related accumulation of finer sediment and associated organisms between streams and rivers of differing order. For example, Anderson and Sedell (1979) noted that 25% of the area of the bed in some small streams was covered by woody structure, with another 35% represented by the organic deposits that are deposited upstream of the wood. However, in larger streams, the wood or wood-created habitat fell to approximately 12% of the bed area. Bilby and Likens (1980) also showed that debris dams contained 75% of the standing stock of organic matter in the first order streams of the Hubbard Brook system in the United States, this was reduced to 58% and 20% in second and third order streams respectively (Bilby and Likens, 1980).

Coarse woody debris was also reported to be a major factor in the deposition of fine particulate organic matter (FPOM) in some Oregon streams (Ward and Aumen, 1986); conservative estimates indicated a contribution of 90 g m^{-2}. However, the authors suggested that the real figure could be several times that contributed by leaves and pine needles.

Aumen *et al.* (1990), using in-situ manipulations, showed that CWD did not affect dissolved nutrient retention directly in streams. Both CWD and cobbles adsorbed nitrates and phosphates more readily than finer substrates under experimental conditions but the low densities of CWD did not affect the total adsorption significantly.

3.3.2 Macro-invertebrates

In Oregon, 40 invertebrate taxa have been shown to be associated with in-stream woody debris (Anderson and Sedell, 1979). Woody debris is a direct food resource for invertebrates, including many aquatic xylophagous invertebrates recorded in the United States, such as the midges, chironomids, other diptera, elmid beetles, caddisfly larvae, and craneflies, which colonise or use wood in its various stages of decay. There is typically a low standing crop and species richness of insects on woody debris compared with leaves and trailing vegetation at stream margins (e.g. Cudney and Wallace, 1980).

3.3.3 Fish

The relationship between fish abundance and that of CWD varies considerably with stream type and species. Many of the studies dealt only with accumulations of CWD, not necessarily formed into dams causing full impoundment. Most of the studies of salmonid habitats and CWD have been at the reach and sub-reach scale and conducted in the Pacific Northwest of the United States. Beechie and Sibley (1997) aimed to identify relationships between the abundance of woody debris and areas of spawning gravel for salmonids, although they found no correlation for the streams they studied. In contrast, Sedell *et al.,* (1984) noted that CWD created "high quality salmonid spawning" by stabilising channel substrate, notably gravel bars and marginal rearing habitats on bends. Side channels formed and protected by CWD had eight times more juvenile coho salmon than side channels without CWD. The CWD at the upstream end of side channels protected the habitat from scouring and spates, though boulders were as effective as CWD in this function. Most juvenile salmonids preferred side-channel habitat which accounted for only 6% of total habitat availability, but 75% of utilisation in one stream, and 25% and 55% in another (Sedell *et al.,* 1982, 1984). Bryant and Sedell (1995) concluded that refuge is probably more important than food where CWD is concerned in natural streams.

Bryant (1985) also showed similar results in Alaskan streams. The densities of 1+ salmonids increased from 0.09 m^{-2} (range 0.00 m^{-2} - 0.10 m^{-2}) where there was no wood, to 0.65 m^{-2} (0.07 m^{-2} – 1.41 m^{-2}) where stream channels contained more than 10 pieces of CWD in a reach. Woody debris habitat in other streams also showed the same pattern, with the main stream containing few salmonids, but the side channels containing large numbers (Bryant and Sedell, 1995).

Coarse woody debris provides seasonally important refugia for salmonids at the mesohabitat and microhabitat scale and is an important refuge at high discharge (Bisson *et al.,* 1987).

Murphy *et al.* (1986) showed that the density of juvenile coho rose by a factor of 10, from less than 0.02 m^{-2} to almost 0.25 m^{-2}, as CWD abundance rose from 0 – 4 to ≥100 m^3 per reach. Murphy *et al.* (1986) in their study on the effects of logging on reaches of forested streams showed that CWD volumes were greater in streams bordered by buffer strips than in those bordered by either old growth or clear cut woodland. Coho salmon fry had the greatest density in the buffered and clearcut streams, in both the summer and winter. Coho salmon and Dolly Varden parr (1+) were densest where CWD was most abundant in the streams with buffer strip, but brown trout parr were generally less abundant in the higher wood densities. Cover, either as CWD or other categories (roots, undercut banks etc.), was considered more important for fish in the winter than in the summer. In summer, food abundance was considered to override the need for shelter from predators.

Hortle and Lake (1983) found that abundance, biomass and species richness of fish were significantly correlated with the number of CWD pieces (snags) and areas of slack water in the Bunyip River in Australia. Channelised sites contained fewer fish, fewer species and a lower biomass than the non-channelised reaches. The absence of habitat diversity was believed to be the reason for the poor fish fauna in channelised reaches. Eels (*Anguilla australis*) and brown trout showed the strongest correlations with CWD.

In Brierly Brook (Nova Scotia) as part of a restoration programme the addition of large woody debris caused the channel to narrow, pools to be scoured, and banks to be undercut. This resulted in increased availability of spawning gravels that was ultimately translated into higher densities of fry and parr in the restored reaches (Floyd *et al.,* 2008)

In small streams in the New Forest, 1+ Atlantic salmon and brown trout, and eels were in higher densities within debris dam matrices than in pools without woody material. It was concluded that salmonids were using the wood matrix or deeper water as refugia.

3.3.4 Fish passage

At the reach scale and above, debris dams cause biological changes in the stream as they form obstacles, steps or waterfalls (Bilby, 1981). In such situations they may impede migrating invertebrates or fish as well as act as retention structures for sediment and organic material. The blocking of migration can occur at very low flows and with very dense wood jams (Bisson *et al.,* 1987), but as flows increase the accumulations of CWD become passable. The migrations of smaller fish may be hindered, but usually dams are in a matrix form with sufficient space between individual pieces to allow free passage. Although these dams are localised phenomena, serious blockage of migratory species could affect distribution at a catchment scale.

Cowx and Welcomme (1998) note that a relatively small obstruction in a stream, with a height of only 40 cm restricted the species richness of the fish community upstream to one compared with eight species downstream by destroying free movement. Turnpenny *et al.* (1988) also indicated that a 5 m waterfall prevented brown trout migrating upstream. Clearly, when considering only migratory species, physical habitat diversity at reach or sub-reach level is of little consequence to fish populations above impassable obstacles, but can be of considerable significance for non-migratory species.

3.3.5 Flow regime

Gregory *et al.* (1985) showed that woody debris dams, with an average density of one per 27m of channel in the Highland Water, New Forest extended the travel times of flood peaks and affected the channel processes in the vicinity of the dams. Over a distance of 4028 m, the presence of some 93 dams causing varying degrees of impedance, delayed the smaller flood peaks by some 100 minutes and the larger flood peaks by about 10 minutes when compared with unimpeded travel.

The removal of timber debris increases current velocities, and the movement of sediment along a stream channel; concurrently the amount and duration of sediment stored decreases, while localised bank erosion increases, and the sequence of pools and riffles becomes less clearly defined (Beschta, 1979; Gregory, 1992).

3.4 Woody debris and cover for fish

The measurement of "cover" or refugia for fish is one of the inconsistencies of habitat analysis, though there have been some attempts to standardise the methods. Coarse woody debris is one of the major categories of cover in most studies but methods of assessing its abundance vary widely (Heggenes, 1988). The definition of cover frequently used is "structures which obscure areas of the stream bed from overhead vision". This usually assumes that protection from predation is the main function of cover. However, for territorial species such as salmonids, objects in the stream can reduce visual contact between conspecifics and thus reduce the probability of aggressive territorial behaviour (Bisson *et al.,* 1982). Cover in two or three dimensions can provide refugia, from which predators can forage. Cover from the adverse effects of flow is also an important component of instream physical structure.

Cover usually implies some physical structure such as overhanging or undercut banks, tree-roots, in-stream vegetation, trailing marginal vegetation, rocks, or woody or other debris (Binns and Eiserman, 1979). It can also include turbulent water (Binns and Eiserman, 1979; Heggenes, 1988; Heggenes and Saltveit, 1990), though this category is by no means universally used (e.g. Heggenes, 1988; Williams *et al.,* 1996; Inoue and Nakano, 1998). The measurement of cover has varied from visual estimates of areas of bed obscured (e.g. Heggenes and Saltveit, 1990; Fausch and Northcote, 1992; Williams *et al.,* 1996; Harvey *et al.,* 1999) to measurements of undercuts, overhangs, tree-root matrices and CWD by width and length (Murphy *et al.,* 1986; Nielsen, 1986; Inoue *et al.,* 1997) to detailed mapping (Lewis, 1969; Hunt, 1976; Moore and Gregory, 1988) and planimetry (Elser, 1968). It is commonly presented as percentage cover of the bed area or bank length or as an absolute value of area (see Milner *et al.,* 1985; Heggenes, 1988).

By definition, "cover" also implies some physical space or refuge in which a fish of a given size may reside either permanently or temporarily. The relevant size of any area of cover is, thus, related to the size of the fish. As most habitat studies relate to salmonids and usually larger salmonids (Binns and Eiserman, 1979; Milner *et al.,* 1985; Heggenes 1988), the definitions of cover have often been restricted to those which will suit individuals over one year old. More recently, studies in the UK have concentrated on other species and given varying definitions of both instream and riparian cover (e.g. Copp, 1990; Ibbotson *et al.,* 1994; Copp and Bennetts, 1996; Prenda *et al.,* 1997; Watkins *et al.,* 1997; Garner *et al.,* 1998).

For CWD accumulations to provide "physical cover" for any given individual, the component pieces of the accumulation must be arranged to provide water-filled spaces. Thus, the actual volume of wood in any accumulation may not be as important in determining the available refugia as the space to wood ratio. It is likely, therefore, that any studies simply using total volumes or biomass of wood, in relation to fish biomass or density, may be based on an incorrect premise. A classification of wood matrices based on the space/wood ratio would, therefore, be preferable.

3.5 Case study: The New Forest (UK)

The New Forest is one of the few remaining areas, especially in lowland Britain, where river channels are influenced by inputs of CWD. A detailed survey of the Lymington River basin (Gregory *et al.,* 1993) covering 110.4 km^2, found a total of 754 debris dams which generally decreased in frequency with distance downstream from the source of feeder streams, though the peak occurrences were in reaches between 3 and 10 km downstream. The loading (standing stock per unit area of stream bed) of wood in the streams followed a similar pattern. The number of dams and the total loading of wood also varied with land use in the catchments, with deciduous forest being the greatest contributor of tree debris. Measured loading, which included only timber actually in the stream and impeding flow, ranged from 0.03 kg m^{-2} to 2.49 kg m^{-2}. The authors estimated that the net timber loadings were only 7% of those which could occur if the streams were not managed and the timber was not cleared.

Differences between CWD loadings in the various streams of the New Forest are marked and could be considered to affect the stream habitat and consequently the various stream ecosytems. For example, in the Highland Water, Bratley Water, and Bagshot Gutter, dominantly wooded catchments, the average numbers of dams per 500 m were 4.99, 5.44 and 11.84 respectively. Net timber loadings were 0.59, 0.43 and 2.49 kg m^{-2} respectively. In contrast, in the Ober Water catchment, with a large proportion of open canopy, there were 2.49 dams per 500 m with a net loading of 0.11 kg m^{-2}. These differences have considerable implications for the fish communities.

3.6 Conclusions

There are a number of clear conclusions from the studies. Debris dams obstruct and impound streams, although these can be permeable to varying extents. The extent of impoundment can be seasonally variable, mainly as a result of leaves, twigs and branches which clog the interstices in the wood matrices during autumn and early winter.

Impoundment extends pool reaches and results in slower, deeper water upstream of the dam, inundating faster, shallower runs and riffles. Conversely, the erosion and scouring of substrates from beneath debris dams can create new riffles areas.

A reduction in water velocity causes suspended solids to be deposited upstream of debris dams resulting in inundation of the substrate with fines to the detriment of spawning salmonids, bullheads, lampreys, stone loach (*Barbatula barbatula*), minnows and any other species requiring well-oxygenated gravels. However, the storage of sediments in impounded reaches may improve the quality of gravels for spawning in reaches downstream of dams.

The increase in pools provides more habitat for lentic and generalist species of fish and invertebrates but less for the rheophilic species due to decreases in riffle areas (Langford, 2001, 2006). In an English context, lentic and generalist forms in smaller streams include larger salmonids (1+), minnows, lampreys, eels and coarse fishes. Rheophilic forms and species include 0+ salmonids, bullheads and small stone loach (e.g. Langford, 2001, 2006; Langford and Hawkins, 1997). The same principles apply to Scotland, although species richness is lower.

Wood matrices trap organic detritus and provide new habitat for invertebrate shredders, for example gammarids, nemourid stoneflies and leptophlebiid mayflies. Whether the fish exploit this additional food resource is not well known.

4 AN EXPERT OPINION SURVEY ON THE IMPACTS OF BEAVER ON FISH POPULATIONS AND ECOSYSTEM PROCESSES

4.1 Abstract

An EOS to assess the impact of beaver on biotic and abiotic ecosystem processes, including the response of fish, and economic and cultural value was conducted by the International Centre for Ecohydraulic Research, University of Southampton during February and March 2009. The EOS was developed to provide supplementary evidence to help understand the potential impacts of reintroducing European beaver to Scotland, principally the potential impact on salmonid fisheries. The EOS was principally based on traditional Likert-type design in which respondents selected a score relating to the degree of positive, neutral, or negative impact beavers are likely to have on a particular item. The survey questionnaire was disseminated by e-mail and completed by 45 prenotified experts from North America and Europe. The participation rate was 70%. Two-thirds of experts were based in North America, and more than 60% considered themselves to be fisheries scientists or managers. Respondents were asked to assign a score of magnitude (neutral, moderate or high) and form (positive or negative) for 24 statements related to the interaction between beaver and fish. The majority (58%) of items received positive responses, including the impact of beavers on the abundance and productivity of migratory salmonids. A negative tendency was exhibited for five (21%) of items related to the impact beaver dams have on the movement of aquatic organisms in tributary streams, including upstream and downstream migrating salmonids, and on the availability of suitable salmonid spawning habitat. Beavers were considered to have no impact on the fish movement in main-stem rivers. Responses indicated a high level of agreement (≥50%) for a single category for half of all items, and polarization of two extremes of opinion was not observed for any item.

4.2 Introduction

For over a decade, extensive consultation and review of current scientific understanding has been conducted as part of the assessment of the feasibility of reintroducing European beaver to Scotland, as required by UK Government obligations under the EU Habitats Directive (European Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna). Based on the results of a feasibility study, a trial reintroduction was sanctioned by the Minister of the Environment in 2008. Nevertheless, fisheries interests have continued to raise concerns about the potential impact of reintroduced European beavers on fish stocks, particularly of economically significant salmonids. This has prompted a further critical review of the literature to better understand the implications of a European beaver reintroduction to Scotland's freshwater fisheries. The literature review and associated meta-analysis form a component of this report (Section 3).

As the arguments for and against a beaver reintroduction are complex, it is useful to supplement evidence provided in the literature and by past experience with the results of public consultation. Since 1998, five consultations have taken place. First, a National consultation (Scott Porter Research and Marketing Ltd, 1998), commissioned by Scottish Natural Heritage (SNH), indicated that 86% of voluntary participants in a "passive" survey were in favour of a European beaver reintroduction. A lower percentage of positive responses was obtained during a "pro-active" survey when public participants were interviewed (63% for, 12% against; 25% did not know). Support was greatest among conservation practitioners, academics, and outdoor enthusiasts who highlighted increased biodiversity, enrichment of Scotland's natural heritage, and ecotourism as benefits of a reintroduction. Strongest opposition was exhibited by those with an interest in fisheries and farming/agriculture who cited negative impacts on fish stocks, damage to the environment, and control of the European beaver population (Scott Porter Research and Marketing Ltd, 1998). This was followed in 2001 by a consultation of local residents conducted by SNH in the mid Argyll area and North Knapdale Community Council area, where the site of the trial reintroduction is located. A third consultation was independently coordinated by the Argyll and Bute Community Planning Partnership Citizens Panel in 2002. A total of 681 (68% response rate) questionnaires were returned. For the whole of Argyll and Bute, 46% supported a reintroduction; 21% were against, and 33% were unconcerned. These results were similar to the SNH local consultation. In 2003, a fourth report was published, this time by the Scottish Economic Policy Network (Scotecon), and considered public attitude towards the control of wild animal species in Scotland and public “willingness to pay”. The survey indicated that 72% of 71 participants supported the reintroduction of European beaver and the average “willingness to pay” for a pilot beaver reintroduction project equalled £24 per household per year for 10 years (Philip and MacMillan, 2003, 2005). The most frequently cited arguments for reintroduction were that European beavers were once native, and that both the wider environment and tourism could benefit. The most frequently cited argument against supporting a reintroduction was that existing wildlife management programmes should be the priority. The most recent consultation of local residents was conducted in 2007 (Scottish Beaver Trial, 2007). Over a two month period, residents from the local vicinity of the site for trial reintroduction, the Knapdale Forest in Mid-Argyll, were provided the opportunity to submit a formal response to the consultation by post or online. The two key questions posed were: 1) Would you like to see beavers in Scotland? and 2) would you support a trial reintroduction of beavers to Knapdale? Respondents were also able to provide comment or ask questions. A total of 466 people submitted a formal response; 72% were in favour of European beavers returning to Scotland and 73% in favour of their return to Knapdale Forest. More than 80% of respondents were defined as being resident of Mid-Argyll. Strongest opposition (31 negative reponses) was from residents living in the immediate vicinity, including 20% of landowners who were adjacent to the proposed reintroduction site.

In addition to surveying the perception of the general public, it is also important to ascertain the opinions, concerns, and reservations of key stakeholders, e.g. fisheries organisations. Collen (1997) canvassed the opinion of fisheries organisations in relation to the reintroduction of European beavers to Scotland, prior to the first public consultation exercises. Responses were received from 32 Scottish District Salmon Fishery Boards (DSFB) and 27 angling associations. Almost 70% of respondents opposed a reintroduction, with the impact of European beaver dams on migrating fish cited as the main concern.

A survey of expert opinion on the effect of European beaver on fish populations was conducted by Collen (1997). An EOS is a form of exploratory research that involves the acquisition of opinions based on the understanding of a person (or a group of people) with experience in a particular subject. A total of 18 respondents (fish and beaver biologists) representing nine countries (Austria, Finland, Lativia, Netherland, Norway, Poland, Russia, Sweden, and Switzerland) returned completed questionnaires. The information obtained proved useful, indicating both positive and negative impacts of beavers on Atlantic salmon and brown trout; benefits for pike (*Esox lucius*); and generally neutral or positive attitudes exhibited by angling communities. However, there was no quantitative analysis of the results obtained and the opinions of experts based in North America (where the majority of research on beaver impacts on fisheries has been conducted) were not sought. To address this gap, we conducted a survey to quantify the opinions expressed by persons with expert knowledge from North America and Europe on the impact of beaver on fish populations (and wider physical ecosystem factors, economics, and cultural value). In addition to the literature review and meta-analysis presented as part of this report, an EOS provides supplementary evidence on the potential impacts of beaver on freshwater fish stocks and the range of opinion exhibited by experts in relation to this issue.

4.3 Methods

4.3.1 Questionnaire design

A Likert scale (Likert, 1932) composed of multiple items was developed to assess expert opinion on potential impacts of beavers on populations of fish, and other ecological and geomorphological processes. Each Likert item, which is a single item or question, is composed of a stem, e.g., a simple statement of attitude or question, and a scale against which the respondent assigns a score (traditionally related to level of agreement). The questionnaire (Appendix 1) was designed so that it should not be onerous to complete, while providing the respondent with the opportunity for additional comment. Scottish Natural Heritage was asked to comment on the draft questionnaire prior to release, and no significant changes were made as a result.

The questionnaire comprised 29 items, followed by a final section that provided the respondents an opportunity to add comments and to state whether or not they wished to remain anonymous. The first 5 items used questions to ascertain the level and nature of previous experience of the respondent.

Item 1 provided respondents with a choice of five categories with which they could describe their profession.

Item 1. In what profession would you describe yourself? (tick as many as appropriate).

- *a. Fisheries scientist/manager*
- *b. Geomorphologist*
- *c. Terrestrial ecologist*
- *d. Beaver specialist*
- *e. Other*

The second question was designed to act as a filter. Respondents were asked to rate their level of expertise. Any response to further questions by respondents who deemed themselves as having no knowledge on the subject were discounted.

Item 2. Can you rate your level of knowledge on the effects of beavers on fish species?

- *a. Expert Knowledge*
- *b. Moderate Knowledge*
- *c. Little Knowledge*
- *d. No Knowledge*

The third and fourth questions sought to ascertain which species of beaver and fish the respondent had experience of.

Item 3. Which beaver species have you most experience (either practical or in theory)?

- *a. European beaver – Castor fiber*
- *b. North American Beaver – C. canadensis*
- c. *Both*

Item 4. Which fish species have you most experience in relation to impacts of beaver?

- *a. Atlantic salmon (Salmo salar)*
- *b. Sea trout (Salmo trutta)*
- *c. Brown trout (Salmo trutta)*
- *d. Other salmonids (please specify)*
- *e. Non-salmonids (please specify)*

The final question of this section was designed to identify whether the respondent had been involved with the previous consultation on the reintroduction of European beaver to Scotland. If they had been involved, respondents were given the opportunity to provide further information

Item 5. Have you been involved in the consultation on the proposed European beaver reintroduction to Scotland?

a. Yes (if so in what extent)
b. No

The remainder of the items (6 –21: composed of a total of 24 items and sub-items, see Appendix 1) were based on a traditional Likert-type design in which a bipolar scale was used to survey respondents opinions (based on subjective or objective criteria) to individual statements (Likert items). Unlike the most common form of scale used, in which respondents are requested to specify their level of agreement with a statement, the degree of impact to each item was considered. Respondents were requested to assign a score ranging from 1 (severe negative impact) to 5 (high positive impact) with a value of 3 indicating “no impact”. Following conventional wisdom, the sequencing and position of Likert items within the questionnaire was designed so that general fields preceded specific areas (McColl *et al.*, 2001). For example, opinions of the impact of beaver activity on freshwater ecosystems as a whole may be considered to be general in nature, while those relating to impacts on downstream movements of migratory salmonids in tributary (rather than main-stem) streams can be considered relatively much more focused and specific. In addition to assigning a score of impact to the suggestion proposed, respondents were provided with the opportunity for further comment. The items in this section were as follows:

Item 6. Beaver activity on freshwater ecosystem
Item 7. Economic impact of beavers on ecosystem
Item 8. Beavers on cultural value of ecosystem
Item 9. Beaver activity on geomorphological processes
Item 10. Beaver activity on patterns of river flow
Item 11. Overall impact of beaver dams on habitat connectivity
Item 12. Beaver dams on movement of aquatic biota
Item 13. Beaver activity on habitat heterogeneity
Item 14. Beaver activity on species richness
- *a. All biota*
- *b. Fish species*

Item 15. Beaver dams on upstream movement of migratory salmonids
- *a. In main-stem rivers*
- *b. In tributary streams*

Item 16. Beaver dams on downstream movement of migratory salmonids
- *a. In main-stem rivers*
- *b. In tributary streams*

Item 17. Beaver dams on movement of other fish species
- *a. In main-stem rivers*
- *b. In tributary streams*

Item 18. Beaver activity on availability of suitable spawning habitat for
- *a. Migratory salmonids*
- *b. Other fish species*

Item 19. Beaver activity on availability of suitable non-spawning habitat for
- *a. Migratory salmonids*
- *b. Other fish species*

Item 20. Beaver activity on abundance of
- *a. Migratory salmonids*
- *b. Other fish species*

Item 21. Beaver activity on productivity of

a. Migratory salmonids
b. Other fish species

Item 22 provided respondents with the opportunity to make further comments, followed by an option to select to remain anonymous.

> *In the space below, please provide additional comment or caveats in relation to any of the above questions, other issues related to beavers, questions, or concerns regarding design of this questionnaire. Details or links to any grey literature source of information would also prove useful.*
>
> *Please indicate below whether you give consent to be identified as a survey respondent or would like to remain anonymous. Aggregate results, and not individual responses, to the short answer questions will be presented. Voluntary "comments" will be reported as part of the report.*
>
> *Would you like to remain anonymous in the final report? Yes / No*

4.3.2 Selection of experts:

North American and European experts were selected based on meeting at least one of the following criteria:

a. Record of publication in relation to beavers (e.g. ecology/economic impacts).
b. Record of publication in freshwater fisheries (particularly in relation to salmonids) in areas within the beaver's range (i.e. judged likely to have expert knowledge on impact of beavers on fish stocks).
c. Record of publication in relation to geomorphological response of rivers to woody structure (especially beaver dams).
d. Demonstrable experience in working within the above areas (e.g. consultants or field operatives that may or may not be required to publish findings in the scientific literature).

The experts selected were either known to the contractors or to SNH, were cited in unpublished reports by the Tweed Foundation (Campbell unpublished a, b), or were identified as part of the literature review. Selection was not based on any preconception of current opinion (i.e. for or against the reintroduction of European beaver to Scotland). Although some appropriately experienced practitioners in the field of beaver and/or fish ecology have undoubtedly not been identified and hence not included in the survey (e.g. because their details were not known to the contractors), it is our opinion that the experts selected (affiliations presented in Table 6) represent a random and unbiased range of opinion.

*Table 6 Affiliation of the selected experts that received prenotification of request to participate in the Expert Opinion Survey on impacts of beaver on fish stocks. Not all those listed responded. *Two of the five experts were retired.*

Institution/ Agency/ Consultancy	Number of experts prenotified
National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, US	9
National Oceanic and Atmospheric Administration, Northeast Fisheries Science Center, US	2
National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center, US	1
School of Aquatic and Fishery Sciences, University of Washington	2
US Geological Survey	3
University of New Brunswick, Canada	3
Norwegian Institute for Nature Research (NINA), Norway	2
Finnish Game and Fisheries Research Institute	1
North Ostrobothnia Regional Environment Centre (NOREC), Finland	1
University of Karlstad, Sweden	1
Swedish University of Agricultural Sciences, Sweden	2
US Forest Service	1
Department of Fisheries and Oceans, Canada	5*
Watershed Technologies Consultancy, Canada	1
Golder Associates Ltd. Consultancy, Canada	2
Telemark University College, Norway	2
Wageningen University, Netherlands	1
University of North Dakota, US	1
Towson University, Maryland US	1
European Beaver Symposium	1
Carpathian Heritage Society - Natural Systems, Poland	1
Ecologic Institute for International and European Environmental Policy, Germany	1
University of Gotthenburg, Sweden	1
New Brunswick Department of Natural Resources Fish and Wildlife, Canada	1
State of Maine Department of Marine Resources - US	1
Philipps University,Marburg, Germany	1
University of Aarhus, Denmark	3
Vilnius University, Lithuania	1
Bureau Ontwikkeling en Beheer, Netherlands	1
Konrad Lorenz Institute for Comparative Ethology, Austria	1
Boston University, US	1
Fisheries Research Service, Scotland	1
University of Oxford, UK	1
University of Helsinki, Finland	1
Palacky University, Czech Republic	1
Beaver Deceivers International - Consultancy, US	1
Danish Forest and Nature Agency, Denmark	2
The Dutch Mammal Society, Netherlands	1
The University of Stirling, UK	1
University of Massachusetts, Amherst, US	1

4.3.3 Delivery of the EOS

The EOS questionnaire aimed to acquire a "snap-shot" of current expert opinion. As it was not the aim of the survey to elicit a consensus view, other traditional techniques such as the Delphi method (Linstone and Turoff, 2002), were not considered appropriate. The Delphi technique usually involves sending a questionnaire to designated respondents a predetermined number of times, with each successive sending of the questionnaire being accompanied by a summary of the results from previous rounds on which the experts are asked to confirm or modify their opinion (Linstone and Turoff, 2002). This questionnaire was designed to be sent to respondents once only.

The need to quantify non-response bias required control over the selection of the number of experts surveyed and for response/non-response to be accurately recorded. Thus, specific individuals identified as experts were targeted only, not the institution for which they worked (i.e. questionnaires were not sent to a key contact at a particular agency with the request to disseminate within the organization with the objective of receiving multiple responses from persons that consider themselves experts).

Previous research has advocated the use of prenotification and reminders to improve probability of response (McColl *et al.*, 2001). All identified experts were initially sent by e-mail a prenotification describing the aims of the survey and request for participation. The prenotification was as follows:

"Dear [Name of expert],

I am a lecturer in Fisheries Ecology at the University of Southampton and I am contacting you with regards to your expertise in relation to beavers and fish.

I hope you can help me with some work we are doing in relation to a proposed trial reintroduction of European beaver to Scotland. Would you be prepared to participate in a survey related to beavers and their potential impacts? This is not an onerous task. If you agree, I will send you the questionnaire which can be completed relatively quickly.

Many thanks for your help in advance.

Best regards

Paul Kemp"

In the event that the expert did not respond to the prenotification a "non-response" was recorded. If the expert agreed to participate, the following e-mail was sent:

"Dear [Name of expert],

Many thanks for agreeing to participate in the "Beaver Expert Opinion Survey".

The aim of this "expert opinion survey" is to develop a "broad-brush impression", based on the experience of practitioners that have direct experience of beaver – fisheries ecology, or the relationship between beavers and their freshwater ecosystem, particularly with regards to impacts on fish populations.

It is well understood that ecology is innately complex and mechanisms that underpin biological responses are convoluted and scale and density dependent. Nevertheless, it remains possible to formulate general impressions of the direction and magnitude of interactions. Response, by assigning scores to the questions posed, should be based on *generalization, e.g. such as in the formulation of phrases like, "On balance, the impact of beavers on the movement of migratory fish is (e.g., negative, neutral, positive)…….." or "in the majority of cases, beavers have (e.g., negative, neutral, positive) effects on habitat heterogeneity".*

I would appreciate it if you could complete the attached questionnaire, which is not too onerous, and return via e-mail to me.

I look forward to your response.

Best regards

Paul Kemp"

Experts that agreed to complete the survey were issued a reminder if no response was received a week or more after delivery. If no response was received one week after the reminder, then a "non-response" was recorded.

Experts were prenotified between 18 and 23 February, and EOS questionnaires were delivered between 18 and 26 February, 2009. Reminders were issued on 2 March. The survey was closed on 10 March 2009 to enable the report completion deadline to be met.

4.4 Results

4.4.1 Participation and anonymity

A total of 65 experts were selected and sent a notification of intention to survey. One e-mail was rejected due to specification of an incorrect address and this was not resolved. Of the 64 remaining, 57 (89%) replied to the prenotification including 9 who declined to participate due either to insufficient expertise, family bereavement, conflict of interest, concerns over political implications, or excessive workload. Eighteen reminders were sent. A total of 45 completed questionnaires were returned (participation rate 70.3%) before the survey closing date, of which 1 was discarded due to the respondent claiming no expertise on the subject. Twenty respondents chose to remain anonymous (Appendix 3 lists respondents and their affiliations excluding those that wished to remain anonymous). Five questionnaires returned after the survey was closed were ignored.

4.4.2 Profession and expertise

Participants were able to select more than one option for item 1 to describe their profession, with 14 choosing to select 2 or more categories. Twenty-eight respondents described themselves as fisheries scientists/managers, 4 as geomorphologists, 8 as terrestrial ecologists, 12 as beaver specialists, and 8 as other. Thirty (66.6%) of participants worked in North America, 11 of whom were based in the Pacific Northwest of the United States. Twenty-six respondents considered themselves to have moderate knowledge of the subject area; 6 described themselves having expert knowledge; and 12 with little knowledge.

Thirty respondents had experience mostly of the North American Beaver, and 12 mostly of the European Beaver. When asked to select the species of fish for which they had experience of beaver impacts, 20 respondents selected more than one category, 17 selected "*Salmo salar*", 12 selected "*Salmo trutta*" (both brown and sea trout), 22 selected "other salmonids", and 12 selected "non-salmonids". Other salmonids included coho and Chinook salmon, steelhead and rainbow trout, Eastern brook trout (charr), cutthroat trout, and Arctic grayling (*Thymallus arcticus*). Non-salmonids included lamprey (*Lampetra* spp.), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), riffle daces (*Rhinichthys* spp.), suckers (*Catostomus* spp.), Clupeids, Cyprinids, stickleback, eel, walleye (*Sander vitreus*), sculpin (*Cottoidea* spp.) and northern pike.

Eight respondents confirmed that, at least to some extent, they had previously been involved in the consultation in relation to reintroduction of European beaver to Scotland (see comments in Appendix 2).

Table 7 Summary of response to Likert items posed in an Expert Opinion Survey questionnaire to assess the impact of beavers on stocks of freshwater fish. Values in bold indicate single categories which the majority of respondents selected, indicating high levels of agreement.Response categories were severe (1), moderate (2) negative impacts; neutral impact (3); and moderate (4) and high (5) positive impacts.

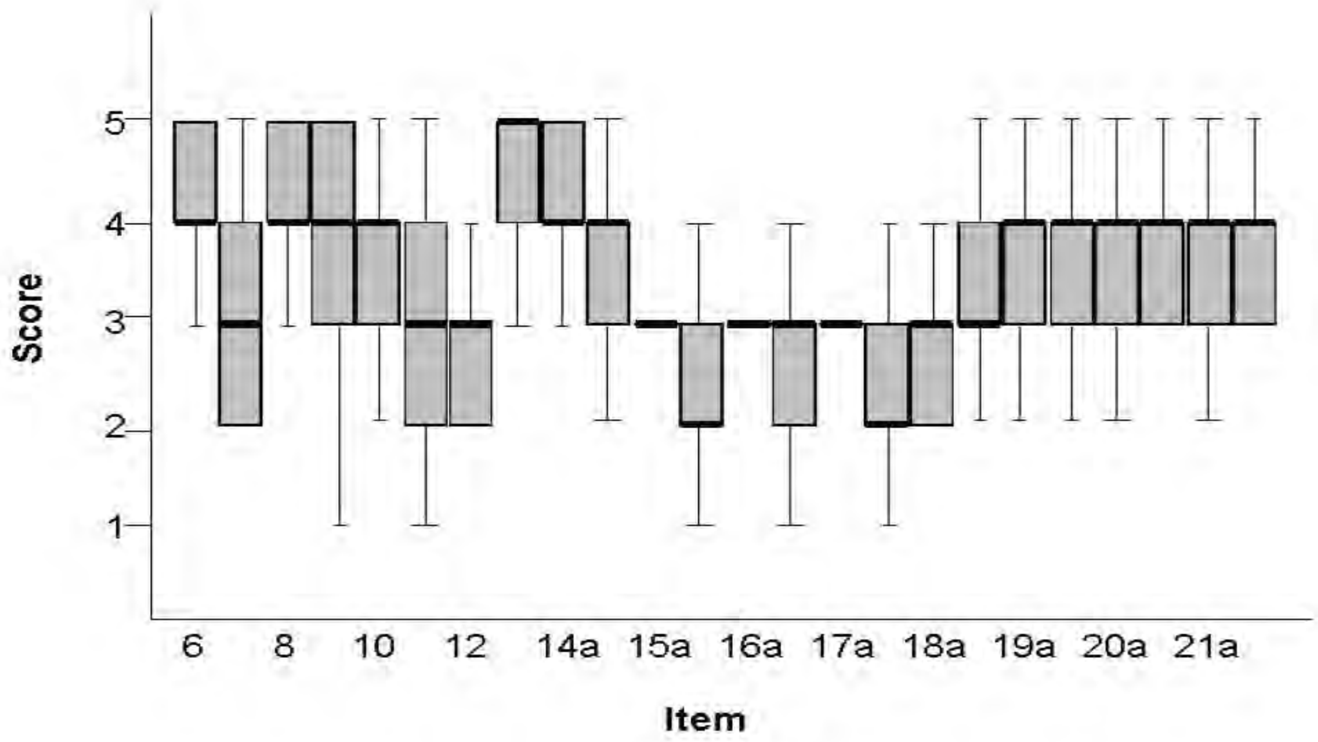
Item	N	Response (%)					Median	Mode
		1	2	3	4	5		
6	44	0%	7%	7%	**50%**	36%	4	4
7	42	0%	33%	31%	24%	12%	3	2
8	39	0%	5%	15%	**51%**	28%	4	4
9	41	2%	5%	20%	46%	27%	4	4
10	43	2%	16%	21%	40%	21%	4	4
11	42	5%	31%	33%	21%	10%	3	3
12	44	0%	48%	41%	9%	2%	3	2
13	43	2%	5%	5%	23%	**65%**	5	5
14a	42	0%	0%	14%	**52%**	33%	4	4
14b	41	0%	5%	22%	**56%**	17%	4	4
15a	42	2%	5%	**88%**	5%	0%	3	3
15b	42	10%	**55%**	31%	2%	2%	2	2
16a	42	0%	0%	**95%**	2%	2%	3	3
16b	41	2%	24%	**61%**	10%	2%	3	3
17a	40	0%	8%	**88%**	3%	3%	3	3
17b	40	3%	**53%**	40%	5%	0%	2	2
18a	40	3%	43%	45%	8%	3%	3	3
18b	37	0%	19%	**51%**	27%	3%	3	3
19a	40	3%	15%	25%	43%	15%	4	4
19b	38	0%	11%	32%	47%	11%	4	4
20a	41	0%	24%	24%	32%	20%	4	4
20b	39	0%	0%	49%	41%	10%	4	3
21a	41	0%	20%	24%	39%	17%	4	4
21b	38	0%	0%	42%	45%	13%	4	4

4.4.3 Impacts of beavers - Likert-scale response to items

A summary of responses to the Likert-scale survey that formed the major part of the questionnaire is presented in Table 7 and Figure 5. Additional comments provided by respondents are listed in Appendix 2.

Thirteen median scores for the 24 items listed were positive (score > 3); 9 were neutral (score = 3); and 2 were negative (score < 3) (Figure 5). Twelve items achieved a positive mode, 8 were neutral, and 4 were negative. Based on reaching a majority threshold (50%),

Figure 5 Likert scale response to Expert Opinion Survey items related to impact of beaver on fish populations and ecosystem processes. Scores of 1 and 2 are negative, 3 represents no impact, and 4 and 5 positive. The solid horizontal lines represent the median, boxes the interquartile range, and whiskers the maximum and minimum scores (excluding outliers and extremes).



high levels of agreement were obtained for 12 items (Table 7). Of those, 5 were positive, 5 neutral, and 2 negative. Polarization of extremes of view was not illustrated for any item.

The response to 14 items exhibited a positive tendency (interquartile range > 3) including two key items designed to illustrate perception of the overall effect of beavers on migratory salmonid populations: the impact of beavers on abundance (Item 20a); and the impact beavers on productivity (Item 21a) (Figure 5). The response to five items exhibited a negative tendency (majority of responses < 3): the impact of beaver dams on the movement of aquatic biota (Item 12); the impact of beavers on upstream movement of salmonids in tributary streams (Item 15b, high level of agreement score 2); the impact of beaver dams on downstream movement of migratory salmonids in tributary streams (Item 16b); the movement of other fish species in tributary streams (Item 17b, high level of agreement score 2); and the impact of beaver activity on availability of suitable salmonid spawning habitat (Item 18a) (Figure 5). There were high levels of agreement (over 87%) in the responses to the 3 items related to upstream and downstream movement of migratory salmonids and other fish in main-stem rivers (Items 15a, 16a, and 17a), i.e. beavers have no impact. The response to a further two items exhibited a neutral tendency in which the interquartile range extended from 2 to 4: the economic impact of beavers (Item 7); and the overall impact of beaver dams on habitat connectivity (Item 11) (Figure 5).

Respondents less frequently selected the extreme response categories for the majority of items, indicating a central tendency bias. However, this was skewed, with selection of severe negative impacts (score = 1) being rare.

Four respondents provided criticisms of the design of the study, or concerns about the application of this methodology (see comments under Item 22 of Appendix 2 for further details).

4.5 Discussion

Previous reviews of the impacts of beaver on ecosystem functioning, including fish population response, and geomorphological processes have emphasized the complex nature of ecological relationships. Results vary with site (e.g. topography and climate), species (of both beaver and fish), and density and scale-dependent factors. An EOS provides additional subjective information to supplement that obtained from analysis of literature, or by direct observation, and is a useful means of identifying the tendencies and levels of agreement or polarization of perspectives. However, the results of an EOS should not be considered in isolation and should be treated with caution as they represent subjective interpretations of perception, and possibly vested interests, even if based on the results of sound scientific investigation. The principle aim of the current EOS was not to develop a scientific consensus by iterative discussion, but to quantify how beavers are perceived by the scientific community to potentially impact fish populations.

Twelve years after the qualitative EOS conducted by Collen (1997), an up-to-date representation of North American and European expert opinion on the impact of beavers on fish stocks was prepared for this report. The tendencies of response for the majority of items presented in the EOS were positive. Nevertheless, key areas of concern, as indicated by a negative response tendency, related to the impact of beaver activity (dam building) on the upstream and downstream movement of aquatic biota, and fish in tributary streams, and the availability of suitable salmonid spawning habitat. This is in line with the results of the meta-analysis of available literature (Section 3). Conversely, a large majority of respondents indicated that beaver activity does not pose a threat to upstream and downstream movement of fish in main-stem rivers. However, negative impacts on fish passage and availability of salmonid spawning habitat were rarely considered to be severe and, based on several comments provided (Appendix 2), tend to operate at local scales, and can be relatively short-lived.

Despite locally negative and short-term impacts on fish movement and the availability of suitable spawning habitat, the general perception is that beavers are either beneficial to, or have no impact on economic, cultural, physical (geomorphological) and ecological processes, including on fish population functioning. Contrary to some arguments, responses tended to indicate that beavers might have positive impacts on the abundance and productivity of migratory salmonids.

Two-thirds of respondents were North American. This bias of expertise and resulting response reflects the weighting of scientific understanding of beaver impacts on fish populations developed in this region (Section 3). Unlike Collen (1997), the current survey captured expert opinion based on both North American and European experience. Several respondents were aware of the intention to reintroduce European beaver to Scotland and provided interesting comments in relation to this issue (Appendix 2). It is also of interest that the results were biased towards the opinion of fisheries scientists/managers (> 60%), and hence the high tendency for positive responses overall may not have been entirely expected.

A participation rate of 70% is considered to be high, and likely reflects the use of a system of prenotification and reminders. The high level of anonymity suggests that individuals did not attempt to portray themselves or their organizations favourably, and hence the results are unlikely to reflect a social desirability bias.

The results of analysis of the Likert items did not indicate polarization of two extremes of view for any item considered. This suggests that, within the scientific community at least, while opinions might differ, the probability of embedded conflict between groups exhibiting extremes of opinion is low. For several items, positive, negative, and neutral, there was a high level of agreement (≥ 50%), indicating the potential for surveys of this nature to identify areas of consensus.

The EOS presented here provides interesting supporting evidence to be considered when assessing potential impacts of a European beaver reintroduction programme in Scotland. The complexity of the issue and both positive and negative impacts are highlighted. Careful consideration of individual comments (Appendix 2) is recommended during the decision making process.

5 DISCUSSION

A trial reintroduction of European beaver to Scotland has been widely supported by the general public for over a decade. Nevertheless, groups that represent the interests of economically significant Atlantic salmon fisheries have continued to raise concerns about the impacts of beaver on fish stocks. The concern that beaver dams can impede the movement of migratory fish, particularly during periods of low flow, has received much attention. It is also suggested that the arguments proposed by the pro-reintroduction lobby are based on insufficient knowledge, or irrelevant evidence based on experience obtained in other regions that is not transferable to the Scottish context. Scottish Natural Heritage commissioned this report to provide an independent review of current understanding of the impact of beavers on stocks of freshwater fish (primarily economically important salmonids) based on quantitative analysis of available literature and review of North American and European expert opinion, primarily that of fisheries professionals.

A meta-analysis of the available literature indicated that the majority (90%) of research on the impact of beavers on fish populations has been conducted in North America, and over the past two decades (69%). As a result, there is a bias to considerations of North American beaver, species of fish that do not occur in Scotland (e.g. Pacific salmonids), and in regions where climate, geography, and land-use is distinctly different. Only 8% of studies considered European beaver. Although there are differences in life-history (Parker and Ronning, 2007), the two beaver species exhibit many similarities in terms of ecology and biology, and thus generalizations can be made.

Evidence provided by the meta-analysis, and supplemented by the EOS, lends support to some of the arguments proposed by the fisheries groups; the most frequently cited negative impact of beaver relates to the impediment created by dams to fish migration (Cunjak and Therrein, 1998; Cunjak *et al.,* 1998; Mitchell and Cunjak, 2007; Scruton *et al.,* 1998; Parker and Ronning, 2007; Taylor *et al.,* 2009 Guignion, 2009). Other negative impacts include impoundment and siltation of spawning gravels (e.g., Müller-Schwarze and Sun, 2003), alteration of temperature (via loss of riparian shade; e.g., Knudsen, 1962; Sayler, 1935; Guignion, 2009) and flow regimes (e.g., Bryant, 1984), and reduction in habitat (Rutherford, 1955) and water quality (e.g., Rupp, 1954). Nevertheless, the analysis of available literature indicated that descriptions of positive impacts on fish populations were more frequently cited than negative effects. Beneficial effects relate primarily to habitat improvement, i.e. enhanced heterogeneity (Bryant, 1984; Lichatowich, 1999) and provision of rearing (e.g., Johnson and Weiss 2006; Swanston, 1991; Taylor, 1999) and overwintering habitat (e.g., Cunjak, 1996), and increased invertebrate productivity (e.g., Gard, 1961; Rutherford, 1955), fish growth (Rosell and Parker, 1996), and ultimately higher fish abundance and productivity (e.g., Pollock *et al.,* 2004).

Beaver dams are rarely constructed on main-stem rivers, and hence do not pose significant impediments to fish passage. Where they do exist they are considered to be semi-permeable structures that allow a proportion of fish to pass both in the upstream and downstream direction. Beaver dams have a higher negative impact on the movement of fish in narrower tributary streams, and especially under low flows. This has the potential to disproportionately impact spring returning adults salmon that tend to spawn in the upper reaches of catchments. Further research to investigate this is warranted. However, the results of the meta-analysis and EOS suggest that, while the impact of beaver dams on fish movements in tributary streams is negative, effects can be short-lived (e.g., Taylor, 1999) and localized. The influence of beaver dams on fish populations remains unclear and is suggested by some to be negligible. If rivers in Scotland are allowed to physically respond to the presence of European beaver dams, which like woody debris dams increase the frequency and extent of overbank flows (Jefferies *et al.*, 2003) resulting in localized flooding, then alternative routes of fish passage will likely become available via back-water or floodplain channels. However, re-establishment of lateral connectivity with the floodplain may be prevented in highly managed and constrained channels designed to minimize flood risk. If these are blocked by dams as a result of European beaver activity, then significant impediments to fish passage may be created, and alternative management options should be considered. Conversely, European beaver structures may provide velocity refuge habitat during high flows in heavily engineered rivers that contain little other off-channel habitat.

If European beaver dams impound spawning areas, then gravels will be covered by deep, slow flowing water conducive to the deposition of fines (Swanston, 1991). This will negatively impact salmonids, but potentially favour others species (e.g. lamprey). However, sediment deposition in impounded reaches can result in improved quality of spawning gravels downstream by reducing infiltration of fines.

The results of the meta-analysis, when considered in conjunction with analysis of the EOS, suggest that the negative impact of beaver activity on fish passage and maintenance of suitable spawning habitat can be at least off-set by benefits associated with increased habitat heterogeneity and resulting increase in fish (including salmonid) abundance and productivity. Brown trout productivity, in particular, is found to be positively related to beaver activity (e.g., Hale, 1966; Müller-Schwarze and Sun, 2003; Gard and Seegrist 1972; Gard, 1961), although enhanced productivity has also been suggested for Atlantic salmon (Scruton *et al.*, 1998; Sigourney *et al.,* 2006). This, however, is likely to vary locally determined by life-history bottlenecks (see Armstrong *et al.*, 2003). For example, long-term persistence of a complex of European beaver dams, constructed immediately downstream of important Atlantic salmon spawning grounds in a river where such opportunities are limited, is likely to have a negative impact on the population. Conversely, enhanced habitat heterogeneity in areas where rearing, overwintering, and adult staging habitat is limited may result in a positive population response, provided that these are not overshadowed by other drivers, such as marine mortality. Management implications should thus be considered on a case-by-case basis.

Several arguments in opposition to a European beaver reintroduction have been mooted. These include misinterpretation (e.g. in relation to translation of findings obtained in regions exhibiting distinctly different climates and geography to Scotland) or misuse as "propaganda" of available literature by those that support a reintroduction; and a lack of scientific understanding of potential impacts, while the value of information gained by conducting a trial reintroduction will prove limited. Some arguments do indeed have merit, e.g. the need to consider potential significance of the impact of European beaver dams on fish movement through tributary streams under low flows.. The arguments are based on a limited literature review (Paper A = 4; Paper B = 9), and do not present a balanced perspective. To address this, the current report presents the results of an independent assessment of 100 sources of information as part of the meta-analysis of available literature.

Concerns regarding the application of the results of studies conducted in regions (e.g., Norway) with distinctly different geography and climate to Scotland (particularly lowland areas) are particularly valid. Indeed one comment provided in response to the EOS (see Appendix 2) suggests that in an intensively managed landscape, such as in the UK in which rivers may be constrained from physically responding to European beaver activity in a natural way, the widely reported benefits of beaver activity on fish stocks may be outweighed by negative impacts. These include a reduction in riparian forest recruitment, costs to human infrastructure (roads and residences) via flooding, facilitation of range expansion of undesirable invasive aquatic and terrestrial species, risks of waterborne pathogens, and local loss of economically significant migratory fishes.

Although the need for more scientific research, at least in relation to some issues (e.g., mechanisms of fish passage at beaver dams; modelling of potential overlap of suitable

Atlantic salmon and European beaver habitat; influence of impediments to fish passage at the population level) is warranted, we find no evidence to suggest that a trial reintroduction is unlikely to yield important information. A trial reintroduction will provide much needed data through the monitoring of effects of European beaver activity on hydrology, geomorphology, ecology, and enterprise in relation to the West-coast of Scotland's forested catchments. SNH recognize that while acquisition of direct information of the impact of European beavers on intensive agriculture and wild salmonid fisheries will be limited through the trial reintroduction in Argyll, the data collected will likely prove useful in predicting the impacts in other regions of Scotland, although these are likely to be complex. Plans to conduct a trial reintroduction, rather than a full reintroduction as has occurred in most other European countries, represent a measured approach that is in-line with best practice. Another important area of research, that should not be neglected, is the prediction of the impact of climate change, particularly in relation to impediments to fish passage created by beaver dams interacting with altered flow regimes (potentially extended periods of low flow) superimposed on changes in timing of fish migration. Further, the development of optimisation modelling techniques (as proposed by Kemp *et al.*, 2008) to identify which combination of barriers (natural and anthropogenic) to fish movement within a landscape may be mitigated for to enable the most cost effective restoration actions to be taken to meet criteria for ecological status (or potential) as required under the Water Framework Directive, should include consideration of potential European beaver activity. The development of these models will highlight areas that may be particularly sensitive to European beaver activity, or where impacts will likely be minimal.

5.1 Implications for European beaver and fisheries management in Scotland

The findings presented in this report indicate that beavers can have both positive and negative impacts on fish populations; that response can be complex and spatially and temporally variable, and that perceived overall effects tend to be positive when viewed from the perspective of productivity. Nevertheless, potential for negative impacts of beaver activity on fish passage, particularly in tributary streams under low flows, and quality of spawning habitat must be appreciated, and management strategies developed.

Localised impacts of European beaver dams on fish passage and spawning habitat, while potentially negligible when viewed from the perspective of populations of the large Scottish East-coast Atlantic salmon rivers (e.g. Tweed, Tay, Spey, and Aberdeenshire Dee), may be significant for less resistant populations that inhabit some small west-coast catchments (note previous discussion regarding disproportionate impacts on spring Atlantic salmon runs). Impediment to movement is also likely to be exaggerated when European beaver activity interacts with anthropogenic river infrastructure, e.g. blockage of culverts with woody debris and silt (Figure 6).

Figure 6 Accumulation of debris upstream of a culvert (a) blocks flow through the structure (b) on the Great Rattling Brook, Newfoundland (Canada) (photographs provided by R. J. Gibson).

(a) North American beaver debris accumulation

(b) Blocked culvert outflow

At a local scale, the management of European beaver dams for the purpose of protecting fisheries interests should be facilitated if necessary. For example, the impact of North American beaver dam complexes that have been shown to impede Atlantic salmon migration can be mitigated for by cutting notches in the structure (see Taylor *et al.*, 2009). In the United States, the Virginia Department of Transportation compensates for the impact of North American beaver activity on culverts by extending the inflow pipe underwater and protecting its entrance with a wire mesh fence enclosure. Debris that accumulates on the enclosure is removed by maintenance crews. A "balanced approach" to management has been suggested for woody debris dams, which should be removed if a significant impediment to fish passage is created, but left when they positively improve habitat quality (Hendry *et al.*, 2003); the same approach could be considered for European beaver structures. However, quantification of porosity of such barriers to fish movement beyond pure speculation can often prove difficult without expensive investigation (e.g., radio-telemetry studies), and in the case of dismantled beaver dams, it is likely that they will be rebuilt relatively rapidly. Management measures have obvious cost implications, and the responsibility for funding mitigation action is likely to result in some debate.

Recent evidence provided by research conducted in the United States suggests that North American beaver behaviour may be manipulated by providing structures that enhance the probability of dam construction in specified areas. The use of BDS structures may provide a mechanism to locally attract North American beavers away from areas considered to be of high sensitivity (e.g. from the perspective of flooding) to more preferred sites.

As part of the trial reintroduction, SWT and RZSS have developed appropriate "exit strategies" which will enable the project to be halted, in consultation with SNH, should negative impacts be sufficiently high to warrant this. Nevertheless, long-term strategies for control of European beaver populations should be considered if a full reintroduction is sanctioned in light of European obligations (and potentially public opinion) that may limit direct action being taken. Lessons should be learned from experience obtained in Massachusetts where increases in North American beaver populations have resulted in human-beaver conflict and negative public opinion (J. Sprules pers. comm.). Maintaining positive public opinion is an essential component of long-term success of any reintroduction programme.

5.2 Acknowledgements

We thank all those that responded to the request to participate in the Expert Opinion Survey, and particularly Professor R.J. Gibson, Dr M. Pollock, and Professor R. Cunjak who provided photographs and data for use in this report. Thanks also go to others who provided comments on the report, including Angus Tree, Dr Martin Gaywood, Dr Colin Bean and Dr Colin Adams.

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APPENDIX 1

Impacts of reintroduced European beaver on fish in Scotland: Expert Opinion Survey

2. In what profession would you describe yourself? (tick as many as appropriate)
   a. Fisheries scientist/manager ☐
   b. Geomorphologist ☐
   c. Terrestrial ecologist ☐
   d. Beaver specialist ☐
   e. Other

3. Can you rate your level of knowledge on the effects of beavers on fish species?

Expert Knowledge	Moderate Knowledge	Little Knowledge	No Knowledge
☐	☐	☐	☐

4. Which beaver species have you most experience (either practical or in theory)?
   a. European beaver – *Castor fiber* ☐
   b. North American Beaver – *C. canadensis* ☐
   c. Both ☐

5. Which fish species have you most experience in relation to impacts of beaver?
   a. Atlantic salmon (*Salmo salar*) ☐
   b. Sea trout (*Salmo trutta*) ☐
   c. Brown trout (*Salmo trutta*) ☐
   d. Other salmonids (please specify)
   e. Non-salmonids (please specify)

6. Have you been involved in the consultation on the proposed beaver reintroduction to Scotland?
   a. Yes ☐ (if so in what extent)
   b. No ☐

Please assign a value based on the below scale to each survey questions and add any comments on reason behind your choice in the adjacent comments space.

Severe negative impact ---No impact-- -----------High positive impact

1	2	3	4	5

Score Comments

7. Beaver activity on freshwater ecosystem
8. Economic impact of beavers on ecosystem
9. Beavers on cultural value of ecosystem
10. Beaver activity on geomorphological processes
11. Beaver activity on patterns of river flow
12. Overall impact of beaver dams on habitat connectivity
13. Beaver dams on movement of aquatic biota
14. Beaver activity on habitat heterogeneity
15. Beaver activity on species richness
    a. All biota
    b. Fish species

16. Beaver dams on upstream movement of migratory salmonids

    a. In main-stem rivers

    b. In tributary streams

17. Beaver dams on downstream movement of migratory salmonids

    a. In main-stem rivers

    b. In tributary streams

18. Beaver dams on movement of other fish species

    a. In main-stem rivers

    b. In tributary streams

19. Beaver activity on availability of suitable spawning habitat for

    a. Migratory salmonids

    b. Other fish species

20. Beaver activity on availability of suitable non-spawning habitat for

    a. Migratory salmonids

    b. Other fish species

21. Beaver activity on abundance of

    a. Migratory salmonids

    b. Other fish species

22. Beaver activity on productivity of

    a. Migratory salmonids

    b. Other fish species

23. In the space below, please provide additional comment or caveats in relation to any of the above questions, other issues related to beavers, questions, or concerns regarding design of this questionnaire. Details or links to any grey literature source of information would also prove useful.

Consent:

Please indicate below whether you give consent to be identified as a survey respondent or would like to remain anonymous. Aggregate results, and not individual responses, to the short answer questions will be presented. Voluntary "comments" will be reported as part of the report appendices.

Would you like to remain anonymous in the final report? Yes ☐ No ☐

APPENDIX 2

COMMENTS SUBMITTED AS PART OF THE EXPERT OPINION QUESTIONNAIRE.

The following sections provide all comments submitted by respondents as part of the EOS. The opinions stated to not necessarily reflect those of the authors of this report or of Scottish Natural Heritage. Comments have been edited to correct errors of spelling only.

Item 5: If you have you been involved in the consultation on the proposed beaver reintroduction to Scotland, to what extent?

- In an informal "advisory" manner, and as the first author of 2 papers on the subject.
- Provided information on beaver reintroduction biology as and when requested.
- I was consulted early on in the 1980s by David MacDonald's group at Oxford. I 've also been in contact with (but not really consulted) the Scottish Natural Heritage.
- Co-author with Peter Collen in a review paper.
- From time to time since the early 90ies.
- SNH staff visited us and we gave them a tour of our reserves and talked about our experiences.
- Informal basis.

Item 6: Beaver activity on freshwater ecosystem.

- Good for many native species, but can limit salmonid spawning habitat in extreme cases.
- I'd guess good for some things, bad for others.
- High positive impact ecologically, for a keystone species.
- Beaver dams impede or prevent ATS migrations preventing them from reaching spawning grounds. Also, the impoundments retain water causing it to warm up unnaturally. These impoundments also allow the beaver to remove or cause the removal of much of the riparian zone which provides shade and nutrient input for juvenile salmon. But, these impoundments can filter water heavy with suspended solids, mitigate pH issues and lessen erosion by slowing the stream velocity.
- Adds to habitat compexity and variation.
- It is a natural component of the freshwater ecosystem. When in balance with the system, the effects are entirely beneficial. Problems only arise when other processes (e.g., lack of predators) are out of balance.
- In river systems that beaver occur naturally (e.g. Canadian Prairies), ecosystems and biota have evolved with them; introduction of beaver in systems which do not occur naturally may be viewed differently.

- Important & interesting part of the fauna.

- Beaver activity generally appears to have positive impacts, such as increasing the structural and species diversity of riparian forest, wetland creation etc, though very occasionally impacts can be negative.

- Adds heterogeneity & biodiversity.

- Mitigate flooding, encourage diversity.

- No impact considering a diversity of all wildlife.

- No Impact - in North America they are part of the ecosystem.

- Low negative impact - habitat alteration;movement blockage.

- Positive score; but depends on species.

- Positive but there may be negative effects on migration of some fish species. In some locations water temperatures may be raised above optimum levels.

- Beaver create important habitat for salmonid overwintering in the Pacific Northwest of the USA.

- Larger negative impact on small streams.

- Adds habitat diversity and structure.

- Generally positive effects, if managed for put and take trout fishery can have some negative impacts for certain species in some areas.

- Where historically present, salmon populations evolved to take advantage of the ponds created…which increased abundance of fish as the ponds provided suitable habitat for juveniles during low-flow periods in the summer, and cold periods during the winter.

- They are a native, keystone species.

- Important aspect to system ecological integrity (Canadian prairie sysems evolved with beaver activity - the species have as well.

- Most often positive except possibly where management may be required to protect anthropogenic created ecosystems.

- Increases species/ecosystem diversity in riparian areas.

<u>Item 7: Economic impact of beavers on ecosystem</u>

- Don't know, but should improve value of areas for fish production and habitat quality..

- interesting sight vs flooding damage, I'd call it a draw.

- Negative economic impact from the standpoint of most landowners; native Canadian trappers would answer just the opposite.
- Positive economic impact due to increased N-retention potential of rivers but often significant losses in tree populations next to the river.
- Other than potential timber loss or extra expense related to working around a beaver impoundment the only real cost are assosiated with road wash outs where beaver have flooded near a road network.
- E.g. Sweden 'no economic impacts on a national scale' (etc.).
- There can be both positive and negative impacts economically.
- Human needs may differ from beaver and ecosystem needs.
- Small game interesting to view & hunt.
- The value of the impact will depend on your point of view, but overall the positive impacts (particularly in relation to ecosystem services) are likely to greatly outweigh the negative impacts.
- Systems with Beaver provide a wider range of ecological goods and services.
- A healthy wetland is more economic.
- They can have limited negative economic impacts especially where the maintance of road systems are concerned.
- Reduced angling opportunites.
- Usually negative because in most cases economic priorities conflict vs ecological priorities.
- Trout fishing may be improved. Biodiversity may be increased. Trees would be destroyed.
- Very difficult to answer without knowing the human and beaver population densities in a given area; I selected 3 as the most neutral choice to reflect this uncertainty.
- Can cause flooding, road wash outs, etc.
- Hard to assess - depends on land use.
- I don't have a way to value this directly, but since the Pacific salmon generally do better with beaver then it seems it would be positive.
- This is a tough one because beaver reintroduction may lead to economic benefits through increased fish production, but some negative economic impacts for farmers if riparian area is heavily managed for agriculture.
- Beaver dams increase areas of flood plains, thus decrease usable land that humans might otherwise utilize for economic gain. The economic gain from land utilization (e.g., building houses near a river) likely is greater than economic loss due to

decreased salmon populations. Placing an economic value on an ecosystem is quite difficult versus assigning an economic value to utilizing land for a specific human activity.

- Peoples interest in Beaver in Holland is big.

- Mainly due to public interest in beaver activity. We arrange more than 100 excursions each year with beavers as the main topic.

- From a human perspective a negitive one - we tend to want constrained systems with known location of water, known flood impacts etc. - beaver tend to add an element we can't control for landscape type of infrastructure (agricultural land, livestock, infrastructure such as roads and buildings etc.) Note; For a limited number of folks it would be a positive impact. Trappers may suppliment their living with beaver, and some outfitters may target terrestrial species using beaver activity habitat (ducks etc.) Overall this would be small compared to the folks that see beaver activity as a problem to their interests.

- Perceived impact may initially be negative but actual impact generally positive, especially when land managers understand and work with beaver activity patterns.

Item 8: Beavers on cultural value of ecosystem

- A really good beaver pond in a high visibility spot becomes an attraction.

- Beaver will usually modify most man-modified (cultural) landscapes in a way most people (other than ecologists) would perceive as negative.

- High positive impact as a tourist attraction.

- The users of this resource vary from those who want beavers removed and those who love to see them. Currently there is very little trapping pressure on beavers in N. America.

- A wildlife species that can easiliy be observed.

- Again, they are part of the ecosystem. If properly functioning ecosystems are valued, then the components (e.g., beaver) should be valued as well.

- Trapping is practiced by aboriginals and others with traditional value to these groups, particularly in some parts of Canada (e.g. Prairies, north, etc.).

- A cursory review of the folklore surrounding the beaver will tell you that they have had a huge impact on human culture wherever humans and beavers shared the landscape.

- Provides a sense of 'Nature'.

- All species have a cultural value.

- Trapping, viewing and resident trout fishing.

- They are a cultural icon in Canada.

- Benefits & losses.

- People do imagine beavers being destructors.

- Natural history observations could be increased. Duck hunting could be increased. Fur trapping would be increased.

- Not clear what is meant by culture here.

- Marked increase of public visitors in areas with beavers.

- The restoration of natural processes and reintroduction of beaver are typically of high interest to public, particularly in heavily modified landscapes or where beaver no longer exist.

- Depends on the culture. Clearly, they had importance to indigenous populations that evolved along with beavers. They have much less importance in cultures where beavers were extirpated.

- In Canada there is still trapping in the north, with some subsistance on traditional life style.

- Dependant to some degree on the history of beaver in the region e.g. Can beaver activity/ presence be remembered in living memory? If so, cultural value is generally increased.

- Species richness increases cultural value.

<u>Item 9: Beaver activity on geomorphological processes</u>

- In this case I am assuming that beaver were historically present and their activity would restore habitat heterogeneity.

- Some rivers have been greatly simplified by past human activity, added complexity in these systems might be a good thing but I really can't say.

- Beaver impoundments have been shown to mitigate low pH issues in a stream because they retain acid water. But when the impoundment drains this can be a negative effect by driving down pH. In streams where beaver dams exist they flood suitable rearing habitats but if these dams are breached during spring freshets, then the on rush of water can scour the substrate cleaning and improving them for use by juveniles.

- Dams may retain sediments, but sediments loads may increase due to cutting of trees.

- In river systems that beaver occur naturally, they are compatible with and play a role in the long-term evolution of geomorphological characteristics of these systems; introduction of beaver in systems which do not occur naturally may raise compatability questions.

- Increased sedimentation.

- Dams store sediment, whereas most other beaver activity doesn't seem to have much impact.

- Dams store sediments, shape channels and provide heterogeneity.

- The impoundment of water has profound impacts on the geomorphology.

- Sediment transport often impinged; bad for aquatic fauna on low sloped streams; also for first and second order streams permanent dams can result if vegetation becomes established througout the dam site.

- They are a natural part of the river processes.

- Negative impact but species dependent.

- Stream discharges are moderated, so that erosion is decreased. Sediment is deposited in the impoundments.

- Difficult to answer without an understanding of the landscape context; depending on the desired state, impact could be very positive or negative.

- Can cause silt to be trapped, deposited in unwanted areas.

- This one's hard to rate positive or negative; but they definitely alter sediment transport regimes and channel morphology in a significant way.

- Retention of sediment, creation of scour pools.

- Again, in my opinion these systems have evolved with beaver activity - if we look at a stream from a longer time frame (100's of years rather than 10's) this activity is important in channel evolution (flooding, meanders etc. Without beaver activity we tend to have channels with less complex development in the prairie/boreal area.

- Site specific and dependant on scale and time, can be either positive or negative.

- Unsure, but probably enhances these processes.

<u>Item 10: Beaver activity on patterns of river flow</u>

- Beaver activity reduces flow rates and flashiness of streams, good for some species bad for others.

- But scale (space and time) needs to be considered here. In the short term, the impact may be slightly negative but over time the effect is neutral.

- Positive impact for undamable rivers. Beaver dammed tributaries tend to buffer runoff.

- I assign positive here assuming native range. As an invasive many of the same processes could be viewed as negative.

- Beaver dams provide in stream checks that prevent severe erosion during high flow periods.

- In river systems that beaver occur naturally, they are compatible with and play a role in seasonal river flow patterns; introduction of beaver in systems which do not occur naturally may raise compatability questions.

- Slow down flows, increased pike habitat.

- Having a system of beaver dams upstream should increase the ability of the landscape to store water and so ameliorate against flooding or drought.

- Probably do not affect overall flow patterns very much but do help recharge/store groundwater for release during dryer periods.

- This really depends on the classification of the river. A large river the impact is essentially 0, a smaller river it can be 5.

- Low negative impact - natural river alignment.

- They are a natural part of the river processes.

- Negative impact but species dependent.

- Create habitat heterogeneity.

- River flow becomes more regulated.

- Depends on the river that is inhabited. In North America, when *C. canadensis* ocurrs in rivers it is usually in bank dens with little or no damming activity, and rivers that are inhabited tend to be intrinsically "undammable" as well.

- Can cause silt to be trapped, deposited in unwanted areas.

- Effect strong - whether it is viewed as positive depends on one's perspective.

- This one's hard to rate positive or negative; but they definitely alter water storage in a significant way.

- Provides areas of slower flow and creates diversity downstream of dams.

- Activity is important in channel evolution - meaders, oxbows, nutrients, riparian maintenance.

- Dependant on size of river; generally no impact on wide/ slow river flows, with either a negative and/ or positive impact on narrow/ fast stream/ river flows dependant on what's considered positive or negative at local level, regional or national level.

- Re-establishes flood plains/ wetlands.

Item 11: Overall impact of beaver dams on habitat connectivity

- Again - time scale should be considered (as above) . Yes, initially, there is fragmentation as a result of dams and inundation, but effect is usually short-lived, at least in Canadian situations for which I am familiar.

- For salmonids, dams disconnect their habitat to some extent for shorter periods of time. For waterfowl and beaver, the opposite is true.

- When in place beaver dams make it more difficult if not impossible for adult salmon to move upstream to spawning habitats. For Juveniles it reduces their ability to move into sutible habitats as they grow and reduces the amount of available rearing habitat. For Brook Trout (*Salvelinus fontinalis*) that depend on movement as they forage and seek cool water refugia in the hot summer months loss of conectivity can be harmful. Brook trout are known to do well in beaver impoundments, but over time being unable to reproduce beacause they are locked into one place without suitable spawning substrates, their populations disappear.

- May occationally create migration barriers.

- When out of balance (e.g., beaver populations too high and salmon populations too low), there can be negative effects. However, it is not the fault of the beavers that wolf populations are diminished and dams limit connectivity.

- There seem to be positive (e.g. water ponding) and negative aspects (e.g. blocking fish movement for a time) with habitat connectivity; a balance usually emerges in systems which have beavers naturally; beaver dams tend to be temporary structures in the long term and they may contribute to habitat complexity (deeper pools for low flow & winter survival; sediment control; shape stream morphological features).

- No impact in larger (>10 m width) streams.

- Where damming occurs, they will create patches of still water which may reduce connectivity. But then again, dams are temporary and so the long term impact would be slight.

- Provide spatially extensive wetted areas.

- All riparian species evolved with beavers in the habitat. Dams should not be a problem (except maybe for humans).

- Good for resident trout; poor for salmon.

- They can degrade connectivity but this usually short lived.

- Negative impact but species dependent.

- Negative impact only in small rivers less than 0,5 cub.m/s.

- Allochthonous inputs are increased.

- In general, beaver dams in North America do not seem to impede connectivity for many vertebrate taxa.

- Some connection and some isolation.

- For pacific salmon, most adults and juveniles move up and downstream with no problem. Some species have reduced upstream migration in the adult stage, but populations were healthy when beaver were abundant.

- Increases lateral connectivity between river and riparian areas.

- They help maintain connectivity of floodplain.

- Their activities tie together, enhance, and expand rich, diverse, native wetland-habitat complexes in areas where that was once the natural condition of the landscape for millenia.

- Habitat connectivity may be somewhat fragmented on a short time scale due to beaver activity, but species we are familiar with are often found on either side of activity, particularly after a few years. Movements are not permanently blocked, and overall habitat is often increased over the long run (for species that benefit from this type of habitat). Habitat connectivity is probably most impacted during low flow periods, or during extended drought periods - although the impacts of this may be offset from the ponding/ dam habitat created by beaver activity - holding water in the system longer and creating deeper refuge.

- Most often positive except where flooding causes loss of habitat/potential commuting corridors for less mobile species such as flora and possible specialist species that may be restricted to certain habitats e.g. insects reliant on certain tree species.

- On-balance, probably increases connectivity.

- Some temporary reduction of longitudinal connectivity outweighed by increases in aquatic-terrestrial and hyporheic- surface water connectivity.

<u>Item 12: Beaver dams on movement of aquatic biota</u>

- I'd guess this varies a lot by species.

- Same comment as for question 11 (initial negative effect,but short-lived impact).

- Because of the storage capacity many nutrients are locked up in the impoundment and not distributed to the sytem until the dam is breached.

- May occasionally create migration barriers, but in general no effect.

- When out of balance (e.g., beaver populations too high and salmon populations too low), there can be negative effects. However, it is not the fault of the beavers that wolf populations are diminished and dams limit connectivity.

- Probably of minor importance.

- Where damming occurs, they will create patches of still water which may reduce connectivity. But then again, dams are temporary and so the long term impact would be slight. Otherwise, beaver dams are quite porous and so anything small enough to squeeze through shouldn't have a problem.

- Surprisingly, most biota are not deterred by dams as most migrations take place during periods of high flows. Most animals can move around or over the dams.

- Again, the aquatic biota evolved with beavers in the environment -- there should be no problems.

- Good initially, poor after 3 years.
- They can degrade connectivity but this usually short lived.
- Annual flow regime dependent.
- Some dams are barriers to upstream migration of salmonids, and other species such as pike.
- Can cause movement, migration barriers.
- Might depend on flow regime.
- May in certain occasions be a barrier to upstream migration.
- Can inhibit upstream migration of some fish species in low flow years/periods.
- An interesting question. We find the ponds attract certain species of fish, and the seasonal movements are different than if the ponds weren't there.
- All native species have evolved in the presence of beavers over thousands of years, so any "problems" with dams have already been worked out. As for fish, I'm no expert, but I believe most large species will likely stop to spawn well before they get to the average beaver dam, which is typically on a small stream near the top of the watershed. If not, most migratory salmonids, at least, are known to be great leapers, and most beaver dams are relatively short. Moreover, unlike many manmade barriers, beaver dams are not huge, permanent, solid structures. Over the years and decades they go unmaintained from time to time, decay, and develop temporary breeches (during all seasons). Even in the presence of beavers, dams also routinely get beat up by floods (and over-topped) or ice and again become breached, at least temporarily. When beaver dams are maintained, the wetlands they create produce a large amount of food and cover for a wide variety of fish species (as well as hundreds of other native species) at various stages of development. In addition, beaver dams only persist, and generally only occur, on relatively small streams in low gradient areas; "beaver blocks" are a minor issue on large streams or rivers, or beyond a certain, fairly moderate gradient. Beavers are energy economists that typically do not dam persistently in high-energy areas where dams might be regularly destroyed during ice and flood events, or where, because of grade, the "wetland return" is poor. Their survival instinct also tells them that broken dams translate to greater vulnerability to the elements and predators.

  Where beavers, beaver dams, and beaver-created wetlands are present in any significant numbers in a watershed, or in a region, there will be a vast amount of aquatic biota produced and sustained that would otherwise never have had the opportunity to "move" at all. So the total volumn of lifeforms travel through and over beaver dams could conceivably become greater along a particular section of stream than it was prior to the return of beavers.
- Increased surface water area above the dams allows increased movement of aquatic biota. Beaver dams themselves are certainly permeable by small aquatic biota and generally by larger aquatic biota.
- Probably a balanced effect.

Item 13: Beaver activity on habitat heterogeneity

- This is both good and bad. The impoundment can back up water in a stream for many kilometers but when breached by a high water event can improve habitat by scouring out embedded substrate and repositioning large wood and sorting substrates.

- Provides the highest spatial diversity at the landscape scale.

- Beavers tend to encourage heterogeneity by their movement patterns.

- For low sloped (less than 1.5%) heterogeneity is often lost; streams with 2% or higher slopes heterogeneity is only temporarily affected where there is high fall or spring flooding.

- Loss of riffle/ run/ pool.

- Beaver ponds create lentic conditions which allow colonisation of invertebrates and some fish species, which would be less abundant in the original lotic conditions. Also extra marshlands are created, providing habitats for associated fauna and flora.

- Depends on the age-class structure of beaver ponds across the landscape; diverse ages of ponds ususally means more diverse biota.

- Can introduce slow moving, standing water areas that can benefit some species (e.g. brook trout).

- As long as one views greater heterogenity as a positive then it's a 5.

- Phenomenal.

- Activity probably increases habitat complexity over the long run. Without it, many streams would be limiting in over wintering habitat (deep pools) etc. Flooding aids in meander changes, riparian development, etc. Without beaver activity - this would occur less frequently.

- Site specific but generally positive unless existing riparian habitat type/ species composition permanently damaged/ destroyed by activity.

- Greatly increases habitat types.

Item 14a: Beaver activity on species richness (for all biota)

- I think there would be winners and losers.

- By increasing the diversity of aquatic environments in the catchment.

- Depends on the scale of examination. Diversity may decline at the scale of the dam/pond but will increase markedly at the landscape scale.

- Beaver areas are much more diverse.

- No impact except on low sloped streams.

- Winners & losers.

- At landscape scale, not locally.

- May provide more diversity in benthos production which could benefit fish feeding.

- Generally the aquatic species are there with or without, but relative abundances of species can be changed dramatically with beaver activity. Wetland plant species likely increase in richness when beaver are present.

- See PhD of Kevin Jones, University of Stirling.

- Typically in areas were beaver have been extirpated there is a reduction in flora and fauna dependent upon wetlands and beaver ponds.

- Really depends on which taxa you are referring to, but generally speaking does improve Species Richness.

- Deeper habitat is created, sediment deposit in deep pool habitat creates substrate that supports different biology than faster flowing rock substrate etc.

- Provided the habitat had an exsisting species source or provided a corridor to a reasonable source, beaver activity generally has a positive effect on species richness.

<u>Item 14b: Beaver activity on species richness (for fish species)</u>

- The impoundments favor non-indigenous warm water species i.e small mouth bass (*Micropterus dolomiue*) over native cold water species i.e. brook trout and Atlantic salmon.

- Can give local problems for brown trout.

- By increasing the diversity of aquatic environments in the catchment.

- Depends on the scale of examination. Diversity may decline at the scale of the dam/pond but will increase markedly at the landscape scale.

- Now, this depends on the species. Since beaver areas increase aquatic insect biomass (and amphibians) and primary productivity they should encourage both herbivores and carnivores -- but for some fish species slow water may not be as desirable.

- No impact except on low sloped streams.

- Winners & losers.

- At landscape scale, not locally.

- Can create habitats for unwanted species (e.g. cyprinids, etc.).

- Generally the species are there with or without, but relative abundances of species can be changed dramatically.

- Beaver ponds must provide a niche for some fish species.

- Typically in areas were beaver have been extirpated there is a reduction in flora and fauna dependent upon wetlands and beaver ponds.

- Depends on what scale you are looking at. I don't know that richness is improved so much as abundance, but some literature points to increased richness.

- Some richness modeling I am familiar with indicates richness goes up when a stream habitat is located close to a waterbody capable of supporting overwinter habitat (usually of a certain size and depth). Beaver activity creates some of this habitat. With out it, richness, and in some cases the presence of game fish (rather than course or forage fish) is less. It also seems to provide for a potential to increase richness/game fish presence higher up a watershed e.g smaller stream orders may have more fish species simply because beaver activity makes it possible to overwinter.

- Generally positive with beaver dams and ponds providing nutrient (food) rich environments and sheltered/ protected areas for many spawn. Although, possible warmer temperatures may impact on salmonids, the positives may outweigh any potential negatives.

Item 15a: Beaver dams on upstream movement of migratory salmonids (in main-stem rivers)

- Beavers do not dam the main stem rivers I have worked in.

- Main-stem rivers won't normally have beaver dams.

- Negative impact but natural part of system, usually contributes to important spatial and temporal heterogeneity.

- Beavers rarely dam mainstem rivers.

- Fish can't move to spawning areas and either don't spawn or choose poorer substrates for spawning.

- Trouts have adapted to beaver generated conditions where they occur naturally.

- Beaver very rarely dam in bigger river channels.

- I know this is always touted as a potential problem, but the reality is that salmonids evolved with beavers on the streams and with beaver dams. There should be no problems.

- Occassionally can disrupt migration on rivers with low slope conditions.

- Usually very limited activity in mainstems.

- Worse in upper reaches.

- Usually beavers are not able to impound rivers biger than 0.5 cub.m/s.

- Pacific Northwest mainstem rivers are generally too large for beaver to dam. Secondary channels on floodplains are dammed, but there are multiple migration pathways available in large rivers with multiple channels.

- Dams not usally constructed.

- Would only possibly affect passage during periods with little flow (drought conditions), but unlikely that beavers could build high enough dams on mainstem rivers to impede passage. Most flow conditions would likely keep dams to a small size.

- See response to 12.

- Not usually permanent blockage.

- Beavers tend not to dam main-stem rivers so not likely to impact on upstream migration. Although, beaver food caches and bank dens may offer some cover for migrating salmonids.

Item 15b: Beaver dams on upstream movement of migratory salmonids (in tributary streams)

- I wouldn't expect it to be a big problem except for perhaps increased predation (if you have animals that prey on returning salmon in the UK).

- A negative impact is highly dependent on water flow conditions. During autumn in most Canadian situations when beavers build dams and salmonids are migrating, there is a high probability that we will get rains and high water that make breach dams, even temporarily, that permit fishes to migrate around the dams. High spring flows typically remove dams so that spring migratory movements are usually not a problem.

- Minor, but some impact.

- Fish can't move to spawning areas and either don't spawn or choose poorer substrates for spawning.

- May temporarliy prevent migration of some sizes of fish.

- Can be significant when beaver populations are too high.

- Local problems can occur.

- Salmon obvioulsy will find it more difficult to get past a stretch with beaver dams than one without, but it is probably not a complete barrier. Combine this with the ephemerel nature of many beaver dams and I would suspect that the overall effect is slight.

- In specific cases they can slow/ stop movements but this has a temporal component. At the scale of seasons or years, nearly all dams are passible.

- Second and third order streams, (if low sloped (less than 1.5-2%) can be blocked by dams to migratory salmonids.

- They can impede upstream movement within tributaries.

- Worse during low flow years.

- Might be a problem if juvenile densities are high and result in marginal habitats (like tributaries) being selected as habitat by dispersers.

- Might block some depending on timing of movement but will also moderate flows.

- I've seen little evidence that fish migration is blocked by beaver dams, although delays in migration sometimes occur when flows are low and adults wait for increased flows. The effects likely vary by species.

- Impact not fully known.

- Can inhibit migration of some salmonid species.

- It depends on flows during the time that adult salmon migrate. Adult salmonids could likely 'jump' or navigate the height of nearly all beaver dams as long as it was during a period with flow in the river. Dams do not stop flow, they just impound water. Historically, salmon that existed in streams with beavers migrated mostly during periods of time when sufficient water existed to provide a passage route over the dams.

- We find the ponds have high rates of juvenile salmonid use and that adults are able to jump most dams.

- Most indigenous species have evolved with this type of activity - short term movement impacts probably occur, but for species like brook trout - may end up using the habitat to its advanatge over the long term.

- Same as 14.b, but possible that dams may be more of an obsticle to migratory salmonids, although smaller dams may not prove much of an obstacle, with gaps in the dams also providing access upstream. Artificial fish runs linked to beaver deceivers can be used to provide salmonids ways around potential obstacles (such as beaver dams) and/or measured direct management of beaver activity can be used, if necessary.

Item 16a: Beaver dams on downstream movement of migratory salmonids (in main-stem rivers)

- No impact because mainstem rivers not blocked.

- Except where the head pond level is much lower than the dam level this is not a problem.

- Trouts have adapted to beaver generated conditions where they occur naturally; usually less interference than upstream movement.

- None, or very few dams.

- If species evolve using the same water courses then they must have been selected for this and should be adapted to the beaver dams.

- Worse in low flow years & for fall spawners.

- Typically fish have few problems migrating downstream over obstructions.

- Very few dams will occur or endure in these rivers. In respect to all dams, however, it is possible that, on average, over the years and decades, they might actually improve fish movement and aid reproductive success. For example, it is easier to swim through a reservoir than a shallow stream. The pools also offer improved protection from predators, a wealth of food, and a refuge from the energy of the stream. If the migrants stop and safely rest and replenish, then the beavers are lending energy to, and improving survivorship in, the overall migratory effort. If the wetlands also act as nurseries for young fish then there may be a lot more fish in the future attempting to negotiate these barriers, which will probably increase the number that are actually successful.

  By necessity, the statements in the survey simplify conditions on the ground. For example, in addition to dam-building activity the presence of beavers means an enormous amount of dredging behavior. They are constantly creating and maintaining canals that could, theoretically, improve fish passage over the unnatural, possibly silted-in, beaver-free streams that existed in the centuries between extirpation and recovery. The dredging also creates more "deep hole" hiding places from predators, habitat diversity, nutrient re-circulation, and many more invertebrates for consumption. The sequestering of silt and other pollutants behind dams that are typically near the top of watersheds could, in downstream areas, improve general habitat quality---possibly increasing the number of spawners that begin the process----and the quality of spawning habitat. It could also help prevent the silting-in, and possible blockage, of downstream sections. The negative-positive formula is incomprehensibly complex, and it differs at every site. However, the positives invariably outweigh the negatives by a long, long margin, particularly when one starts to talk about all the lifeforms in an ecosystem.

Item 16b: Beaver dams on downstream movement of migratory salmonids (in tributary streams)

- Salmonids are able to get past them, particularly during spring flows, but some obstruction possible.

- The same would apply here except in smaller tribs brook trout would be more prevelant.

- Can be significant when beaver populations are too high.

- No problems in larger streams.

- I hadn't considered this one before, but given that dams will have deeper water on the upstream side with some flow over or through the dam, I'd imagine that they would not present much of a barrier to smolt.

- No real impact due to seasonality of flows.

- Migration on low sloped streams can be adversely affected.

- Worse in low flow years & for fall spawners.

- Neutral or weak negative impact; usually there are gaps in a dam.

- Impoundments created by beavers may provide safe areas/ rest sites for downstream movement of migratory salmonids and beaver dams become less of an obstacle.

<u>Item 17a: Beaver dams on movement of other fish species (in main-stem rivers).</u>

- May be a problem for some.

- Juvenile sea-run alewives have been observed holding upstream of a dam waiting for high water to get to the ocean.

- I guess some problems for larger white-fish species.

- There are rarely dams on main channels.

- I don't see any long-term problems here since beaver dams are not the permanent structures that human dams are. They are porous at times (due to increased stream flow) and beavers do move out after a time and dams readily break down.

- Worse in upper reaches.

- Usually beavers are not able to impound rivers bigger than 0.5 cub.m/s.

<u>Question 17b: Beaver dams on movement of other fish species (in tributary streams)</u>

- Temporary isolation may be a good thing, so I say negative impact here because movement is reduced, but this may be a good and natural feature of native systems.

- Can be significant when beaver populations are too high.

- Beaver dams are ephemerous, and so have no effect on the long term population dynamics of non-migratory species.

- Positive impact except low sloped streams.

- Worse during low flow years.

- Up to no impact, because beaver dams are the short-lived structures and usually broke to some extent even within one year.

- Resulting isolation may increase biotic diversity, however, so the affect may be positive or negative depending on the desired state.

- Depends on species.

- At some times of the year and for smaller species, beaver dams are of sufficient height that they can preclude the ability of fish to move upstream. They likely do not affect downstream passage.

- Prairie species are sometimes blocked by new activity (poorer swimmers than salmonids), but again, over a longer period they move around during higher flow periods (or move through it), and then often benefit from the activity with more complex habitat, better over wintering habitat etc.

- May provide temporary obstacles to movement. But long term probably positive, with beaver dams and ponds providing nutrient (food) rich environments and sheltered/ protected areas for many spawn and adult fish to build up energy reserves before moving on.

Item 18a: Beaver activity on availability of suitable spawning habitat for (migratory salmonids)

- Could impound all spawning areas if there were enough of them.

- Only in rare circumstances, in tributary streams with limited spawning substrate might this be an issue.

- The impoundments flood habitat but often in the scour pool and shoal below the dam Atlantic salmon have been observed spawning.

- Dams can silt behind but reduce silting downstream; on whole watershed scale trivial in any case.

- Can be significant when beaver populations are too high.

- A balance usually develops in systems that beaver occur naturally.

- I have no knowledge of any problems on this.

- On one hand, beaver ponds are not suitable spawning habitat, but on the other, sediment retention by dams should keep downstream gravel-beds clean and improve existing spawning grounds. Also, no dams on big channels, so the overall affect might be neutral.

- This depends on the stream order and period of flow. I've seen both introduced salmonids in small mountain stream spawn in beaver areas as well as a migratory species. The only problem I could see would be if the stream is very slow moving and has a great deal of sediment. But I've never observed this in the US.

- Minimal on larger (4th order + streams); negative impact on low sloped, smaller streams.

- Beavers tend to create dams at outlets or at the end of steadies, both these locations can also have suitable spawning gravel.

- 1 - grayling; 2 - browns; 3 - brook trout.

- Negative impact - sediments usually cover the bare mineral substrate.

- Damming may inundate spawning habitat, but any negative effects would depend on whether spawning habitat was limiting or not in the main stream.

- Some loss in the ponds but perhaps some gain in flow regulation and channel complexity.

- May be a slight impact where ponds drown out reaches with spawning.

- Dammed areas typically have little spawning habitat as they accumulate fine sediment though occasionally fish spawn downstream of dams or in gravel accumulated at upper end of beaver pond. Also lowering of stream gradient by construction of many dams can lead to a meandering channel with considerable suitable spawning areas.

- It would depend on the number of beavers. If populations were so high as to turn a stream system into just a series of pools, with little to no free-flowing water with suitable gravel, then they could eliminate spawning habitat. On the other hand, the benefits of having some pools for rearing might offset and actually improve overall abundance of species.

- There are both positive and negative effects. The negative effects come from siltation following dam construction, and the positive effects follow dam abandonment after the pond fills with sediment. In our systems we find the surface substrate contains good spawning gravels. Also, downstream of the dams there appears to be increased steelhead spawning, possibly due to increased upwelling.

- With brook trout, for example (and in my experience), "beavers in the system" means a lot more, healthier fish available to spawn in the first place. I have measured the extent of beaver-damming habitat in a watershed in Maine, USA (gently rolling hills). It was only 1.5 % of the entire watershed (again, low-gradient areas on small streams). Therefore, the vast majority of overall brook mileage in most watersheds will continue to babble regardless of the presence of beavers. This is why, even if dams were a serious impediment, native fish species would likely do just fine (notwithstanding the potential "human factor": destroyed habitats and enfeebled, over-exploited populations).

- Not often a net gain in this type of habitat.

- Beaver dams on gravel bottomed streams will reduce the availability of spawning habitat for migratory salmonids, however, beavers tend not to dam on fast flowing gravel bottomed streams as the surrounding environment/ habitat is often too resource poor and the banks unsuitable for bank dens. Also, the velocity of the water makes the damming and maintenance of the dam difficult.

Item 18b: Beaver activity on availability of suitable spawning habitat for (other fish species)

- Depends on species.

- My guess is that if they could get into an impoundment, alewives could use the slow deadwater for spawning habitat. Bass could make use of it as well. Brook trout habitat would be flooded as a result of beaver dams.

- Dams can silt behind but reduce silting downstream; on whole watershed scale trivial in any case.

- A balance usually develops in systems that beaver occur naturally.

- It would depend on the species, but I'd imagine you have the same balance of issues as 18a (On one hand, beaver ponds are not suitable spawning habitat, but on the other, sediment retention by dams should keep downstream gravel-beds clean and improve existing spawning grounds. Also, no dams on big channels, so the overall affect might be neutral).

- 4 - northern pike & cyprinids; 1,2 – sculpins.
- Positive for species that spawn in shallow water, on underwater vegetation.
- Depends on species.
- Depends upon spawning habitat preferences of other species.
- Depends on species and whether they require pools or streams with riffles for spawning.
- Species that like flooded vegetation or slow water habitat may see some gain for the time a dam is in place.
- Generally positive on beaver dams as the debris from cut/ fallen wood and the warm pond edges provide a variety of suitable refuge and spawing areas as well as a suitable environment for alevin/ fry growth.

Item 19a: Beaver activity on availability of suitable non-spawning habitat for (migratory salmonids)

- Sometimes inundated areas, especially in small tributaries provide suitable winter habitat.
- The impoundments flood juvenile rearing habitat.
- Can be significant when beaver populations are too high.
- A balance usually develops in systems that beaver occur naturally.
- Woody debris, both from dams and from beaver felled trees, are likely to be very good for fish. A greater diversity of flow types as a result of damming may also benefit fish. However, increased water-temperature in ponds may reduce oxygen availability in dam sections.
- Usually provide the best rearing habitat for several species of juvenile Pacific salmon.
- Beavers should increase the total fish biomass.
- Aquatic insect production areas negatively impacted.
- Generally due to a reduced ability to migrate to the upstream side of beaver dams.
- Species dependent; worse for Arctic grayling.
- More prey in beaver ponds.
- Increase in off-channel rearing.

- Can be both positive and negative depending on the species. Increased availability of lentic habitats for those species that require them. For those species or life stages that require higher velocity habitats and coarser substrates, habitat availability is slightly reduced.

- Evidence from USA that woody debris can increase densities.

- Depends on habitat preferences of species, those that like slow water areas tend to benefit from beaver activity.

- Historically beaver dams provided good pool habitat that increased survival of juveniles.

- We see a lot of use by juvenile salmonids, primarily steelhead and coho, but also chinook.

- For brook trout in our area this habitat is often winter habitat - and sometimes the only winter habitat for the smaller stream that have been stocked.

- Generally positive with the slower water velocity and edge to surface area ratios creating a more productive environment which provides both food and shelter for migratory salmonids which allows them to conserve more energy than when foraging in higher velocity streams. However, beaver ponds may provide predators with easier pickings.

<u>Item 19b: Beaver activity on availability of suitable non-spawning habitat for (other fish species)</u>

- Impoundment would increase habitat for small mouth bass, chain pickeral (*Esox niger*) and cyprinidae species. Conversely, chain pickeral and bass are predators on juvenile salmonids.

- Can be significant when beaver populations are too high

- A balance usually develops in systems that beaver occur naturally.

- Woody debris, both from dams and from beaver felled trees, are likely to be very good for fish. A greater diversity of flow types as a result of damming may also benefit fish. However, increased water-temperature in ponds may reduce oxygen availability in dam sections.

- Resident species (cyprinids and resident brook trout) usually benefit.

- Beaver ponds are actually highly productive areas and tend to be hotspots for resident fish (especially brook charr).

- Better for brook trout.

- Better feeding conditions.

- Depends on species.

- Can be both positive and negative depending on the species. Increased availability of lentic habitats for those species that require them. For those species or life stages that require higher velocity habitats and coarser substrates, habitat availability is slightly reduced.

- Depends on habitat preferences of species, those that like slow water areas tend to benefit from beaver activity.

- Likely increased populations because of favorable habitat for prey eaten by fish.

- I think the literature shows a number of North American fish species that utilize beaver ponds.

- Beaver activity creates habitat that species like northern pike use (slower water, with emergent vegetation etc). Forage fish (various minnow species) also benefit from this type of habitat.

<u>Item 20a: Beaver activity on abundance of (migratory salmonids)</u>

- Depends on the number of beavers and the species of salmonid.

- This can be a problem in low gradient streams and where beaver density is high such that dams are not seasonally breached and displaced by seasonally high streamflows.

- Increased beaver activity has a negative impact on salmoninds due to loss of rearing and spawning habitat.

- It may limit distribution in some instances, but beavers also influence nutrient flow and other ecosystem processes. When in balance, these effects are generally positive.

- A balance usually develops in systems that beaver occur naturally.

- On one hand, dams may slow migration in smaller tributaries, but the benefits of increased woody-debris throughout the whole system may outweigh this.

- Coho smolts from beaver ponds are generally in better condition than those from stream habitat. The assumption is that there is a better smolt-to-adult survivorship in the smolts from beaver ponds.

- I see beavers as actually encouraging these fish since they evolved together and it is artificial to not have beavers in the systems.

- Negative impact due to small, lower sloped streams.

- Negative impact due to reduced spawning habitat.

- They usually spawn in larger rivers, where beavers have very weak impact on spawning conditions.

- Our studies show dramatically increased abundance of both coho salmon and steelhead when beaver dams are present.

- Overall it tends to be positive, but may lead to changes in dominant species.

- Quite important historically for coho salmon, possibly for some trout species.

- For brook trout in our area beaver activity is something that enhances local populations - sometimes it is specifically protected to ensure their survival locally.

- The potential benefits of increased foraging (protection) and smolt growth offered by beaver ponds may increase abundance levels.

Item 20b: Beaver activity on abundance of (other fish species)

- Depends on the species. For example, lamprey can benefit from increased siltation resulting from woody debris in streams.

- A balance usually develops in systems that beaver occur naturally.

- Via increased prey abundance from woody debris and ponds.

- Winners & losers.

- It depends on species, small salmonids could suffer from beaver activity in small rivulets, some cyprinids could benefit.

- Depends on species.

- Overall it tends to be positive, but may lead to changes in dominant species.

- I do not know in context of overall changes in abundance for all species. Anecdotally, when I was young and went fishing with my father, we would seek out beaver ponds as that was where we were most likely to find the highest abundances and the biggest trout.

- Benefits for some species such as pike.

- As discused above the more productive (protection) environmant created by beaver ponds will generally increase abundance levels.

Item 21a: Beaver activity on productivity of (migratory salmonids)

- In the long term, when considering river systems and riverine fish populations, I consider the effect to be positive for all fishes.

- Reduced habitat due to increased beaver activity means less production.

- A balance usually develops in systems that beaver occur naturally.

- Stream size dependent.

- On one hand, dams may slow migration in smaller tributaries, but the benefits of increased woody-debris throughout the whole system may outweigh this.

- Historically, rivers in North America (east and west) had abundant beaver and salmon populations. They had thousands of years to 'adapt' to each other and did quite well. The data available suggest that beaver provided productive habitat for salmonids at a variety of spatial and temporal scales, and through a number of biophysical pathways and processes. In my opinion, the removal of beaver has been highly detrimental to salmonid productivity.

- I think the effects will be profound. The return of the beaver will begin to restructure the riparian systems and the salmonids should be beneficiaries of this.

- Siltation and access problems to smaller streams.

- Worse for grayling.

- Overall it tends to be positive, but may lead to changes in dominant species.

- Productivity is really hard to quantify in salmonids, and demonstrating that beaver ponds have had a quantifiable effect on salmonid productivity. I think it is likely, but I sure don't know of any data that convincingly demonstrate this.

- Brook trout in Saskatchewan probably have increased productivity due to increase in habitat complexity associated with ponding etc..

- Positive effects on nutrient dynamics (P release), overwintering habitat potentially outweigh beaver dams as partial barriers**.**

Item 21b: Beaver activity on productivity of (other fish species)

- I would guess that impoundments would help warm water species.

- A balance usually develops in systems that beaver occur naturally.

- Via increased prey abundance from woody debris and ponds.

- Beavers seem to support most fish species in most habitats.

- Species dependent.

- Depends on species.

- Overall it tends to be positive, but may lead to changes in dominant species.

- Forage fish population probably icrease with some of the habitat created by beaver activity - this may translate into increased productivity of larger bodied fish as well.

Item 22: In the space below, please provide additional comment or caveats in relation to any of the above questions, other issues related to beavers, questions, or concerns regarding design of this questionnaire. Details or links to any grey literature source of information would also prove useful.

- I did not like the valuation portion of these questions. As in any response to a perturbation in a natural system, some elements benefit and some lose. For example, beaver dams can reduce access to spawning areas and reduce spawning substrate for salmonids or lampreys. However, increased siltation provides habitat for juvenile lampreys and spawning areas for alosids. If beavers are allowed to completely impound an area, they can significantly reduce habitat for some species. However, the absence of beavers has been linked to coho salmon reductions because beaver impoundments are needed for juvenile fish rearing. Some good examples are available in recent work by Phil Roni.

- Beaver are a factor in the US Pacific Northwest. They are generally thought to be a good thing on balance, but of course the changes they effect in the habitat are good for some purposes and bad for others....and it's all a matter of how much beaver activity, large numbers of them can totally alter the character of a stream (obviously).

- There is still a lot that we don't understand about the role of beavers in stream ecology and productivity.

- This questionnaire would have been of much greater value to the reintroduction process had they been directed to Scottish riparian ecosystems, instead of aquatic ecosystems in general. Most of these questions have been impossible to answer accurately.

- Most of my comments are based on the presence of beavers in their native range. They are known to have dramatic effects on the ecosystem level, affecting many facets of diversity, forest structure, sedimentation, etc. They trap sediments and form meadows, improving rearing conditions for a number of fish species by keeping gravels clear in free-flowing reaches. Beaver ponds support a diversity of fauna, much of which becomes food for fish. They are problematic for humans, though, and can do substantial damage to septic systems, roads, etc. So economic impacts will vary and depend on context.

- Here in Maine beavers are reviled to some degree. They cause road wash outs because they plug culverts or build dams near bridges. Brook trout fishermen like to fish beaver ponds beacause trout that live there can grow to large size. But without access to spawning gravels they are unable to reproduce. Some of the problems with beavers stem from current forestry practices that allow cutting to with 200 feet of a stream. This distance is well with in the zone of comfort beavers have to move away from water. They then take advantage of the new tree growth that occurs in riparian zone where pioneer species such as red maple and alder grow. Anecdotally, I have noticed over the years that where forestry practices (determined by individual landowners) were implemented where the buffer was much greater that 200 feet, beaver activity was diminished possibly because they could not safely get to a food source and so moved out. It is my opinion that if beavers already exist in Scotland that they be left to distribute themselves on their own. Many times when humans try to "fix" something they broke the result can be even worse that the intial problem. Actions in the Florida Everglades for mosquito control come to mind.

- I would rate my knowledge of this issue as expert as I have gone into it in depth, as far as the limited research done permits (entirely because of British concerns on the issue. It is not an issue in Norway or elsewhere in Scandinavia, though beaver are well established on many salmon rivers - e.g. on 6 of the top 10 by catch weight in Norway), because I have lived and worked for 15 years in a region containing both many beavers and a number of economically important salmon rivers (e.g. Orkla, Gaula, Namsen, Stjørdalselva, all of which have well established beaver populations), and because I conduct research on beavers and beaver management. I don't think anyone is an expert in terms of having an in depth scientific knowledge of the issue because the body of data doesn't exist. This is itself a proxy for how seriously the issue is perceived in places that have anadromous salmonids and beavers.

My main concern with the design is the issue of scaling. An individual Eurasian beaver dam or group of dams may in certain circumstances (and not in others) hinder upstream migration to some degree, and/or provide a refuge in drought conditions, and/or beaver pond habitat in which Atlantic salmon fry grow larger, faster: there are individual studies to suggest or indicate these and other effects at individual sites and time periods (e.g. Sigourney *et al.*, 2006). But for this to affect the overall population of adult fish returning to spawn on the whole watershed is another scale entirely. Most Eurasian beavers do not build dams, most tributaries are not dammed in fact, even where beaver populations are at capacity on a watershed. Only if, e.g., spawning habitat or fry growth habitat were limiting at a watershed scale and damming then lead to a reduced/enhanced number and/or quality of smolts proceeding to sea to a significant degree, would the adult population be likely to be affected either positively or negatively. No one has ever demonstrated anything even approaching such a major effect from what is, in Eurasian beavers especially, a relatively uncommon and peripheral activity. I have therefore chosen 3 as my response to most of these questions. The detailed effects of an individual dam or dam series can be complex, positive, negative, and/or neutral, and variable over time; but either way, the sum of all dam effects is trivial on the scale of a whole watershed.

It is immensely hard to prove a negative, in the absence of very thorough scientific investigation of the issue, of which there is almost none on Eurasian beaver damming, and little on N. American beaver damming. Given the lack of perception of a problem sufficiently significant to spend research money on in what is otherwise a heavily monitored and researched field (factors affecting salmonid populations), in Scandinavia and elsewhere, one falls back on anecdote, or, as in this case, opinion polls.

As an anecdotal example, the Namsen is the no.3- no. 5 watershed in anadromous salmonid catch weight terms depending on the year - of several hundred such watersheds - in Norway (source: Statistics Norway, www.ssb.no) and the sport fishery of major importance economically and socially in the district. Beavers are common, so much so that hunting is 'quota free' in season (usually quotas are set in most of Norway). The salmonid population is closely monitored, and salmon spawn on every one of the tributaries assessed in the annual monitoring program, most of which are potentially dammable. The annual report on salmonid population spawning and factors influencing it, 'Spawning and fry of salmon and trout in the Namsen, North Trøndelag, in 2006' (Berggård & Berger 2008; online at http://www.namsenvassdraget.no/filer/20080515162142.pdf) does not mention beavers even once (Norwegian for beaver is 'bever').

Similarly, on the Orkla (no. 4 in catch weight) the 'Management plan for beavers along the Orkla and its larger tributaries' (Bonvik & Rønning 2006; http://www.meldal.kommune.no/download.asp?dafid=1179) mentions in passing that it has occasionally been suggested that the beavers might affect salmonid populations, but that there is no evidence of this; the subject occupies 3 sentences of a 43 page management plan working at the scale of individual beaver territories. In 'Orkla, a national reference watershed for studies of population regulating factors in salmon' (Hvidsten et al 2004; http://www.nina.no/archive/nina/PppBasePdf/fagrapport/2004/79.pdf), summarising a great deal of research on the Orkla watershed, beaver or their dams are again not mentioned once, in 96 pages.

In 15 years working on beavers in Norway I've perhaps heard 2 or 3 times, at second hand or from a paragraph in a local paper, that someone thought a dam might be hindering sea trout migration; in each case the evidential base appears to have been casual observation. I then heard no further on it. An internet survey of Norwegian angling blogs found nothing on beavers, apart from an anecdote about snagging a fishing fly in a beaver's fur.

Parker & Rønning (2007), in a refereed paper on a capacity population of beavers on the Numedalslågen (no.8 in anadromous salmonid catch weights) found that even if dams were assumed to always hinder migration (which they did not test), they were so uncommon and peripheral structures at a watershed scale as to be 'insignificant' for anadromous salmonid populations.

It should be noted that one of the significant differences between Eurasian and N American beavers is in damming behaviour. To summarise, N. American beavers build more often, and their dams are deeper and longer on average (this is not to deny extreme cases in *C. fiber*, e.g. from a mountain region of Poland (Zurowski 1989) where 24 dams were constructed along a 1.3km reach).

I have never seen a Eurasian beaver dam series approaching the number, length, and depth of some of the series I know from N America, and I know *C. fiber* much better than *C. canadensis*. The incidence of dam building in *C. fiber* varies with the terrain. In my region of Norway, reminiscent in relief of e.g. Atholl or Strathspey, the modal and median number of dams per territory is zero; where they are built the mode is 1 and the median either 1 or 2; the maximum I have seen 4. In flat NW Russia, *C. fiber* beaver dams were found on 19, 26, 29 or 53% of territories, depending on the region (Danilov & Kansh'iev, 1993). On gently rolling terrain in NE Poland Zurowski and Kasperczyk (1986) found damming at 50 of 257 territories, or 19.5%, in a population at or near capacity numbers. In hilly terrain (similar to the central Highlands of Scotland) in SE Norway, Parker & Rønning (2007) found of 29 territories in their capacity population that 3 (10.3%) had actively maintained dams. There were also two dams no longer maintained, which would have been breached at the next spate; on average there was one dam per 14.3km of tributary stream length suitable as beaver habitat. More anecdotally, a colleague who works professionally on beaver dams in the US, and is familiar with *C. fiber*, (name on request) states: "While reading about the relative paucity of damming behavior in Europe, my North American bias is revealed as I find myself wondering how "one" can even be a beaver without building dams all over the place". Danilov & Kan'shiev (1993), discussing a mixed population of *C. canadensis* and *C. fiber* in northwest Russia, state that in contrast to *C. fiber*, where construction seems facultative (see also Hartman & Törnlov 2006), "in Canadian beavers, high building activity (of dams and lodges) seems to be due rather to ecological characteristics of this species than to habitat conditions" .

As an example at the higher end of *C. canadensis* damming behaviour, take the Mitchell & Cunjak (2007) paper recently cited in Britain as evidence of a barrier effect of damming on salmonid migration (though inferences are, as the authors clearly state, confounded by the differing environments resulting from a systematic change in hydrology unrelated to the dams, see discussion second sentence; and salmon remain common - the commonest species of all in riffle and run habitats - above the dams - see Figure 6). It concerns a series of in any year between 6 and 12 dams, at least one of which was 2m high. Hartman & Törnlov (2006) provide a quantification of the usual characteristics of Eurasian beaver dams; in them the water level was raised on average 0.46m (SD: 0.21m); average depth before damming 0.36m (SD: 0.14m); average width of the stream dammed 2.5m (SD: 1.1m). I have never seen a Eurasian beaver dam series of the magnitude of the series reported by Mitchell & Cunjak, although I have seen many, mostly in terrain of Caledonian orogeny geology, strongly reminiscent in landforms of parts of the Scottish Highlands (the main salmon rivers of Norway are not in the classic fjordland landscape, and neither are the main beaver populations).

Naïve extrapolation of *C. canadensis* damming behaviour to a different species should therefore be avoided, in the same way as, e.g., naïve extrapolation between coho and Atlantic salmon behaviour.

A corollary is that Eurasian beaver dams are rarely of significance to the conservation biology of a population - beaver preferred habitat is habitat in which damming is not necessary, and dams are, in the majority of territories where they occur, not crucial to the viability of the territory. I am very relaxed about dams being removable at landowner discretion, except perhaps in the period where there are dependent young in the lodge/burrow and its entrance is kept below water by a dam (only 10% of dams had this function in Hartman & Törnlov's (2006) study) . This is primarily for human social, and not economic or ecological, reasons. In Parker & Rønnings (2007) study, 5 of 14 riparian landowners had removed beaver dams at least once in the 49 years since recolonisation (though never for suspected hindrance to fish migration).

In summary, Eurasian beaver damming effects on watersheds are on a larger scale generally underwhelming. There are of course significant impacts, most often on bankside vegetation and sometimes highly conspicuous to humans, but these are normally intensely local in scale. Visitors I have from the UK sometimes seem slightly disappointed with the reality.

- Beavers have expanded tremendously in Noway in recent years after being more or less extinct. As a central salmon researcher in Norway (including leading the Standing Scientific Committee on Atlantic salmon Management) I get all sorts of questions and reports from locals all over the Norway. I have never had any concerns/complaints related to the interaction between beavers and salmonid fishes (anadromous or resident).

- Several reports from the grey literature suggest that beaver activity can limit spawning and rearing habitat use, particularly in small tributaries. However in my view, it must be understood that these are proximal not ultimate causes of salmon declines. In the U.S., salmon populations are at all time lows because of a myriad of other factors (dams, pollution, marine survival, etc.). Beaver were a part of the freshwater ecosystem that salmon evolved to cope with. They should be viewed in that light; that is, part of the solution, not part of the problem.

- Beavers where they occur naturally are a factor in the evolution of natural ecosystems; usually they are contributing to the maintenance of healthy ecosystems in several parts of Canada which are characterized by colder climatic conditions and low slope rivers; beavers may assist with low flow & the winter survival of fish.

- Obviously there are a miriad of effects that beaver will or might have on the aquatic ecosystem. Overall, I would imagine that these effects will sum up to being if not positive, then at least not negative since all native aquatic species must have co-existed with beavers in the past.

- Note: many of my responses are rated 3-5 meaning that I think there would be no impact or a highly positive impact.

My view is simple. Beavers were an active and important component of the riparian systems along with all fish species for thousands of years. They evolved together and I'd expect no negative impact of beaver activity. My own observations in both the western and eastern US indicate that the fish community is both richer and higher in biomass when beavers are present. While not related to fish (directly) the case of the wolf reintroduction into Yellowstone NP in Wyoming illustrates how ecosystems can be influenced by a keystone species. In the Lamar Valley beavers had been present in the late 1800s but not present by the 1900s. When wolves were introduced beavers came back to this area in a few years? Why? The wolves (who do prey on beavers when they can) reduced the elk (American elk, not moose) population along with the deer population. This reduced the pressure on the riparian vegetation and beavers moved back in. The point? A keystone species can and does have tremendous positive impacts on the ecosystem function. I'd bet that beavers being reintroduced in the UK would have positive ecosystem impacts.

- In Canada we are fortunate to have high fall and spring flood conditions that usually provide fish passage especially on larger streams; we have many beaver that we call "bank beaver" that live in the shoreline gravel-mud rather than houses built from sticks as they are on smaller lower sloped streams or headwater streams. Perhaps the most important problem is silt build-up in smaller, lower sloped streams that can last for years; secondly, sea-run trout home to one or several pools in smaller headwater streams, and beaver dams constructed in June can block migration and endanger the run of several hundred fish to predators.

- The effects of beaver on salmonids are highly species-dependent. For this reason, many of my answers are based on "average conditions". My personal experience is that beaver are much more detrimental to Arctic grayling than to brook trout; with brown trout being intermediate. Therefore my ratings reflect these differences. It may have been better to have the respondents complete a separate form for each species (or species group). I would be willing to do this if requested. The major adverse effects on fluvial salmonids in my experience include: delay or blockage of spawning migrations, and inundation of riffle/run/pool assemblages. The latter results in lower habitat diversity and reduced availability of spawning habitat. Again, the movement and spawning habitat issues appear to be more detrimental to grayling than brown trout and brook trout; the latter species appear to me more adapted to exist in beaver-controlled systems. Much of this I believe to be due to the fact that brown trout and brook trout are late fall spawners, are less migratory, and are already located in relatively close proximity to their spawning areas. Grayling, on the other hand are entering the spawning streams in the spring and are dependent upon freshet-flows to breach or partially breach active beaver dams. In low flow years, access to the spawning areas can be restricted. There is much evidence to indicate that beaver populations have increased substantially across their range in Alberta (likely Western Canada) in the last 20 years. This has resulted in a substantial increase in the abundance of flat, depositional habitat (at the expense of r-r-p type habitat) in small to medium-sized grayling streams (second to third order systems). The situation may be partially linked to the effects of climate change (reduced spring flows and lower summer baseflows) which have encouraged the accumulation of dams and increased the need for additional dams. If so, the density of beaver dams (and resulting habitat alteration) can be expected to increase in the future. As with anything related to climate change, their will be "winners and losers". It would be prudent to consider how the target fish species (assumed to be brown trout) might be affected by climate change related effects in tandem with the re-introduction of the beaver.

- My general knowledge of the literature says that beavers have a positive influence on salmon habitat by providing rearing habitat for juveniles and provide structure in streams that is used by both anadromous and resident fishes. In my field research systems, beaver dams are short lived and thus do not block habitat for extended periods of time. They are also permeable so some fishes can pass up and downstream. The construction of dams leads to the creation of pool habitat and also reconnects aquatic and riparian habitats, sometimes leading to the development of new off channel habitat.

- Beaver dams are natural feature of streams. If some of fishes cannot cross them - this shows they are too weak. Or stupid. Both should be eliminated from gene pool.

- We always should consider the impact of scale (local vs. landscape). Beavers always increase the habitat heterogeneity on the landscape scale.
  Size of rivers also is very important. In every region we should find the critical value of river yield, where the damming intensity changes essentially. In Lithuania this critical value is somewhere at 0.5 cub.m/s, so, beaver impact on migratory salmonids is minimal, as they spawn in larger rivers. Certain negative impacts could be expected to brown trout, which inhabits small rivulets.

- Stable streams are more productive than "flashy" streams, so the general effect of beaver dams is positive. Also increased allochthonous sources of nutrients would be positive. Dams can creat barriers for upstream migration of salmonids, but depending on size of fish and height of the dam. The location of the beaver colony could affect its value. For example mature trees on an estate could be felled and therefore the beavers would be a problem. Also beavers can block culverts to increase the size of their impoundments. On small lakes with a small outlet stream beavers can dam the outlet stream and raise the level of the lake, which can be a nuisance for the use docks and boat houses.

- When beaver population densities become high, they are difficult to manage without a reliable source of mortality (predation, trapping, etc.) and, in areas of dense human habitation, human-beaver conflicts are an inevitable result. Sadly, we have seen this very situation arise in Massachusetts. Since legislation changed our trapping laws, beaver populations have grown to the extent where public opinion of this species is very negative. Thoughtful and proactive management strategies are absolutely necessary if beaver are to be a desired and appreciated part of a landscape.

- It is very difficult to evaluate the impact on 'other species as the species composition can be highly variable. The habitat requirements of some species would be benefited by beaver alterations to natural habitats and this would probably be the case for many, but not all, non-salmonids.

- Beavers were clearly a key part of the habitat complexity that supported high levels of abundance and productivity of salmonids in western North America, where I work. The devastation of the beavers was the first in a series of assaults on salmonids, and resulted in highly simplified channels with fewer ponds, wetlands and other sources of off-channel rearing. These kinds of habitats are clearly important for some species such as coho salmon and cutthroat trout, and less so for others such as pink and chum salmon. There is a notion that beaver dams block upstream migration, and in some cases this is true but it depends on the timing of salmon migration and the overall habitat complexity. I see salmon getting under, over, or around dams all the time. The loss of some spawning habitat is usually more than offset by the increase in flow stability from the ponds and wetlands, and the increased production from nutrient cycling processes. I realize that the re-establishment of this animal can be controversial for many reasons, including land-use management and fish and wildlife ecology. In situations where they were not native (e.g., southern Aragentina) they are viewed as a serious problem but in western North America I think most biologists would agree with me that their overall effect on salmonids is positive. Indeed, many of our habitat restoration efforts are aimed at accomplishing what beavers do naturally - stabilizing flow regimes, creating habitat complexity and off-channel rearing options for periods of high flows, and retaining nutrients.

- I am not quite clear about what you are asking for in the questions above. Is it how I judge the situation/impact in my part of the world? Or is it how I guess a possible impact in Scotland would be? Or do you want my view on the issue in general? I have chosen to answer the questions so the answers give you my opinion about the impact of beavers on ecosystems in my country.

  A second problem is that the answers will give you some kind of average. But an average is a severe oversimplification if variance is not taken into account. The impact of beavers will vary extremely between different areas in spite of equal beaver population density. I have seen areas where beavers have been living for decades at maximum density where people pass without seeing a trace of beaver activity. In other areas a modest population may have a great impact on the landscape and diversity.

  A third problem is that you ask for "negative" or "positive" impact. These words indicate values which not necessarily have anything to do with magnitude of impact. A great impact may be considered as "negative" by one person but "positive" by another. Foresters, hunters, conservationists and anglers will not have the same opinion about what is "negative" or "positive".

  Last, but not least, we must remember that very little research has been done on the impact of beavers in Europe. We are still guessing a lot and trying to extrapolate from North American studies, in combination with general impressions from our own experiences in the field.

- For many questions the answer is really that the effects on habitats are significant, but the effects on biota are completely dependent on the species examined. Therefore it is often hard to rate positive vs. negative, because both occur simultaneously -- positive for some species and negative for others. I rated 4 and 5 where there were significant effects for certain species of Pacific salmon, but for other species the effect is probably equally negative. In aggregate, beaver dams increase overall habitat diversity and almost certainly increase biocomplexity of any river system.

- [In Denmark] Most beaver dams has been constructed at small, previously heavily regulated tributary streams <2 m. A few dams has been constructed at larger main rivers, but usually beavers do not dam rivers >2m wide.

  Around the few dams at larger rivers - and at a large number of dams on the tributaries – the flowing water has created a dynamic network of small brooks bypassing the dams. Dams at main-stem rivers often collapse during spates.

  Overall the beaver dams have increased the area and volume of freshwater in the affected areas and increased the overall area of suitable freshwater habitats for most fish species, incl. brown trout, and probably increasing the fish biomass in the affected areas. Glass eels and small lampreys has been observed migrating up through dams at sites where water is flowing through the dams.

The damming of small streams has increased freshwater and wetland habitat heteogeneity on a fine scale, i.e. shorter dispersal distances and potentially better connectivity between ‘micro-‘habitats, though migration in streams is restricted for some aquatic species.

- Salmonids and beavers have co-existed for thousands of years in many environments. There appears to be no significant volume of literature that the existence of beavers in stream systems are detrimental to fish populations but a reasonable volume of scientific literature showing biodiversity benefits. Undoubtedly some beaver dams may block the upstream passage of migratory fish but so do natural accumulations of woody debris. My professional opinion as a river scientist is that the benefits the beaver can bring to stream system far outweigh any disbenefit. Benefits could include increases in biodiversity and beaver dams being construed as natural flood management measures and diffuse pollution best management practice.

- The literature on beaver in the North America demonstrates the importance of beaver in riparian and floodplain areas. The literature for salmonids fish production is generally very positive, though there have been a few limited studies done in Wisconsin that reported that removal of beaver dams lead to increase in catchable brook and brown trout. In contrast, studies in the western US have shown that beaver ponds are very important rearing areas for juvenile coho and to a lesser extent for other salmonid species. The difference in these studies likely has to do with the narrow focus of the Wisconsin studies and perhaps that they were dealing with very low gradient slow moving stream and that they were focused on catchable resident trout. Beaver reintrodution is seen in western US as a cheap and natural method to restore fish habitat and recover riparian areas.

- Brook trout flourish in beaver habitats. A site on a small stream known to have very few, and small, trout can experience an amazing transformation when dammed by beavers. The trout population, and the average size of individuals, grows rapidly and significantly. Many anglers, including myself, who have done massive amounts of sampling, will attest to this fact!

  Another anecdote: on several occasions I have observed where beavers in winter excavate holes, or canals, through their dams. Why? Access, under the ice, to neighboring wetlands? Creation of air spaces under the ice? Creation of warmed, unsupported, and weakened ice that increases breakout potential to upland food sources around the shore? It doesn't really matter for our purposes. Depending on the severity of the winter, there may be many months during which fish can freely move back and forth through these types of gaps. When beavers survive the winter, and stay around, the holes are patched when the ice melts.

  And another… as the co-evolution argument would suggest, by all accounts there was an enormous abundance of beavers and salmon (and probably trout) sharing North America when Europeans arrived.

- It is my impression that the long, harsh winter encountered in much of Canada (or many northern areas) probably creates a unique habitat requirement - over winter habitat that does not freeze, and is of sufficient size that a reasonable population of fish can inhabit it through the winter months. Beaver activity can aid in the creation of this type of habitat through ponding etc. In Saskatchewan introduced species such as Brook Trout rely on the pool habitat created by beaver activity, and in some cases this habitat is protected from regular removal (e.g. dams are often removed to protect road infrastructure or farm land from flooding in the spring, however, where Brook Trout are present, this work may be prohibited.

Our local species in Saskatchewan have evolved with the presence of beaver activity. We alter the landscape in many areas, and in some cases remove/prevent beaver activity to maintain creeks/channels to prevent flooding etc. This would appear to ensure stream connectivity (superficially a good thing), but it also changes the way the smaller creeks (and some larger creeks) develop. Regular flooding is beneficial from an ecological integrity point of view; nutrients are accessed, riparian and stream habitat is diverse (some species such as cottonwoods need flooding). Pool habitat can be beneficial for some life stages, and it can buffer drought periods by maintaining pool habitat in dryer periods.

- My work has been on European beaver population dynamics. My field studies have taken place in the Czech Republic with occasional visits/ work in other mainly European countries.

  Fish/beaver relationships in the Czech Republic are mainly dominated by commercial carp fish ponds and leisure carp fishing. Obviously, the Czech Republic is land-locked and salmonids are not a high management priority. Therefore, my opinions given above on salmonids are based on previous general discussions with American/ European colleagues and periphery research on fish/ beaver interactions.

  Although I have informally consulted on the Scottish beaver release, I did not offer an opinion on effects of beaver activity on salmonids.

  For many of the questions I would have liked to give a 2 - 4 score as often beaver activity can be both positive and negative. The effect of beaver activity in general is extremely positive in the long term, however, it can be negative in the short term if not managed correctly. There will always be site specific instances where beaver activity is extremely negative, however, mitigation and/or management can prove effective in these instances.

- An overall observation in the fisheries field in the western USA is that the good-beaver/ bad-beaver issue has been debated over the last few decades. I believe it is now generally accepted that with respect to the overall ecosystem richness and productivity, it is good-beaver.

- My responses to the questionnaire are relevant to the environmental setting that I am most familiar with: forested areas of northeastern and northcentral North America. In these environments, with a high percentage of native forest cover and fairly low human settlement densities, with some level of potential control of beaver populations (via human trapping or by large mammalian predators) the relevant studies (particularly by Naiman and colleagues) point to a largely positive impact of beaver on ecosystem structure and function . In highly altered and intensively managed landscapes in the UK, I would be very concerned that these benefits would be outweighed by some potentially negative impacts on native riparian forest recruitment, human infrastructure (roads and residences), potential facilitation of undesirable invasive aquatic and terrestrial species, risks of waterborne pathogens, and local elimination of highly valuable migratory fishes. It is important to keep in mind that you are considering introducing a potential 'game-changer' with respect to some very complex and unpredictable interactions, and that this agent of change has a very high intrinsic population growth rate and a high dispersal capacity. Integrated conservation plans, drawing on a wide range of sources, and presenting multiple scenarios with explicit acknowledgement of uncertainties, would be essential to any restoration effort.

APPENDIX 3

List of EOS respondents and their affiliations (excluding those that wished to remain anonymous)

Respondent	Affiliation
Phil Roni	NOAA Northwest Fisheries Science Center, US
Eric Hockersmith	NOAA Northwest Fisheries Science Center, US
Thomas Quinn	University of Washington, Seattle, US
Ted Castro Santos	United State Geological Survey Conte Laboratory
Rick Cunjack	University of New Brunswick, Canada
Torbjorn Forseth	Norwegian Institute for Nature Research (NINA)
Hans Lundqvist	Swedish University of Agricultural Sciences
Keith Clarke	Department of Fisheries and Oceans, Canada
Bill Hooper	Watershed Technologies (Canada)
Robert Naiman	University of Washington, Seattle, US
Duncan Halley	Norwegian Institute for Nature Research (NINA)
Andrzej Czech	Carpathian Heritage Society - Natural Systems, Poland
Ingo Bräuer	Ecologic Institute for International and European Environmental Policy, Germany
Rory Saunders	NOAA - NorthEast Fisheries Science Center, US
John Gibson	Department of Fisheries and Oceans, Canada (retired)
Ernie Atkinson	State of Maine Department of Marine Resources, US
Jaap Rouwenhorst	Bureau Ontwikkeling en Beheer, Netherlands
Peter Busher	Boston University, US
Shaun Baker	Palacky University, Czech Republic
Skip Lisle	Beaver Deceivers International (Consultancy)
Dave Gilvear	University of Stirling, Scotland
Morton Elmeros	University of Aarhus, Denmark
Jen Strules	University of Massachusetts, Amherst, US
Jim O'Neil	Golder Associates Ltd.

Scottish Natural Heritage is a government body responsible to the Scottish Government.

Statement of principles:

Scottish Natural Heritage – the government body that looks after all of Scotland's nature and landscapes, across all of Scotland, for everyone. Our 5 strategic priorities are:

- Caring for Scotland's nature and landscapes
- Helping to address climate change
- Delivering health and well being
- Supporting the Scottish economy
- Delivering a high quality public service

Find out more at **www.snh.gov.uk**

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Scottish Natural Heritage
All of nature for all of Scotland