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Qualitative and quantitative effects of reintroduced beavers on stream fish

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Abstract

Reintroduction of beaver (*Castor* spp) may facilitate rehabilitation of freshwater habitats providing a cost-effective sustainable means of improving ecological conditions. Despite extensive research, debate and consultation, a general consensus on the impact of beaver on fishes has proven elusive because of variability in biological response. This paper provides a systematic review of the impacts of beaver dams on fishes and fish habitat based on a meta-analysis of the literature and expert opinion. Research is regionally biased to North America (88%). The most frequently cited benefits of beaver dams were increased habitat heterogeneity, rearing and overwintering habitat and flow refuge, and invertebrate production. Impeded fish movement because of dams, siltation of spawning habitat and low oxygen levels in ponds were the most often cited negative impacts. Benefits (184) were cited more frequently than costs (119). Impacts were spatially and temporally variable and differed with species. The majority of 49 North American and European experts considered beaver to have an overall positive impact on fish populations, through their influence on abundance and productivity. Perceived negative effects related to the movement of aquatic organisms in tributary streams, including upstream and downstream migrating salmonids, and the availability of suitable spawning habitat.

Keywords Beaver dams, fish migration, meta-analysis, public perception, salmon, species reintroduction

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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 implement species protection measures (Maunder 1992; Hodder and Bullock 1997; Seddon 1999; Seddon *et al.* 2007). Reintroduced species may also provide significant economic benefits, such as through ecotourism (Maunder 1992; Rees 2001), to regions where other types of activity may be limited. Elevated interest in species reintroduction has recently been driven primarily by obligations set out under international agreements (e.g. Convention on Biological Diversity 1992).

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. Further, reintroduction often 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 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). It is important to gain public support. This is more likely where clear objectives have been established after consultation, during which attitudes and opinion, especially of key stakeholders most likely to be affected by the reintroduction, are recorded and considered (Rees 2001). The reintroduction of grey wolves (*Canis lupus*, Canidae) to Yellowstone National Park, Wyoming (USA), was forestalled for two decades by strong opposition from stakeholders within the region (Fritts *et al.* 1997). Conversely, acceptance by local people was crucial to the success of reintroducing brown bears (*Ursus arctos*, Ursidae) to the Pyrenees (Arquilliere 1998). Thus, accounting for public/stakeholder perception is important in project implementation. Without support for conservation from the local population and stakeholders, the reintroduced 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 (Fritts *et al.* 1997; Breitenmoser 1998).

The North American (*Castor canadensis*, Castoridae) and Eurasian (*C. fiber*, Castoridae) beaver suffered major reductions in numbers and contraction in range because of overexploitation for the fur trade. Since the 1920s, both species have seen a dramatic revival as a result of increased legislation and reintroduction programmes (Rosell *et al.* 2005). During the 20th century, the numbers of Eurasian beaver had increased from approximately 1200 animals in eight isolated populations to a minimum of 639 000 in 2003. This includes significant increases throughout the former European range (with the exception of Britain, Portugal, Italy and the southern Balkans) as a result of reintroduction and range expansion (Halley and Rosell 2003).

In Europe, legislation (the EU Habitats Directive 92/43/EEC, EU 1992) provides for the assessment of the desirability of reintroducing listed species, including the Eurasian beaver, to areas where they were once native. The legislation requires that any reintroduction should take place only after proper consultation with the public concerned, which therefore includes key stakeholders. From the perspective of a Eurasian beaver reintroduction, key stakeholders include those groups that represent fisheries interests. Unfortunately, it has proven difficult to provide fisheries groups with the information they require on which to base opinion because a clear consensus of impacts of beaver on fish populations is difficult to achieve because of the inherent variability in biological response observed depending on scale, space, time and biotic factors.

Previous reviews have consistently recognized that the ecological (and socio-economic) impacts of beaver can be perceived as either positive or negative depending on the viewpoint of the stakeholder (see Scott Porter Research and Marketing Ltd, 1998). However, it has previously proven difficult to generalize beneficial or detrimental effects of beaver reintroduction on fisheries because of high levels of uncertainty. This study is the first to combine the results of an expert opinion survey with a systematic meta-analysis of the literature to develop an argument based on the 'weight of evidence' for positive or negative impacts of beaver activity on fish populations. It is intended that this approach will provide information of interest to those tasked with considering the reintroduction of beaver and inform fisheries groups of the implications of beaver activity for fish populations.

Methods

Meta-analysis and review of the literature

The impact of North American and Eurasian beaver on fish populations was reviewed to identify potential threats and benefits posed by beaver reintroduction to freshwater fisheries. A vote-counting meta-analysis (e.g. Haxton and Findlay 2008) was conducted to highlight biases within the literature, gaps in understanding and positive and negative aspects of beaver/fish interactions.

Peer reviewed and 'grey' literature relating to the impact of beavers on fish was collected via two routes. First, the bibliographic search engines 'Google Scholar' and 'Web of Science' were interrogated using search keywords that included 'European beaver AND Atlantic salmon', 'European beaver AND salmon', 'European beaver AND trout', 'European beaver AND salmonid', 'European beaver AND fish', 'beaver reintroduction AND fish', 'beaver AND reintroduction AND fish', 'beaver AND reintroduction AND salmon', 'beaver AND impact on fish' and 'beaver AND impact on salmon'. Second, additional relevant articles listed in the bibliographies of retrieved papers were sourced and added to the database. The articles were interrogated for sections of relevance to the impacts of beaver on fish populations. The journal title, year of publication, location of the study area or region described, beaver and fish species and impact of beaver on fish (classified as positive or negative) were entered into a database.

A vote-counting methodology (Gates 2002) was selected in which the number of statistically significant results highlighting positive or negative impacts of beaver interactions, or explicit statements that an effect had been detected (in the absence of quantitative statistics), was counted. To provide an assessment of the weight of evidence, once highlighted each of the positive or negative impacts was evaluated to determine whether the statements cited were supported by the research's methodological approach or were based on speculation or general opinion. This inclusive methodology considers the results of a wider range of publications that might otherwise be excluded (e.g. because of inadequate or missing statistical information) in more quantitative meta-analyses (Haxton and Findlay 2008).

Expert opinion survey

Questionnaire design

Questionnaires are used increasingly as a means of collecting data in ecology (White *et al.* 2005), and Likert scales (Likert 1932) have been used previously to assess public perception to species reintroduction (e.g. Worthington *et al.* 2010 in relation to burbot, *Lota lota*, Gadidae to the UK). In this study, a Likert scale composed of multiple items was developed to assess expert opinion of potential impacts of beavers on populations of fish, and other ecological and geomorphological processes. Each Likert item (a single item or question) was composed of a stem, e.g., a simple statement of attitude or question, and a scale against which the respondent assigned a score (traditionally related to level of agreement).

The questionnaire was designed so that it should not be onerous to complete. Respondents were provided with the opportunity for additional comment; the results of which are presented in Kemp *et al.* (2010).

The questionnaire comprised of 28 items. The first four 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 (fisheries scientist/manager, geomorphologist, terrestrial ecologist, beaver specialist and other) to describe their profession. The second question was designed to act as a filter. Respondents were asked to rate their level of expertise (expert, moderate, little or no prior knowledge). The third and fourth questions sought to ascertain which species of beaver and fish the respondent had experience of.

The remainder of the items (5–20: composed of a total of 24 items and sub-items, see results) 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). Respondents were requested to specify the degree of impact associated with each item by assigning a score ranging from 1 (severe negative impact) to 5 (high positive impact) with a value of 3 indicating 'no impact'. Following conventional wisdom (McColl *et al.* 2001), the sequencing and position of Likert items within the questionnaire was designed so that general fields preceded specific areas.

Selection of experts

North American and European experts were selected based on fulfilling at least one of the following criteria: record of publication in relation to (i) beavers (e.g. ecology/economic impacts), (ii) freshwater fisheries in areas within the beaver's range (i.e. judged likely to have expert knowledge on impact of beavers on fish stocks), (iii) geomorphological response of rivers to woody structure (especially beaver dams) and/or (iv) demonstrable experience in working in the above areas (e.g. consultant or field operative that may or may not be required to publish findings in the scientific literature).

The experts selected (Table 1) were either known to the authors or were identified as part of the literature review. Selection was not based on any preconception of current opinion (i.e. in favour of or against beaver reintroduction programmes or management).

Delivery of the questionnaire

The aim of the expert opinion survey was to clarify current perspectives and range of opinion. It was not intended to elicit a consensus view, e.g., by employing traditional techniques such as the Delphi method (Linstone and Turoff 2002; Plummer and Armitage 2007). The questionnaire was sent to respondents once only.

To identify the potential for non-response bias, the number of experts surveyed was controlled to enable accurate response verification. This was achieved by identifying and targeting specific individuals rather than the institution for which they worked (i.e. key contacts were not requested to disseminate questionnaires within their institution with the objective of receiving multiple responses from persons whom consider themselves experts).

Previous research has advocated the use of pre-notification and reminders to improve probability of response (McColl *et al.* 2001). All identified experts were initially sent by e-mail a pre-notification describing the aims of the survey and a request to participate. A 'non-response' was recorded if no reply to the pre-notification was received. The questionnaire was sent only to experts who agreed to participate, followed by a reminder if no response was received after a minimum of 1 week. A 'non-response' was recorded if no reply to the reminder was received after 1 week. Experts were pre-notified between 18 and 23 February 2009, and questionnaires were delivered between 18 and 26 February 2009. Reminders were issued on 2 March 2009. The last survey response received was returned on 28 March 2009.

Results

Meta-analysis

One-hundred and eight articles containing information on the interactions between beavers and fish were identified. The majority (79) were published after 1989 (Fig. 1). The earliest studies identified were published in 1935.

Publications were regionally biased. Ninety-five were based on North American research; the majority of which (72) were conducted in the United States. Nine studies were based on European experience (three in Norway, and one each in Poland, Germany, Estonia, Latvia, Sweden and Denmark). Two studies examined introduced North American beaver populations in Chile, while two

Table 1 Affiliation of the selected experts that received pre-notification of request to participate in the Expert Opinion Survey on impacts of beaver on fish stocks in Scotland. Not all those listed responded.

Institution/Agency/Consultancy	*N* experts pre-notified
NOAA, Northwest Fisheries Science Center, US	9
NOAA, North East Fisheries Science Center, US	2
NOAA, 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 Gothenburg, Sweden	1
New Brunswick Department of Natural Resources Fish and Wildlife, Canada	1
State of Maine Department of Marine Resources - Bureau of Sea-run Fisheries and Habitats, 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
Environment Agency, UK	1
The University of Stirling, UK	1
The Dutch Mammal Society, Netherlands	1
University of Massachusetts, Amherst, US	1
No affiliation	2

NOAA, National Oceanic and Atmospheric Administration.
*Two of the five experts were retired.

studies took a global perspective. Clearly, as the majority of research was conducted in North American, there was a corresponding bias to consideration of the North American beaver and fish species.

Fifty-six species and sub-species of fish were recorded in the literature on beaver/fish interaction reviewed. The total number may have been higher because some articles discussed fish assemblages rather than individual species. The most frequently cited species were brook trout (including eastern brook trout) (*Salvelinus fontinalis*, Salmonidae) (22 records), coho salmon (*Oncorhynchus kisutch*, Salmonidae) (15), rainbow trout (*O. mykiss*,

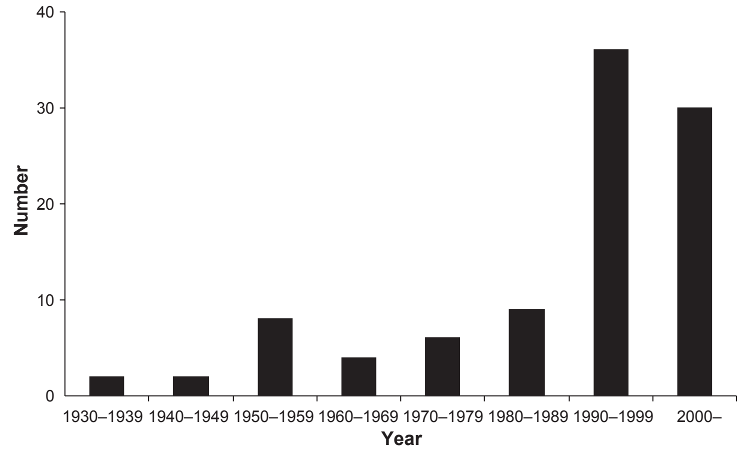

Figure 1 The number of studies considering beaver/fish interaction published since 1935.

Salmonidae, including the anadromous steelhead trout, and the golden trout sub-species) (14), cutthroat trout (*O. clarki*, Salmonidae, composed of several sub-species) (14), Atlantic salmon (*Salmo salar*, Salmonidae) (13) and brown trout (*Salmo trutta*, Salmonidae, including anadromous sea trout) (12). Rather than stipulating specific species, a number of studies considered the impact of beavers on generic 'trout' (10 records), 'salmonids' (5), 'all anadromous species' (1) or 'all species in the study location' (16). When species were categorized into groups (e.g. if more than one species of trout was cited in an article, then all were considered a single record for the 'trout' group), 'trout' were recorded in 26% of articles, 'charr' in 25% and 'salmon' in 30% (12% considered Atlantic salmon).

The number of times positive impacts of beavers on fish populations were cited was higher (184) than for negative impacts (119) (Fig. 2). Twenty articles cited only negative impacts vs. 40 that described only positive effects.

The most frequently cited positive impacts were increased fish productivity or abundance, followed by increased fish habitat or habitat complexity, the provision of overwintering habitat, increased rearing habitat and enhanced fish growth rates (Table 2). Barriers to fish movement were the most frequently cited negative impact, followed by reduced spawning habitat, lower oxygen concentrations and altered temperature regime (towards the upper range of a species thermal tolerance) (Table 3).

The analysis of the 'weight of evidence' found a disparity between the percentage of the negative and positive impacts that were based on speculation rather that quantitative assessment. Over half (51.1%) the positive impacts cited were based on data, whereas for negative impacts, 71.4% were speculative. For positive impacts, the conclusion that the presence of beavers increased fish productivity, overwintering habitat and habitat complexity was more frequently based on quantitative analysis, while the provision of rearing habitat was more speculative (Table 2). The commonly cited negative impact of beaver dams impeding fish movement was supported by data on 21.6% of occasions (Table 3).

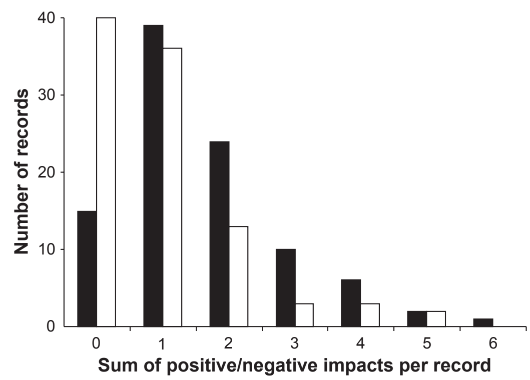

Figure 2 The total number of positive (solid bars) and negative (clear bars) impacts of beavers on fish cited in each reference.

Literature review: impacts of beaver activity on fish

Habitat

Both North American and Eurasian beaver influence freshwater ecosystems (Naiman *et al.* 1988; Pollock *et al.* 1995) via their effects on hydrology, geomorphology, water chemistry and temperature (see Collen and Gibson 2001; Rosell *et al.* 2005). Arguably, it is the effects of beaver activity on

Table 2 Citation of positive impacts of beaver activity on fish populations and the percentage of citations based on quantitative analysis or speculation. Different impacts are expressed as the number of times they are cited in 108 literature sources and as a percentage of the total number of citations.

Positive impacts	Number	% of total citations	Data driven (%)	Speculative (%)
Enhanced habitat availability/complexity	19	10.3	52.6	47.4
Enhanced overwintering habitat	17	9.2	64.7	35.3
Enhanced rearing habitat	16	8.7	31.2	68.8
Provision of cover	5	2.7	20.0	80.0
Enhanced diversity/species richness	8	4.3	87.5	12.5
Enhanced abundance/productivity	50	27.2	58.0	42.0
Provision of habitat under low flows	11	6.0	27.3	72.7
Provision of high flow refuge	3	1.6	0	100
Provision of temperature refuge	13	7.1	53.8	46.2
Enhanced water quality	2	1.1	0	100
Sediment trap	3	1.6	0	100
Enhanced invertebrate productivity	16	8.7	56.2	43.8
Enhanced growth rates	16	8.7	62.5	37.5
Enhanced fish condition	1	0.5	100	0
Provision of fishing areas	4	2.2	25.0	75.0
Total	184	100	51.1	48.9

Table 3 Citation of negative impacts of beaver activity on fish populations and the percentage of citations based on quantitative analysis or speculation. Different impacts are expressed as the number of times they are cited in 108 literature sources and as a percentage of the total number of citations.

Negative impacts	Number	% of total citations	Data driven (%)	Speculative (%)
Barriers to fish movement	51	42.9	21.6	78.4
Reduced spawning habitat	20	16.8	40.0	60.0
Altered temperature regime	11	9.2	9.1	90.9
Reduced oxygen levels	12	10.1	50.0	50.0
Reduced habitat quality	2	1.7	0	100
Altered flow regimes	4	3.4	75.0	25.0
Loss of cover	5	4.2	0	100
Reduced productivity	9	7.6	33.3	66.7
Retarded growth	2	1.7	50.0	50.0
Abandonment of beaver settlements	1	0.8	100	0
Reduced water quality	2	1.7	50.0	50.0
Total	119	100	28.6	71.4

physical habitat that provides the greatest benefit in enhancing 'ecological status' by enabling persistence of a varied riverine habitat mosaic (Hanson and Campbell 1963) through the creation of lentic patches within a corridor of lotic habitat (Snodgrass and Meffe 1999). The resulting habitat heterogeneity benefits a multitude of organisms, including fish.

In shallow, ice-covered streams, beaver ponds provide fish with important overwintering habitat (Cunjak 1996) and refuge because of their low current velocities, reduced ice cover and stable temperature regimes (Chisholm *et al.* 1987; Lindstrom and Hubert 2004). Beaver ponds represent key winter habitat for bull trout (*Salvelinus confluentus*, Salmonidae) and cutthroat trout (Rasmussen 1941; Jakober *et al.* 1998), coho salmon (Swales and Levings 1989; Nickelson *et al.* 1992; Miller and Sadro 2003) and Dolly Varden (*S. malma*

malma, Salmonidae) (Gregory 1988). Survival of overwintering coho salmon in beaver ponds was approximately twice that observed for the rest of the river system on Vancouver Island, Canada (Swales and Levings 1989). Jakober *et al.* (2000) observed a positive preference exhibited by bull trout and cutthroat trout for beaver ponds, as more than 70% of fish congregated in five ponds that represented 30% of the area sampled.

Beaver ponds represent important rearing habitat for andromous species (Swanston 1991; Taylor 1999; Johnson and Weiss 2006), including coho salmon (Swales and Levings 1989; Leidholt-Bruner *et al.* 1992; Rosenau and Angelo 1999; Beechie *et al.* 2001; Lang *et al.* 2006), Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) (Rosenau and Angelo 1999), steelhead trout (Lichatowich 1999) and Atlantic salmon and brook trout (Scruton *et al.* 1998). Indeed, Grasse (1979) went as far as to propose that beaver ponds should be stocked with trout to increase productivity.

Structures formed as a result of beaver activity can provide fish with cover (Salyer 1935; Rasmussen 1941; Rutherford 1955; Beedle 1991; Burchsted *et al.* 2010) from adverse flows and predators.

A frequently cited negative impact of beaver activity was the inundation of spawning gravels with the fine sediment deposited when currents are reduced (Swanston 1991). The impact of siltation is particularly problematic for salmonids because of their requirement for clean, well-oxygenated water to pass through redds (Salyer 1935; Cook 1940; Rasmussen 1941; Patterson 1951; Christenson *et al.* 1961; Gard 1961; Knudsen 1962; Dumke *et al.* 2010). In the Californian Sierras, the deposition of silt on spawning gravels within impounded reaches may have resulted in the displacement of native golden trout (*Salmo irideus*, Salmonidae) by brown and rainbow trout (Müller-Schwarze and Sun 2003). A study conducted in Nova Scotia indicated that redds were typically absent between 100–300 m upstream of beaver dams because of the poor spawning habitat quality in impounded reaches (Taylor *et al.* 2010). In Norway, recolonization of the Litlelva stream area of North Trondelag by Eurasian beaver during the 1990s is thought to have reduced the availability of Atlantic salmon and brown trout spawning habitat because of the siltation of gravels (Halley and Lamberg 2001).

Conversely, the influence of beaver dams on sediment budgets may benefit stream-dwelling fish (Halley 1995). Storage of sediment behind dams, while locally detrimental to salmonid spawning gravels, will reduce sediment transfer downstream (Grasse 1951; Halley 1995), protecting spawning gravels located between impounded reaches, particularly in low order tributaries (Beedle 1991). The volume of sediment that may be trapped in this manner is not insubstantial. For example, a series of three Eurasian beaver dams on the Sumka River (Tartarstan Republic, Russia) trapped 4250 tons of solid particles during a period of flooding in 2001. This resulted in a reduction in the sediment mass per litre of water flowing downstream of the dams by 53% (Gorshkov 2003). Of particular interest is that this study reflects monitoring of impacts of beavers that were deliberately reintroduced for the purpose of reducing the input of agriculturally derived sediment into a lake ecosystem. Even relatively small North American beaver dams (e.g. 4–18 m^3 of wood) have been found to retain between 2000 and 6500 m^3 of sediment (Naiman *et al.* 1986).

In addition to habitat availability, beaver have the potential to impact habitat quality. Rutherford (1955) argued that recently constructed beaver impoundments provided food and cover conducive to the maintenance of larger numbers of brook trout than neighbouring stream sections, although conditions tended to be poor in older ponds because of habitat deterioration over time. Rohde and Arndt (1991) cited habitat deterioration because of the activities of humans and the successful reintroduction of beavers as one of the main reasons for range contraction of the sandhills chub (*Semotilus lumbee*, Cyprinidae) and pinewoods darter (*Etheostoma mariae*, Percidae) in North and South Carolina.

Beaver reintroduction and management may provide a low-cost (and sustainable) strategy for improving salmonid habitat (Andonaegui 2000). Indeed, recent research conducted by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service has attempted to manipulate beaver behaviour by providing Beaver Dam Support (BDS) structures with the intention of attracting beaver to specific predefined areas (M. Pollock personal communication; Beechie *et al.* 2010). A lack of overwintering habitat on the Lower Bridge Creek, an anthropogenically incised tributary of the John Day River (Oregon), was thought to limit populations of juvenile steelhead. By encouraging beavers to construct dams, pool habitat for juvenile steelhead should be provided in the short term. Over longer time-scales, it was hoped that streambed aggradation will be enhanced, resulting in elevation of the floodplain water table and increased summer flows, decreased stream temperatures, a narrower and more sinuous stream channel, and expanded riparian forest (Pollock *et al.* 2003). Indeed, these expectations have been at least partially achieved, with vertical aggradation (based on assessments of 13 beaver dams 1–6 years old), initially estimated to be rapid (up to 0.47 m year^{-1}) and then to decline to lower rates (e.g. 0.075 m year^{-1}), resulting in increased area of riparian habitat (Pollock *et al.* 2007). Several BDS structures have been installed, and early results have indicated that they can be employed successfully to initiate dam construction in areas not previously utilized by beavers, resulting in beneficial physical response from the perspective of river management/restoration (M. Pollock personal communication; Beechie *et al.* 2010).

The majority of research has focused on the importance of beaver created habitat for salmonids because of their economic and conservation importance (Bryant 1984; Lichatowich 1999). For example, beaver ponds in Wyoming are considered critical to the continued survival of sensitive species such as the Colorado River (*O. c. pleuriticus*, Salmonidae) and Bear (Bonneville) River cutthroat trout (*O. c. utah*, Salmonidae) (Collins 1993). Despite this focus, the benefits of beaver created habitat are realized also by non-salmonids (Ray *et al.* 2004) such as Oregon chub (*Oregonichthys crameri*, Cyprinidae) (Scheerer *et al.* 2004), lake chub (*Couesius plumbeus*, Cyprinidaei) (Murray and Innes 2009) and minnow (*Phoxinus phoxinus*, Cyprinidae) (Hägglund and Sjöberg 1999).

As a component of a dynamic fluvial system, beaver dams and ponds are continually abandoned, destroyed and reconstructed. In one study, an influx of lentic fish species followed the collapse of a beaver dam and resulted in a short-term increase in abundance and species richness (Stock and Schlosser 1991), followed by a subsequent decline to lower than pre-disturbance levels. This was accompanied by a dramatic (>90%) decrease in the density of benthic invertebrates (Stock and Schlosser 1991).

Barriers to fish movement

Beaver dams, comprising of wood partially sealed with mud and vegetation, create semi-permeable barriers to the upstream and downstream movement of fish. This may result in reduced access to essential spawning and rearing habitat, inhibited colonization and increased isolation of populations (Table 4). The magnitude of impact is not easily predictable; fish can be delayed at barriers that appear passable or may quickly pass those that may at first seem difficult (Thorstad *et al.* 2008).

Several studies emphasize the potential for beaver dams to impede fish movement (Table 4) and significantly impact populations. However, the majority (78.4%) of these studies are speculative rather than being data driven (see Tables 3 and 4). The re-establishment and expansion of beaver has been blamed for the loss of Atlantic salmon from several river systems on Prince Edward Island (Canada) and their reduced abundance in others (Guignion 2009). Others, however, qualify statements relating to negative impacts by indicating that the magnitude is both temporally and spatially variable (Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007).

The ability of beaver dams to impede the movement of fish varies with flow (e.g. Schlosser 1995a; Snodgrass and Meffe 1998), life-span of the structure and species. In Nova Scotia (Canada), dams blocked the upstream migration of Atlantic salmon under low flow conditions, when fish were clearly seen to congregate below them, but had limited effect during most years when precipitation rates were average or above as indicated by distribution of spawning redds (Taylor *et al.* 2010). Similar observations have been recorded for steelhead (Lowry 1993), cutthroat and rainbow trout (Grasse 1951). In Estonia, beaver dams formed a major impediments to downstream fish movements during a drought (Tambets *et al.* 2005), and most fish (with the exception of nine-spined stickleback *Pungitius pungitius*, Gasterosteidae) stranded in the small ponds upstream of the beaver dams did not survive.

The life-span of beaver dams varies with gradient and magnitude of flow. In the North-western United States, beaver dams represent temporary structures often washed out during the same freshets used by Pacific salmon species to reach their spawning grounds (Taylor 1999). In Norway, it is suggested that any impacts of beaver dams on the upstream and downstream movements of Atlantic salmon and sea trout would be negligible because of their low density, small size and short life-span (Parker and Ronning 2007).

With the return of beaver to Europe, interspecific variation in relation to the impact of their dams on

Table 4 The impacts of beaver dams on fish and the methods used to assess the impact.

Species	Effect of beaver dams	Method of assessment	Reference
Atlantic salmon	Limit spawning distribution	Electrofishing and seine netting	Mitchell and Cunjak 2007
Atlantic salmon	Some beaver dams pose serious obstacles to migrating salmon, especially when discharge is low	Redd counts	Taylor *et al.* 2010
Atlantic salmon, brook trout	Partial to complete blockage	Anecdotal evidence	Scruton *et al.* 1998
Atlantic salmon, brook trout, alewife	Prevent both upstream migrants from reaching spawning grounds also impacts seaward movements for some species	Observed/speculative	Guignion 2009
Atlantic salmon, sea trout	Obstruct upstream and downstream migration	Quantified amount of habitat behind dams/speculative	Parker and Ronning 2007
Bull trout	Blocked or delayed downstream movements	Radio telemetry	Dupont *et al.* 2007
Brook trout	Dam removal leads to range expansion but not abundance increase	Dam removal and electrofishing	Avery 1991
Brook trout	Fall spawners blocked from reaching spawning grounds	Discursive/observation	Grasse 1951; Doucett *et al.* 1999;
Brook trout	Dam impede upstream and downstream migration, but not totally impassable	Fish trapping	Rupp 1954
Brown trout	Block downstream movement	No data	Tambets *et al.* 2005
Brown trout, minnow, bullhead, burbot, pike	Barriers to colonization and migration, especially for slow dispersing species	Discursive	Hägglund and Sjöberg 1999
Coho salmon	Dams (one = 2 m height) did not block migration. Movement facilitated by fall freshets	Fish trapping	Bryant 1984
Coho salmon, steelhead trout	Impact ability to colonize new areas	Seine netting	Murphy *et al.* 1989
Cutthroat trout, rainbow trout	Fish usually pass because of high spring flows	Discursive	Grasse 1951
Lahontan cutthroat trout	Seasonal blockage of at least upstream movement	Anecdotal and observational	Talabere 2002
Lake whitefish (*Coregonus clupeaformis*, Salmonidae), walleye	Reduce access to spawning grounds	Discursive	Bertolo and Magnan 2006
Northern pike, walleye	Block spawning runs	Speculative	Knudsen 1962
Oregon chub	Population isolation	Speculative	Scheerer *et al.* 2004
Roach, sticklebacks, brook lamprey	Total barrier to movement	Methods not stated	Elmeros *et al.* 2003
Salish suckers (*Catostomus* spp., Catostomidae)	Species rarely crossed beaver dams	Radio telemetry	Pearson and Healey 2003
Sea trout	Partially block spawning run	Methods not stated	Elmeros *et al.* 2003
Sockeye salmon	Block access to spawning sites	Observational/speculative	McPhee *et al.* 2009
Steelhead trout	Fish appeared able to cross barriers	Observational	Lowry 1993
Steelhead trout, rainbow trout	Upper extent of distribution fluctuates with occurrence of dams		Andonaegui 2000
Trout spp.	Adults unable to return downstream after spawning	Methods not stated	Rasmussen 1941
Trout spp.	Block spawning runs or upstream migration	Discursive/speculative	Bradt 1935; Cook 1940; Knudsen 1962; Grasse 1979
Trout spp.	Tagged fish did not pass upstream over dams but were able to move downstream to spawning grounds	Tagging	Salyer 1935

fish movements has been illustrated. Dams constructed by reintroduced Eurasian beaver in Denmark, most on streams with a width <2 m, are capable of impeding roach (*Rutilus rutilus*, Cyprinidae), stickleback (*Gasterosteus aculeatus*, Gasterosteidae) and brook lamprey (*Lampetra planeri*, Petromyzontidae), while brown trout are only able to pass them during periods of high flow (Elmeros *et al.* 2003). The movement of eels (*Anguilla anguilla*, Anguillidae) appears to be unaffected, while the upstream movement of small fish is considered possible via back-water channels. Overall, however, the reintroduction of Eurasian beaver does not appear to have negatively affected eel or brook lamprey populations, while roach and stickleback have benefitted because of the increase in the density of ponds. Impacts on sea trout migration, however, remain a cause for concern (Elmeros *et al.* 2003).

In Norway, Atlantic salmon are thought to primarily spawn in the main Numedalslågen river, recolonized by beaver in 1957, while sea trout tend to utilize tributary streams (Parker and Ronning 2007). As a result, the impact of beaver activity on access to spawning grounds of the two salmonid species may differ substantially. For example, in one case, the construction of five dams (all <0.5 m high) on the tributary streams could potentially prevent Atlantic salmon and sea trout from reaching 3 and 18% of their spawning habitat, respectively (Parker and Ronning 2007). Nevertheless, the impacts are considered localized, and overall, the relative increase in lentic habitat is thought to benefit sea trout because of their reliance on pools, while Atlantic salmon reproduction in the catchment appears to be unconstrained by the presence of beaver.

In Sweden, the colonization and migration of slow dispersing species such as bullhead (*Cottus gobio*, Cottidae) appear to be disproportionately impacted (Hägglund and Sjöberg 1999).

Flow

Beaver dams stabilize river flow (Grasse and Putnam 1955; Halley 1995) by increasing the water-holding capacity of the watershed, dampening peaks in the hydrograph (Finnigan and Marshall 1997) and elevating the water table enabling the slow release of groundwater to maintain stream flow during periods of drought (Finnigan and Marshall 1997).

Flow stabilization may, under some situations, benefit fish populations. In response to concerns raised by Lever (1994) regarding the effect of a future reintroduction of Eurasian beaver on Atlantic salmon fisheries in Britain, Halley (1995) describes the expansion of the Norwegian population from approximately 100 individuals in 1900 to over 50 000 in 1995. He speculates that Eurasian beaver may have had a mildly beneficial effect on Norwegian Atlantic salmon stocks, partly as a result of flow stabilization.

Beaver ponds provide fish refuge during periods of low flow and drought (Cook 1940; Knudsen 1962; Bruner 1990; Hägglund and Sjöberg 1999). This is particularly important in the arid regions of North America. In Wyoming, the negative impacts of drought on populations of Bonneville cutthroat trout were to some extent mitigated on tributaries where beavers were active and livestock grazing was less intensive (White and Rahel 2008). Conversely, during high flows, juvenile fish utilize areas of slack water, more common where beavers are active, as a velocity refuge (NRC 1995; Taylor 1999).

Dewatering of the stream section downstream of dams during low flows can negatively impact both fish movements and habitat availability (e.g. for juvenile salmonids, Bryant 1984). Changes in flow regime and the increase in lentic habitats can prove detrimental for lotic species such as the sandhills chub and pinewoods darter (Rohde and Arndt 1991).

Temperature

Beaver activity can influence stream temperature regimes in two ways: by increasing the area of impounded reaches and thus increasing the time available for water to be heated by solar radiation, and by opening the river to sunlight (Cook 1940).

The influence of beaver ponds on fish populations via their effects on water temperature varies spatially. Higher water temperatures because of the presence of beaver ponds may benefit species in areas where fish distribution or productivity is temperature limited (Rasmussen 1941; Grasse and Putnam 1955; Gard 1961; Swales and Levings 1989; Baker and Hill 2003), as suggested for Lahontan cutthroat trout (*O. c. henshawi*, Salmonidae) in Oregon (Talabere 2002). Higher temperatures may prove detrimental in areas where streams and rivers temperatures are close to the upper limit of thermal tolerance for the species of interest. In a study of thermal characteristics of a beaver impacted stream in Wisconsin (USA), while a slight increase in temperature was detected, no consistent relationship between size or number of beaver impoundments and the degree of downstream warming was apparent (McRae and Edwards 1994). Nor did the removal of dams appear to influence upstream/downstream temperature differences. Instead, the main influence of beaver ponds was a reduction in river temperature fluctuations. McRae and Edwards (1994) argue that attempts to manage local thermal regimes of headwater streams by removing dams may be outweighed by disruptive effects on the composition of fish and invertebrate communities downstream.

The loss of riparian canopy as a result of beaver activity can cause stream temperatures to increase. This can prove detrimental to fish, such as trout (Salyer 1935; Knudsen 1962; Guignion 2009), when temperatures rise towards the upper limit of thermal tolerance for the species (Swanston 1991). Unlike other impacts, which may be localized, the reduction in shade because of tree felling can occur over considerable stream length (Parker and Ronning 2007). Problems associated with high stream temperatures are most acute during summer months (NRC 1995; Guignion 2009) and can affect fish downstream of dams in addition to those frequenting beaver impoundments (Shetter and Whalls 1955). Baker and Hill (2003) suggest that trout populations in the eastern United States are limited by high water temperatures, and that beaver activity may increase temperatures beyond tolerable limits. Interestingly, an early study suggested that spawning of brown and brook trout in Michigan is negatively affected by beaver activity as temperatures are lowered below the spawning threshold of the two species, because of greater exposure to the air (Salyer 1935).

Water quality

Beaver activity influences biogeochemical processes of watersheds because of the creation of ponds (e.g. Cirmo and Driscoll 1993; Correll *et al.* 2000). Detrimental effects on water quality within and below impoundments have been described (Rupp 1954), with reduction in dissolved oxygen the most frequently cited negative response (Cook 1940; Call 1966; Bryant 1984; Dolloff 1987; NRC 1995; Guignion 2009; Burchsted *et al.* 2010), resulting in transient anoxic conditions (e.g. Minnesota: Schlosser and Kallemeyn 2000; Ontario: Bertolo *et al.* 2008). Schlosser and Kallemeyn (2000) found virtually all beaver ponds were hypoxic, with oxygen concentrations throughout the water column being <0.4 mg L^{-1}. In Ontario, pumpkinseed (*Lepomis gibbosus*, Centrarchidae) populations fluctuated drastically as hypoxia in beaver ponds resulted in winter mortalities that eliminated as much as 96% of the older fish (Fox and Keast 1990).

In addition to influencing oxygen budgets, the deposition and retention of sediment and organic material can increase acidity within beaver ponds over time, potentially to levels that surpass the tolerance of trout species (Salyer 1935). Conversely, by trapping this organic-rich sediment, overall stream acidity levels might decline (Cirmo and Driscoll 1993) to benefit fish communities (Halley 1995).

Species richness

In North America, beaver activity is associated with high fish species richness and diversity (Hanson and Campbell 1963; France 1997). Active and abandoned beaver ponds provide conditions conducive to high species richness (Snodgrass and Meffe 1998, 1999; Schlosser and Kallemeyn 2000) because of the provision of habitat diversity and increased complexity of food webs (Ray *et al.* 2004). In New Brunswick (Canada), the disturbance caused by beaver activity is the key driver for high diversity in systems that would otherwise be dominated by Atlantic salmon (Mitchell and Cunjak 2007).

Productivity, abundance and growth

The response of benthic invertebrate productivity to the presence of beaver is a key factor in determining the nature of beaver–fish interactions (Rutherford 1955; Gard 1961). Biological production is often enhanced as a result of beaver activity (Salyer 1935; Duncan 1984; Swanston 1991; Anderson *et al.* 2009), resulting in a high standing crop of aquatic invertebrates (Rasmussen 1941; Call 1966; McCaffery 2009). The abundance of some invertebrate species may be reduced when beaver ponds are formed, partly because of increased selective predation by trout, but overall productivity tends to increase (Cook 1940; NRC 1995). Indeed, the benefit to fish of increased invertebrate abundance has been cited as an argument for beaver reintroduction in Germany (Harthun 1999). Rupp (1954), however, estimates that unit-area invertebrate production is lower in Colorado (USA) beaver ponds than in non-impounded reaches, although total production is more than doubled because of

Table 5 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 (*Culaea inconstans*, Gasterosteidae)	+	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 and Sun 2003; Gard and Seegrist 1972; Gard 1961; Kukula and Bylak 2010
Bull trout	+	Andonaegui 2000
Chinook salmon	+	Andonaegui 2000
Coho salmon	+	Bustard and Narver 1975; Pollock *et al.* 2004; Lang *et al.* 2006; Leidholt-Bruner *et al.* 1992; Nickelson *et al.* 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 (*Semotilus* spp., Cyprinidae)	+	Schlosser 1998; Rupp 1954
Cutthroat trout	+	Grasse 1951; Harig and Fausch 2002
Dolly Varden	+	Gregory 1988
Eastern brook trout	+	Rupp 1954; Grasse 1951
Fallfish (*S. corporalis*, Cyprinidae)	+	Rupp 1954
Fathead minnow (*Pimephales promelas*, Cyprinidae)	+	France 1997
Finescale dace (*P. neogaeus*, Cyprinidae)	+	France 1997
Golden trout	–	Müller-Schwarze and Sun 2003
Lahontan cutthroat trout	+	Talabere 2002
Lake whitefish	–	Bertolo and Magnan 2006
Minnow (Cyprinidae spp.)	+	Knudsen 1962
Mudminnow (Umbridae spp.)	+	Knudsen 1962
Muskellunge (*E. masquinongy*, Esocidae)	+	Frohnauer *et al.* 2007
Ninespine stickleback	+	Rupp 1954
Northern pike	+	Bertolo and Magnan 2006; Knudsen 1962
Northern redbelly dace (*P. eos*, Cyprinidae)	+	Rupp 1954; France 1997
Pinewoods darter	–	Rohde and Arndt 1991
Puye (*Galaxias maculatus*, Galaxiidae)	+	Moorman *et al.* 2009
Rainbow trout	+	Müller-Schwarze and Sun 2003; Grasse 1951; Andonaegui 2000; Gard 1961
Sandhills chub	–	Rohde and Arndt 1991
Slimy sculpin (*C. cognatus,* Cottidae)	+	Mitchell and Cunjak 2007; France 1997
Sockeye salmon	+	Murphy *et al.* 1989
Steelhead salmon	+	Andonaegui 2000
Walleye	–	Bertolo and Magnan 2006
White sucker (*C. commersonii*, Catostomidae)	+	Rupp 1954; France 1997
Yellow Perch (*Perca flavescens*, Percidae)	+	Balon and Chadwick 1979

greater area of substrate, resulting in higher fish abundance.

A relationship between beaver activity and fish abundance and productivity, possibly operating via influences on invertebrate production, is of obvious interest to fisheries managers (Table 5). Enhanced fish growth in beaver ponds because of high invertebrate productivity and elevated water temperatures (Rosell and Parker 1996) has been observed for sockeye (*O. nerka*, Salmonidae) and coho salmon (Murphy *et al.* 1989; Swales and Levings 1989) and a variety of trout species (Cook 1940; Patterson 1951; Rutherford 1955; Shetter and Whalls 1955; Christenson *et al.* 1961; Knudsen 1962; Hale 1966; McCaffery 2009; Kukula and Bylak 2010). In New Brunswick, Atlantic salmon parr recaptured from a beaver pond exhibited higher growth rates and were better able to maintain condition during the summer, than individuals sampled from above or below the pond (Sigourney *et al.* 2006). Conversely, excessively high densities of brook trout in beaver ponds in Colorado led to their stunting (Rabe 1970).

In Sweden, Hägglund and Sjöberg (1999) found low abundance of brown trout in stream reaches where beaver were active, although those caught in beaver ponds tended to be larger than those from riffle sections.

Extensive beaver activity in wetlands provides stable salmonid habitat and buffers variability in abundance (Lichatowich 1999). Prior to European settlement in the Pacific Northwest of the United States, fluvial systems exhibited a mosaic of beaver created wetland complexes, active side channels and riparian forests that provided highly productive habitat for Pacific salmonids (Andonaegui 2000). Based on aerial photography, Pollock *et al.* (2004) estimate that the summer Pacific salmonid smolt production potential of the Stillaguamish River Basin (Washington) has declined by 61% of historic levels because of the loss of suitable rearing habitat associated with beaver ponds. At the landscape scale, beaver ponds may provide reproductive 'source' habitats while adjacent stream environments act as 'sinks' (Schlosser 1993, 1995a,b). The full functioning of the entire spatial and temporal mosaic of successional habitats associated with beaver activity, including those because of the creation and abandonment of beaver ponds, is required to maximize potential benefits for fish populations (Schlosser and Kallemeyn 2000).

Expert opinion survey

Participation and anonymity

A total of 68 experts were selected and sent a notification of intention to survey. One notification was rejected because of specification of an incorrect e-mail address, and this issue was not resolved. Of the 67 remaining, 61 (91%) replied to the pre-notification including 9 who declined to participate. Eighteen reminders were sent. A total of 50 completed questionnaires were returned (participation rate 74.6%), of which one was discarded because of the respondent claiming no expertise on the subject. Twenty-one participants wished to remain anonymous.

Profession and expertise

Participants were able to select more than one option for item 1 to describe their profession, with 15 choosing to select two or more categories. Thirty-one respondents described themselves as fisheries scientists/managers, 5 as geomorphologists, 8 as terrestrial ecologists, 15 as beaver specialists and 9 as other. Thirty-two (64%) participants worked in North America, 11 of whom were based in the Pacific Northwest of the United States. Twenty-eight respondents considered themselves to have moderate knowledge of the subject area; 8 with expert knowledge; and 13 with little knowledge.

Thirty-three respondents had experience primarily of the North American beaver, 15 predominantly of the Eurasian beaver and one with both. When asked to select the species of fish for which they had experience of beaver impacts, 25 respondents selected more than one category, 18 selected '*Salmo salar*', 15 selected '*Salmo trutta*' (both brown and sea trout), 25 selected 'other salmonids' and 15 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*, Salmonidae). Non-salmonids included lamprey (*Lampetra* spp., Petromyzontidae), alewife (*Alosa pseudoharengus*, Cluipeidae), blueback herring (*Alosa aestivalis*, Cluipeidae), riffle daces (*Rhinichthys* spp., Cyprinidae), suckers (*Catostomus* spp., Catostomidae), general Clupeids, general Cyprinids, stickleback, eel, walleye (*Sander vitreus*, Percidae), sculpin (Cottoidea spp.) and northern pike (*Esox lucius*, Esocidae).

Impacts of beavers – response to Likert-scale items

Twelve median scores for the 24 items listed were positive (score >3); 10 were neutral (score = 3); and 2 were negative (score <3) (Table 6). Eleven items achieved a positive mode, eight were neutral, four were negative, and one was bimodal for scores of 3 and 4. Based on reaching a majority threshold (50%), high levels of agreement were obtained for 12 items (Table 6). Of those, four were positive, six neutral and two 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 19a); and the impact of beavers on productivity (Item 20a) (Fig. 3). The response to five items exhibited a negative tendency (majority of responses <3): the

Table 6 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	Item description	*N*	Response (%)					Median	Mode
			1	2	3	4	5		
5	Beaver activity on freshwater ecosystem	46	0	7	7	**50**	37	4	4
6	Economic impact of beavers on ecosystem	44	0	30	34	25	11	3	3
7	Beavers on cultural value of ecosystem	43	0	5	19	49	28	4	4
8	Beaver activity on geomorphological processes	44	2	7	18	48	25	4	4
9	Beaver activity on patterns of river flow	46	2	17	20	41	20	4	4
10	Overall impact of beaver dams on habitat connectivity	45	4	36	31	20	9	3	2
11	Beaver dams on movement of aquatic biota	47	0	47	43	9	2	3	2
12	Beaver activity on habitat heterogeneity	46	2	4	7	24	**63**	5	5
13a	Beaver activity on species richness - all biota	44	0	0	14	**52**	34	4	4
13b	Beaver activity on species richness - fish species	44	0	5	25	**55**	16	4	4
14a	Beaver dams on upstream movement of migratory salmonids in main stem rivers	45	2	4	**89**	4	0	3	3
14b	Beaver dams on upstream movement of migratory salmonids in tributary streams	45	9	**56**	31	2	2	2	2
15a	Beaver dams on downstream movement of migratory salmonids in main stem rivers	45	0	0	**96**	2	2	3	3
15b	Beaver dams on downstream movement of migratory salmonids in tributary streams	44	2	23	**64**	9	2	3	3
16a	Beaver dams on movement of other fish species in main-stem rivers	43	0	9	**86**	2	2	3	3
16b	Beaver dams on movement of other fish species in tributary streams	43	2	**56**	37	5	0	2	2
17a	Beaver activity on availability of suitable spawning habitat for migratory salmonids	43	2	42	47	7	2	3	3
17b	Beaver activity on availability of suitable spawning habitat for other fish species	40	0	18	**53**	28	3	3	3
18a	Beaver activity on availability of suitable non-spawning habitat for migratory salmonids	43	2	19	26	40	14	4	4
18b	Beaver activity on availability of suitable non-spawning habitat for other fish species	42	0	10	33	45	12	4	4
19a	Beaver activity on abundance of migratory salmonids	44	0	23	30	30	18	3	3 and 4
19b	Beaver activity on abundance of other fish species	42	0	0	**50**	40	10	3.5	3
20a	Beaver activity on productivity of migratory salmonids	44	0	18	30	36	16	4	4
20b	Beaver activity on productivity of other fish species	41	0	0	41	46	12	4	4

impact of beaver dams on the movement of aquatic biota (Item 11); the impact of beavers on upstream movement of salmonids in tributary streams (Item 14b, high level of agreement score 2, Table 6); the impact of beaver dams on downstream movement of migratory salmonids in tributary streams (Item 15b); the movement of other fish species in tributary streams (Item 16b, high level of agreement score 2, Table 6); and the impact of beaver activity on availability of suitable salmonid spawning habitat (Item 17a) (Fig. 3). There were high levels of agreement (over 85%) with a score of 3 given in response to the three items related to upstream and downstream movement of migratory salmonids and other fish in main-stem rivers (Items 14a, 15a and 16a). 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 6); and the overall impact of beaver dams on habitat connectivity (Item 10) (Fig. 3).

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

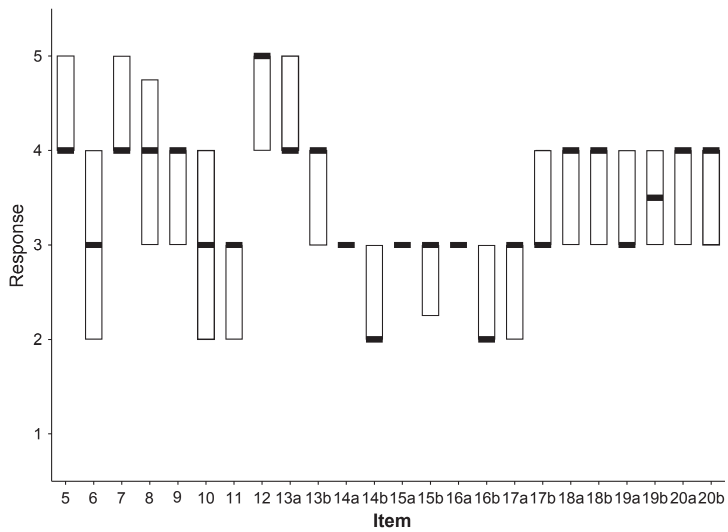

Figure 3 Response of experts to survey questions related to the impact of beaver on fish populations and ecosystem processes (see Table 6). Likert-scale item response scores range from severe negative (1) to high positive (5), with a score of 3 representing no impact. Solid horizontal lines represent medians and boxes interquartile range.

(score = 1) being rarer than for high positive impacts (score = 5).

Discussion

The interaction between beaver activity and freshwater fisheries has been the subject of several reviews (e.g. Collen 1997; Collen and Gibson 2001; Pollock *et al.* 2003; Rosell *et al.* 2005; Venturini 2006). Descriptions of costs and benefits have highlighted the intrinsic uncertainty and complexity of response that varies with temporal and spatial scale, species and density. As a result, clear generalized guidance on which to base management decisions has been difficult to obtain. Fisheries groups continue to raise concerns about beaver reintroduction and management (Cramb 1998; Bau 2001), particularly in relation to the impact of beaver dams on the movement of migratory fish during periods of low flow. Based on combined results of an independent and systematic review of the literature and survey of expert opinion, this paper attempts to enhance certainty and develop generalizations based on weight of evidence. Although the complexity of response to beaver/fish interactions was again highlighted, broad general patterns emerged.

The most regularly cited significant negative impact of beaver activity is the impediment created by dams to fish migration (Cunjak and Therrien 1998; Cunjak *et al.* 1998; Scruton *et al.* 1998; Mitchell and Cunjak 2007; Parker and Ronning 2007; Guignion 2009; Taylor *et al.* 2010), although little research quantifying the magnitude of this impact was found (see Tables 3 and 4). On main-stem rivers, beaver dams are rarely constructed and hence do not pose significant impediments to fish passage, a suggestion supported by the response of a large majority of the experts. Where dams 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 narrow tributary streams, and especially under low flows. For example, 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 (Elmeros *et al.* 2003). However, 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 and appear to have negligible long-term impacts on Atlantic salmon and brown trout populations (Parker and Ronning 2007).

Impoundment and siltation of spawning gravels (e.g. Müller-Schwarze and Sun 2003) was also identified as a significant negative impact of beaver activity, particularly for salmonids (Swanston 1991). Non-salmonid species, however, may benefit (e.g. Snodgrass and Meffe 1998; Schlosser and Kallemeyn 2000). Conversely, sediment deposition in slow-flowing beaver ponds can result in improved quality of spawning gravels located between impounded reaches by reducing infiltration of fines (Beedle 1991).

Other negative impacts include alteration of temperature (via loss of riparian shade; e.g. Salyer 1935; Knudsen 1962; Guignion 2009) and flow (e.g. Bryant 1984) regimes, and reduction in habitat availability (Rutherford 1955) and water quality (e.g. Rupp 1954).

Based on qualitative assessment of 'vote-counting', positive impacts of beaver activity were more frequently cited than negative effects, although potential for publication bias (Gurevitch and Hedges 1993; Thornton and Lee 2000) should be recognized. Beneficial effects related primarily to habitat improvement, i.e., enhanced heterogeneity (Bryant 1984; Lichatowich 1999) and provision of rearing (e.g. Swanston 1991; Taylor 1999; Johnson and Weiss 2006) and overwintering (e.g. Cunjak 1996) habitat, and increased invertebrate productivity (e.g. Rutherford 1955; Gard 1961), fish growth (Rosell and Parker 1996) and ultimately higher fish abundance and productivity (e.g. Pollock *et al.* 2004).

For the majority of items to which experts responded, a positive score was given. On balance, beavers are perceived to be either beneficial to or have negligible impact on, economic, cultural, physical (geomorphological) and ecological processes, including fish population dynamics. The high tendency for positive responses to the majority of items is interesting considering that over 60% of participants described themselves as fisheries scientists or managers. The high percentage (42%) of requests for 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 survey did not indicate polarization of two extremes of view for any item considered. 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. Nearly three-quarters of those invited to participate in the expert opinion survey did so. This high response rate may likely be explained, at least partly, by the use of pre-notification and reminders.

Research and management implications

The ecological impacts of beaver activity, whether positive or negative, are often difficult to quantify with a high degree of certainty. For example, demonstrating the impact of beaver dams on fish movement using traditional methods (e.g. based on presence/absence or density of juvenile fish, or redd counts, both upstream and downstream of dams) can sometimes provide some indication of broad change, although they might not necessarily be able to provide a detailed level of resolution. Alternatively, fine-scale techniques (e.g. telemetry) can prove prohibitively expensive when employed for anything more than to assess local impacts. The mechanics of fish passage at beaver dams requires more intensive research, using both experimental- and field-based empirical approaches. Research is also warranted to improve understanding of how potential overlap of suitable salmonid and beaver habitat may be modelled, and the influence of impediments to fish movement at the population level. Further research should also consider how predicted shifts in climate, and related flow and temperature regimes, may interact with the impact of structural impediments to fish movement, including beaver dams.

The balance between costs and benefit of beaver activity when viewed from a fisheries perspective will vary locally determined by life-history bottlenecks (see Armstrong *et al.* 2003). Localized impacts of beaver dams on fish passage and spawning habitat, while potentially negligible from the perspective of long-term dynamics of resistant populations, may impose additional pressures on stocks that are already stressed as a result of anthropogenic factors. Further, the spatial bias in understanding can prove problematic when knowledge obtained in regions, and for species, that differ from those where future reintroductions are proposed is applied. Much of the current understanding of beaver/fish interactions relates to the North American beaver and Pacific salmonids, a bias also highlighted by the expert opinion survey. It is important to recognize that, although similar, the two species of beaver differ in terms of their life-history and behaviour, and thus, ecological impacts will not be identical. For example, the North American beaver appear to build larger dams, and more frequently, than the Eurasian species, even where the two occur in sympatry (e.g. in Russian Karelia: Danilov and Kan'shiev 1983; Danilov 1995). The Eurasian beaver tend not to construct dams on streams with a gradient >2% (maximum recorded = 2.5%, Schulte 1989; Hartman and Törnlöv 2006), while the North American beaver utilize steeper channels up to c. 3% (see review in Curtis and Jensen 2004) and on occasion as high as 4% gradient (McComb *et al.* 1990). Further, the litter size tends to be larger for the North American than the Eurasian beaver (Rosell and Parker 1995) which may influence frequency of dam building and ultimately the density of beaver structures within the landscape. As a result, these and likely other interspecific differences, inferences about the effects of one of the species based on evidence provided in relation to the other should be considered with caution.

In regions where rivers can respond in a 'natural' way to the activity of beaver, e.g., increased frequency and extent of overbank flows (Jeffries *et al.* 2003) and localized flooding as a result of dams, alternative routes of fish passage become available via back-water or floodplain channels. In intensively urbanized regions, the re-establishment of lateral connectivity with the floodplain is prevented in highly managed and constrained channels designed to minimize flood risk. In engineered channels, beaver dams can sometimes significantly impact fish passage, and this can be exaggerated as a result of interaction with anthropogenic river infrastructure, e.g., blockage of culverts with woody debris and silt. The widely reported benefits of beaver activity may be further outweighed by other negative effects such as the possible reduction in riparian forest recruitment under certain circumstances, and flooding of human infrastructure (roads and residences).

There are several management options available. Culverts may be protected by extending the inflow pipe underwater and screening the entrance within a wire mesh enclosure. Notches are often cut in dam structure (see Taylor *et al.* 2010), or they may be dismantled entirely. Unfortunately, the latter can prove ineffective in areas where the beaver activity increases the probability that they will be rebuilt. Conversely, not all beaver dams block the entire channel, and some structure may provide velocity refuge during high flows in heavily engineered rivers that contain little other shelter. Alternatively, BDS structures may be employed to locally attract beavers to preferred areas away from sensitive locations (Pollock *et al.* 2003).

Reintroduction programmes should incorporate appropriate 'exit strategies' that enable the project to be halted during the trial stage if necessary, and for populations to be controlled over the longer term if densities are considered sufficiently high as to be detrimental to other interests. Lessons should be learned from experience obtained in Massachusetts where increases in beaver populations have resulted in human–beaver conflict and negative public opinion (J. Sprules personal communication). Maintaining positive public opinion is an essential component of long-term success of any reintroduction programme (see Reading and Kellert 1993; Fritts *et al.* 1997).

Expert opinion in combination with meta-analysis, techniques commonly employed in the social sciences (e.g. Glass 1976), helps improve certainty and generalization through the consideration of weight of evidence and identify areas of agreement or polarization of perspectives. However, there is a need to identify, appreciate and account for differences in quality of information between studies which are influenced by whether arguments and conclusions formed are based on primary data, models or speculation. Mechanisms to successfully assess quality of information and weight interpretation accordingly are important. Nevertheless, better integration of social sciences into ecological research has been recognized as an urgent priority (e.g. Redman *et al.* 2004), and novel interdisciplinary approaches such as adaptive comanagement (Plummer and Armitage 2007) may prove useful when developing conservation strategies despite complex and uncertain ecological interactions. By concentrating on the impact of beaver activity on fisheries, this study reflects a focused approach to facilitate decision-making by managers who will, by necessity, also consider wide-reaching implications of other social, economic and political factors. Nevertheless, despite the many arguments for or against reintroductions of species, whether based on sound scientific evidence, speculation or public opinion, legislation is increasingly acting as an important driver in the decision-making process and can constrain management options.

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