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Independent Review of: "REVIEW OF EVIDENCE OF INTERACTIONS BETWEEN BEAVERS AND FISH AND FISHERIES IN ENGLAND AND WALES by Professor Ian G. Cowx"

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Introduction

Context

The author, Dr. Malison was funded by the Devon Wildlife Trust to complete an Independent Review of the report authored by Professor Cowx "Review of evidence of interactions between beavers and fish and fisheries in England and Wales." Dr. Malison was contracted to conduct this review to **ensure that the impact of beavers was assessed in an independent, objective and unbiased fashion**. Dr. Malison is a researcher in the USA with expertise and experience researching beaver-salmonid interactions in both North America and Scandinavia. **Dr. Malison has published about both potential positive and negative impacts of beavers on salmonids** (see more about the author below). Dr. Malison has not been involved in the ROBT, not is she a member or contributor to the funding organization in any way. In conducting this review, Dr. Malison provided detailed comments on the review authored by Prof Cowx. Dr. Malison viewed the River Otter Beaver Trial Science and Evidence Report and utilized the peer-reviewed literature and included additional citations as needed. Dr. Malison did not comment on opinions regarding management or government decision making processes in general, but rather focused on statements related to the interactions between beavers and fish/fisheries and the robustness of scientific data collection. Throughout the review text from the Cowx review is quoted in italics and responses follow in regular font.

About the Author

Dr. Rachel Malison is a freshwater ecologist with expertise in stream and floodplain ecology. She uses a systems approach to investigate what factors drive and control the structure and function of freshwater systems. Much of Dr. Malison's work focuses on linkages within and among lotic systems and encompasses scales from genes to ecosystems. She is an expert on the interactions of beavers and salmonids and has conducted research on the impact of both *Castor canadensis* in North America and *C. fiber* in Norway. She completed her MS degree at Idaho State University where she investigated the influence of wildfire on aquatic-terrestrial connectivity of linked stream-riparian habitats in the Frank Church Wilderness. She completed her PhD in Systems Ecology at the University of Montana where she studied the influence of beavers (*C. canadensis*) on freshwater habitats and food resources for juvenile salmonids (macroinvertebrates) and how beavers influence the growth, survival and production of juvenile salmonids in a large river floodplain in Alaska. She also investigated potential negative impacts of introducing salmon to a productive river floodplain where beavers have never been present, to illustrate that each potential case for beaver restoration should be examined critically on salmon rivers. Following her PhD, she was awarded a Marie Curie International Incoming Fellowship from the EU to study the influence of beavers (*C. fiber*) on juvenile Atlantic salmon and trout

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populations in the Trøndelag province of Norway. Following her work in Norway she returned to the Flathead Lake Biological Station in Montana, USA where she has been researching the vulnerability and adaptations of stoneflies (Order: Plecoptera) in river floodplains and streams using a variety of genomic and physiological techniques. Dr. Malison also has research underway investigating changing temperatures of freshwater salmon habitat in Alaska and is starting a new research project in summer 2021 to investigate how beaver dam analogs alter aquatic macroinvertebrate communities in small streams and what consequences this might have on aquatic-terrestrial linkages.

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Detailed Review of the review authored by Professor Cowx

Summary

Summary statements from Professor Cowx's report (shown in italics) and responses:

- *In recent years, beavers have been reintroduced into the UK, mostly in enclosed (fenced) environments. Several 'wild' populations have also established, including one in the River Otter in Devon, which is being used as a trial to assess the likely impacts (positive and negative) on riverine ecosystem functioning and biodiversity. There are concerns, however, that the River Otter trial is too narrow in scope to provide robust evidence to inform decisions on further reintroductions, especially into the wild.*

  The concerns about the ROBT being too narrow in scope and not relevant to wild reintroductions are unfounded. The ROBT beavers are not contained within enclosures, they are free to move. This would be the case in other wild reintroductions as well.

- The aims of his review were to*:*1) *re-examine the evidence base on the scale and intensity of impacts from beaver reintroductions on river ecosystems, and specifically on fish and fisheries;* 2) *review evidence from the River Otter Beaver Trial and associated studies to understand the impact of beavers on fisheries under 'wild' conditions;* 3) *provide conclusions and recommendations about the potential impact of beavers on fish and fisheries with particular reference to UK rivers.*

  Though the aims of Prof Cowx's review were simply focused on the impacts of beaver on fish and fisheries, the overall conclusion of his review was that beavers should not be reintroduced until a wide number of factors are addressed. However, the impacts of beavers and their creation of dams are strongly beneficial to other organisms and aquatic ecosystem biodiversity and this is supported by peer-reviewed literature (detailed in sections below).

- *A review of the literature and other materials related to beaver reintroductions, with specific reference to fish and fisheries, was carried out. There is considerable emphasis in the literature and media on the positive benefits that beavers can bring to aquatic ecosystems and biodiversity, but the reintroduction of beavers can also cause a number of potential problems, such as disruption to fish migration and fish recruitment, damage to trees, loss of agricultural production, and damage to banks and other infrastructure, with concomitant impacts on biodiversity, stakeholder conflicts and management costs. The fish and fisheries problems mainly occur because of construction of dams that impede fish migration and flood spawning and nursery habitats. It also appears that most of the costs associated with dealing with the impacts of beavers are borne by the*

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stakeholder, including land/riparian owners, fishery owners and river conservation bodies.

Prof Cowx did indeed conduct a literature review. However, the review and this summary primarily focused on the potential and/or perceived negative impacts of beavers and dams, when a large body of the literature supports positive impacts. A balanced summary of the impacts of beaver reintroductions and their influence on fish and fisheries should list both potential positive and negative impacts.

- *The River Otter Beaver Trial [ROBT] studies, which ran for 5 years, provided considerable information on changes in the distribution of beavers in the catchment over the study period and into the future, and illustrated the benefits, in terms of nature-based solutions to flooding and to biodiversity, arising from construction of dams. Emphasis was put on benefits from beavers to the rural economy and ecotourism and less on the impacts of beaver activities on agriculture, fisheries and property. Unfortunately, the* ***5 year timeframe of the study was insufficient to understand the full implications of reintroducing beavers into open catchments.***

  Long-term ecological studies (lasting 5+ years) are extremely important to science and for informing policy, yet the majority of funding and conducted research are short term studies conducted in 4 years or less (Hughes et al., 2017). The fact that the ROBT lasted 5 years, makes in longer than most ecological studies and additional long-term monitoring is on-going and also planned for the future. As such, it is a robust study, supported by multiple case studies and peer-reviewed papers that focused on both positive and negative impacts. A combination of the ROBT study, as well as inference from a plethora of other studies can be used to infer the "full implications" of reintroducing beavers.

- *In particular, the evidence collected on the interaction between beavers and fish and fisheries was limited, and lacked the rigour expected of a robust impact assessment, and in some cases was only based on observation data, especially movements of fish past dams. The fisheries surveys focussed on a single dam structure on the River Tale over a four-year period and only one survey on the main River Otter in 2015, despite considerable beaver activity in this latter zone of the river. The findings of the fisheries surveys were largely inconclusive. The ROBT fisheries studies should have, at minimum, examined the fish population/community dynamics above and below a range of dams in different locations and used control reaches to account for variability in the impact of dams between different river types.* ***It is also important that future studies on the impact of beavers on fish and fisheries cover areas where beavers are active not just where***

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***dams have been constructed**, i.e. in the main river channels and lower reaches of larger tributaries.*

Unsurprisingly, beavers did not build dams on the main river channel. The magnitude of water flow precludes this from happening and as such fish are able to access the entire length of the main river with no potential obstacles form beavers (though of course all the man-made weirs are a known problem). This is commonly the situation in larger rivers in both North America and Europe and as such beavers have very limited ability to influence fish and fisheries in the main river because their dams are located on tributaries or off channel habitat (Malison & Halley, 2020; Malison et al., 2014, 2015). The concern regarding impact where beavers "are active" but not building dams in larger main river channels is unfounded.

- *Studies on fish migration were also inconclusive and based on videos of five adult sea trout passing one structure under what appear to be optimal hydraulic conditions. To address the conjecture surrounding fish migration past beaver dams, which must include both up and downstream movements, **there is a clear need for more robust studies on the barrier effects and otherwise of beaver dams on fish migration and recruitment processes**. Further, the coarse resolution rapid barrier assessment tool developed within the project is limited in scope and needs to be field tested for validity with a range of dams in different water courses, and with a range of migratory species, before any confidence can be placed in its application. Thus, **before any definitive conclusions can be drawn about passability of beaver dams, fully funded research, including telemetry studies, on a range dam types, including cascades of dams, and for a full range of species, must be undertaken.***

One of the most commonly held concerns regarding the impacts of beavers, especially held by angling related interests, is that beaver dams are barriers that block fish migration (Auster et al., 2020; Kemp et al., 2012; Morzillo & Needham, 2015). Though there is definitely need for additional research to be conducted on both adult and juvenile fishes, and the suggestions provided in the review by Prof Cowx would provide a strong study design (with the addition of PIT-arrays and tags for juvenile fish), a large body of research from North America and Europe has demonstrated that beaver dams and beaver dam analogs are not impassable barriers (Bouwes et al., 2016; Bylak & Kukuła, 2018; Lokteff et al., 2013; Malison & Halley, 2020). Rather than being impassable like large weirs or manmade dams, beaver dams vary in their passability. Beaver dams regularly overtop with high flow and rain events, they often break and/or have water flowing through in places (Collen & Gibson, 2001; Malison & Halley, 2020). A greater understanding of how changes in the seasonality or degree of fish movement is modified by beaver dams would be useful, as well as actual long-term studies documenting whether these changes modify population dynamics or productivity of different fish species. Generally beaver dams are very "leaky" and offer many pathways for fish

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movement (though this may not be the case in more extreme situations where tens or hundreds of dams are present in large alluvial floodplains; see Malison & Stanford, 2016). Furthermore, though other studies haven't made direct measurements of movement, the continued use of habitats upstream of beaver ponds should not be discounted as evidence for passability (e.g. Bylak et al., 2014; Malison et al., 2015; Wathen et al., 2018). These studies also show how beneficial beaver related habitats can be for juvenile fish rearing (including salmonids). For example, Malison et al (2015) documented thousands of juvenile salmonids utilizing beaver ponds as rearing habitat in summer months and in some cases all individuals were documented leaving the ponds in the fall, providing additional evidence they were able to move past the dams. Wathen et al. (2018) documented the importance of beaver complexes for rearing steelhead in a system where beaver dams are passable and Bylak et al. (2014) found all dams were passable, though this varied with flow and some were only passable with relief channels.

- *A number of mitigation and management measures were found in the literature and proposed and tested in the ROBT Science and Evidence study to address problems arising from beaver activity. Most of the potential negative effects of beavers on fish are related to dam construction, but these dams may be difficult to modify or destroy because of the beavers' inherent response to rebuild them. Other measures related to flow management ('beaver deceivers') require rethinking as they could potentially exacerbate problems with fish migration.*

There is an assumption that dams will negatively affect fish populations, yet many publications illustrate that beaver dams can be passed by fish (Bouwes et al., 2016; Bylak & Kukuła, 2018; Collen & Gibson, 2001; Cunjak et al., 1993; Lokteff et al., 2013; Malison & Halley, 2020; Malison et al., 2015).

- ***In conclusion, based on the review of potential interactions between beavers and fish and fisheries, and on the current science and evidence available, further reintroductions of beavers into the wild should not take place until the recommendations made herein have been fulfilled. Once these knowledge gaps have been filled and management issues resolved, it may be possible to find solutions that would allow further controlled introductions of beaver, where their location, activities and numbers can be managed to curtail any damage to fish and fisheries or other economic or social sectors.***

This recommendation is not justified because a balanced view of the positive and negative benefits of beavers is not presented. Detailed comments and additional references are included in this review to provide a more balanced view that could potentially help inform policy recommendations.

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1 Introduction

1.1 Context

The author provides information about how beavers were reintroduced to the River Otter in Devon and the duration of the ROBT. The author notes that Natural England is also currently analyzing the result of the ROBT, along with other data on beavers across the UK and in other countries to help inform decisions. **This should highlight the fact that data from other countries is useful in making inferences about beaver reintroductions, and that long-term studies in England alone need not be required before reintroductions of this native species occurs.**

The aims of the review by Prof Cowx were to:

- *"re-examine the evidence base from the UK and elsewhere in Europe and North America to determine the scale and intensity of impacts from beaver reintroductions on river ecosystems (structure and functioning), and specifically on fish and fisheries supported by them;*

- *review the evidence from the River Otter Beaver Trial and associated studies, together with supplementary information gathered for the River Otter, in terms of understanding the impact of beavers on fish and fisheries under uncontrolled, 'wild' conditions;*

- *provide conclusions about the information reviewed and the potential impact of beavers on fish and fisheries with particular reference to UK river systems to inform decisions on the potential management and licencing of beaver introductions in England."*

Unfortunately, the review by Prof Cowx was not balanced and did not include a review of many of the positive impacts of beavers. Furthermore, the review did not comprehensively review the impacts of beavers on the structure and function of river ecosystems as stated in point one, rather it focused primarily on the perceived negative impacts of beavers on fish and fisheries. **Conclusions about the potential impacts of beavers on fish and fisheries should not be based on the review by Prof Cowx because previous comprehensive reviews have shown that the benefits of beavers are more often cited than costs** (Collen & Gibson, 2001; Kemp et al., 2012)**.**

1.2 About the Author

Professor Cowx is a world-renowned Fisheries Biologist, but he has not conducted research on beavers or the interactions of beavers and fish/fisheries.

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2 Review of beaver-fish interactions

2.1 Methodology

The review by Prof Cowx included a review of the peer-reviewed literature, with specific reference to fish and fisheries, however some of the keywords themselves (mortality, barrier) focus on potential negative impacts and were not balanced by keywords that would have selected for positive impacts. For example, dams should not simply be considered barriers. Very commonly they are passable to fish. Other useful keywords to include with 'beavers' would have included 'biodiversity', 'community composition', 'freshwater fish/salmonid habitat,' 'rearing habitat', 'species richness', 'fish/salmonid growth,' 'fish/salmonid production*,'* etc. Methodology used in the review by Kemp et al. (2012) suggests that the search terms 'beaver AND reintroduction AND salmon' would have also been useful.

Notably, this review did not include a significant number of references which illustrate the positive impacts beavers (*C. canadensis* and *C. fiber*) can have on fishes, including salmonids (some of which are included here). Beaver ponds provide important rearing habitat for juvenile salmon and other fishes (Bryant, 1983; Grasse, 1979; Hägglund & Sjöberg, 1999; Leidholt Bruner et al., 1992; Malison et al., 2015; Murphy et al., 1989; Scruton et al., 1998). Beaver ponds have lower maintenance costs for juvenile fishes (Enders et al., 2003), which can contribute to higher growth rates. Beaver ponding can increase survival (Bustard & Narver, 1975; Malison et al., 2015; Quinn & Peterson, 1996), growth rates (Bustard & Narver, 1975; Malison et al., 2015; Peterson, 1982; Swales & Levings, 1989), and production (Bouwes et al., 2016; Layman & Smith, 2001; Malison et al., 2015; Nickelson, Rodgers, et al., 1992) of juvenile salmon. The presence of beaver ponds promotes higher fish species richness (Snodgrass & Meffe, 1998). Beaver habitat is considered generally beneficial to fishes in a number of other publications, though benefits can be lost after sites are abandoned in some systems (Collen & Gibson, 2001; France, 1997; Gard, 1961; Huey & Wolfrum, 1956; Neff, 1957). Beaver ponds also provide important winter rearing habitat for fishes (Chisholm et al., 1987; Richard A. Cunjak, 1996; Jakober et al., 1998; Lindstrom & Hubert, 2004; Miller & Sadro, 2003; Nickelson, Nicholas, et al., 1992; Nickelson, Rodgers, et al., 1992), though winter kills of pumpkinseed fish associated with hypoxia have occurred in at least one system (Fox & Keast, 1990). Furthermore, woody structures provide fish with cover (Burchsted et al., 2010).

The positive impacts listed in the studies above do not include all the other organisms that benefit from the presence of beaver ponds (Dalbeck et al., 2014), increases in system biodiversity (Law et al., 2016, 2017, 2019; Nummi et al., 2019; Willby et al., 2018), and how beavers can increase habitat heterogeneity and connectivity of wetland environments (Hood & Larson, 2015).

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2.2 Review of beaver fisheries interactions

The review by Prof Cowx notes that there were 796 citations reported in WoS with the basic search term "fish* AND beaver*" as of November 2020 and that additionally, numerous other reports existed in the grey literature. However, the review by Prof Cowx references only 125 of the 796 publications in section 6.2 References.

His review does not include references from many publications that show positive impacts of beavers on fishes or aquatic systems. Examples of publications illustrating positive impacts are cited above in section 2.1 Methodology (though this is an underestimate because a comprehensive review to list them all was not undertaken as part of this effort)..

Text describing the analysis depicted in Figure 2.1 of the review by Prof Cowx is presented as showing the "main issues arising from the reintroduction of beavers". "Main issues" comes across negatively, when in fact a few of the factors in the table are positive and many other positive impacts are missing entirely. Additionally, "Damage to riparian vegetation and agricultural crops" does not belong in Figure 2.1. As depicted there are no references specifically included in Figure 2.1 and it is impossible to know the relative weight of positive and negative impacts for a given category.

Table 2.1 as presented in the review by Prof Cowx cannot be used to determine the relative weight of positive and negative impacts of beavers on fish and fisheries because **1) there are no references included in the table**. It is impossible to weigh the evidence for different impacts without citing primary literature. 2) Many positive impacts are not included in the table. 3) Negative impacts are included that are not supported by peer-reviewed literature. 4) Prof Cowx's reviews seems not to take spatial scale into consideration. Within a river or stream system, relatively small areas behind dams generally become lentic, while the majority of the system remains lotic (flowing). In lentic areas behind some dams some negative impacts may occur, but the magnitude of the impact needs to be assessed in the context of the river system or watershed. The later example/s of entire stream reaches being transformed from lotic to lentic systems occurred in fenced situations where beavers are not able to move on the landscape.

Table 2.1 has been recreated and improved below to demonstrate what should have been included (but it still not comprehensive of all the literature). An effort was made to better represent both positive and negative impacts, all referenced by peer-reviewed literature. Text in *italics* was copied or summarized from the Prof Cowx review table 2.1. Comments regarding assumptions, considerations or problems with the impacts listed by Prof Cowx are noted in the new adjacent columns "Assumptions/Notes". Additional categories and impacts have been added to the table where relevant. Text with ~~strikethrough~~ is not relevant or in the wrong category. To determine the relative importance of positive and negative impacts references for impacts have been included in "Reference" columns.

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Beaver activity and outcome	Positive effects on fish and fisheries	Assumptions/Notes	References	Negative effects on fish and fisheries	Assumptions/Notes	References
Felling of trees and shrubs						
Changes to riparian woodland and bankside cover and shifting of riparian tree species composition	*Penetration of light may allow new plant communities that may better stabilize banks and reduce erosion* *Potential increase in terrestrial input of food items with shift in riparian species* By coppicing trees understory is more abundant and diverse	Citations? Potentially (Law et al., 2017)		*Change in canopy could reduce quantity/quality of terrestrial leaf litter stream inputs* *Change in canopy could reduce macroinvertebrate diversity and quantity of terrestrial prey inputs (food for salmonids)* ~~*Shift in fish species composition towards non-salmonid species which have higher tolerance to low dissolved oxygen*~~	Or it may not Or it may not This is not a potential effect of “felling trees and shrubs”	
Opening up the canopy and increasing canopy patchiness	*Increased light penetration may increase primary production (PP) within rivers and ponds.*	Some trees are well adapted to the coppicing effect of beaver foraging and may rapidly regenerate, reducing magnitude of canopy change	(Jones et al., 2009)	*Reduced shading may result in increased water temperature, causing thermal stress for some fish species*	May – warmer temperatures are not always a result and/or temperature do not rise enough to cause stress. Also reduced shading may not occur (see Halley et al., 2009)	(Knudsen 1962)

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	Increased PP and temperature may increase macroinvertebrate food production and increase fish production	Or invertebrate food production is increased by improved habitat (woody structures) and habitat complexity (see below)		*Increased instream plant growth may block rivers and cause upstream flooding and loss of connectivity during summer months*	**Citations?** What evidence is there for plant growth blocking fish movements. This seems highly unlikely.	
	Stream temperatures can marginally increase, increasing fish growth without unfavorable conditions for rearing salmon	(Malison et al., 2015)		*Elevated temperatures could contribute to reduced dissolved oxygen in some cases, which would be unfavorable for salmon*	**Citations?**	
	Increased light could lead to instream macrophyte establishment which shelter some fish species (pike, perch, roach, stickleback) but also support non-native colonization	Or not				
	Cooler temperatures at the bottom of beaver ponds can provide refugia	(Means, 2018)				
Changes in the amount/diversity of woody	*Greater quantities of large* (and small) *wood in rivers and ponds can increase habitat*		(Beedle, 1991; Burchsted et al., 2010; Collen & Gibson, 2001;	*Possible reduction in the size and quantity of large woody material entering watercourses*	**Citations?** Doubtful, Jones et al. 2009 found 12 times more annual growth in	

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material in watercourses	*diversity, availability of prey items, and fish cover* Greater quantities of wood can increase prey availability and fish growth rates ~~*Possible increase in terrestrial invertebrate prey entering the aquatic environment*~~ Woody debris is a fundamental part of natural stream geomorphology and inputs from beavers will benefit aquatic organisms	More "instream wood" will not result in more terrestrial prey fluxes, this belongs in "shifting riparian species section" and "dam construction"	Gurnell et al., 2002; Levine & Meyer, 2019) (Sigourney et al., 2006) (Collen & Gibson, 2001; Gurnell et al., 2002; Harvey et al., 2018; Thompson et al., 2018)	*in longer term may affect habitat structure and adversely affect some fishes* *The establishment of large log jams could temporarily hinder the movement of some fish species <u>if they act as barriers</u>* *Large quantities of large and small wood items may result in blockages that effect the transport of coarser sediments (see note above)*	felled trees compared to unfelled. **Citations?** What evidence is there that "large log jams" hinder fish movement or that beaver activities create them? Furthermore, these are not solid barriers. **Citations?** Woody debris are well known to be beneficial to fish and can create additional habitat complexity in streams. It is unlikely that additional woody debris alone will result in blockage that limits longitudinal connectivity	
Foraging						
Feeding on specific terrestrial herbaceous & aquatic plant species	*Changes to aquatic macrophyte community structure may favor some species of non-salmonid fish and their prey*	Conversely, reduction of macrophytes may result habitat improvement for some fish species.		*Decrease in macrophytes may negatively impact species depending on them for food or shelter (e.g. pike). Salmonids*	**Citations?** Or they may not.	

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		Rivers with beavers will like have greater variation in aquatic vegetation (macrophytes and other wetland plant species, see summary in Brazier et al. 2020).		*are rarely associated with macrophytes* *Altered riparian vegetation may allow invasive plant species to proliferate* *Loss of trees and shrubs may result in reduction of quantity/quality of terrestrial material into the river* *Change in riparian vegetation may reduce capacity to regulate sediment and nutrient run-off into river*	 **Citations?** Or they may not. **Citations?** Or they may not. **Citations?** Or it may not.	
Construction of dams						
Change of upstream habitat from flowing (lotic) *to stillwater* (lentic) *system*	*Increase in habitat diversity, which may favor some fish species or life stages and increase species richness of fish and invertebrate prey* *Increased temperatures, changes in habitat availability, feeding opportunities and refugia from low flows*	 Temperature may also not increase (Orr et al., 2020)	(Benke et al., 1999; Bush & Wissinger, 2016; Law et al., 2019; Wissinger & Gallagher, 1999)	*Possible shift in species composition towards non-salmonid species which have higher tolerance to low DO (such as cyprinids and sticklebacks)* *Increased habitat diversity may favor some species over others, including non-*	Only sometimes. Also, spatial context important, this can occur in small patches of habitat relative to entire river length Again, very scale dependent and one can argue that increased diversity at the watershed scale is	

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	may result in increased growth rates, fish condition and overall production			*natives or benefit only some life stages*	beneficial, with different species benefitting in different patches.	
	Deeper pond water is occupied by larger trout, lentic species such as minnow or roach and predatory species like pike		(Hägglund & Sjöberg, 1999)	*Creation of lentic habitats may result in habitat loss for species favoring lotic water*	Again, scale is important, entire streams are not converted to beaver ponds	
	Increased prey abundance, biomass or density		(Benke et al., 1984; Czerniawski & Sługocki, 2018; France, 1997; McDowell & Naiman, 1986; Osipov et al., 2018)	*Loss of spawning habitat for rheophilic species*	In habitat patches	
				Reduction of spawning habitat for salmonids (via sedimentation of substrates)	In habitat patches, most often just upstream of beaver dams	(Grasse, 1951; Taylor et al., 2010)
				Reduction of flow may occur which may result in lower dissolved oxygen and increased temperature	Strongly site dependent, varies with system and groundwater influxes	
	Ponds offer greater habitat complexity, foraging and sheltering habitats and protection from aquatic predators		(Collen & Gibson, 2001; Rosell et al., 2005)			
	Possible increase in terrestrial invertebrate prey entering the aquatic environment due to increased habitat perimeter and		(Malison et al., 2015)	*Possibly increased opportunities for fish predators and poachers*	**Citations?**	
				Winter fish kills can occur in beaver ponds if dissolved oxygen levels drop		(Fox & Keast, 1990)

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	aquatic/terrestrial connectivity Create habitats that are important winter refugia Ponds provide important rearing habitat for juvenile salmon and other fishes Beaver impoundments result in a plethora of positive ecosystem level benefits from increased biodiversity, habitat creation that benefits	Though not a fish/ fisheries response, this needs to be mentioned if potential negative impacts of non-fish	(Chisholm et al., 1987; Richard A. Cunjak, 1996; Jakober et al., 1998; Lindstrom & Hubert, 2004; Miller & Sadro, 2003; Nickelson, Nicholas, et al., 1992; Nickelson, Rodgers, et al., 1992 (Bryant, 1983; Grasse, 1979; Hägglund & Sjöberg, 1999; Leidholt Bruner et al., 1992; Malison et al., 2015; Murphy et al., 1989; Scruton et al., 1998) (Dalbeck et al., 2020; Stringer & Gaywood, 2016; Willby et al., 2018)	*Increased opportunity for invasive species to colonize altered habitat, including skunk cabbage or signal crayfish*	**Citations?** If potential negative impacts outside of fish and fisheries are to be noted, then the extensive literature on wider ecosystem benefits of beavers should also be cited. This positive impact has been added	

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	waterfowl, and many other organisms	non-natives are included in the review.				
Change in hydrological processes on riparian & downstream habitat	*Reduction of fine material transport may improve spawning habitat quality downstream* *Impoundments may create low and high-flow refuges for fish* *Flooding of riparian and wetland habitats can provide spawning opportunities for species like pike and additional habitat for species like eel and lamprey ammocetes* Impoundments can raise the water table, result in increased base flows and greater floodplain connectivity		(Beedle, 1991; Gorshkov, 2003; Grasse, 1951; Naiman et al., 1986; Puttock et al., 2018) (Cook, 1940; Hägglund & Sjöberg, 1999; Knudsen & J., 1962) (Gorczyca et al., 2018; Hood & Bayley, 2008; Hood & Larson, 2015; Majerova et al., 2015; Michael M. Pollock et al., 2014; Puttock et	*Changes in flow may result in reduction of gravel for downstream spawning (affecting salmonids and lamprey)* *Reduction of flow downstream may result in reduced wetted width and loss of juvenile fish habitat* *Attenuation of flows may reduce capacity of flow to clean gravels downstream of dam*	**Citations?** See Woo & Waddington (1990) re **widening of the channel** below dams. **Citations?** Hydrological effects differ based on dam structure and number of dams but localized increases in gradient and stream power downstream of dams enhances erosion and scour (Gurnell, 1998; Hering et al., 2001; Woo & Waddington, 1990) and see Brazier et al. 2020.	

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	Reduction of stream incision and reconnection with floodplain Accumulation of fine sediments may increase the volume of available habitat for lamprey ammocetes		al., 2017; C J Westbrook et al., 2006) (Gorczyca et al., 2018; Hood & Larson, 2015; Orr et al., 2020; M M Pollock et al., 2007; Michael M. Pollock et al., 2014) (Levine & Meyer, 2014; Puttock et al., 2018)			
~~*Creation of barrier*~~ Dams as possible barriers	*Moderates upstream movement of invasive species*	**Citations?** This assumes that dams are impermeable and impassable, which they are not		*Prevention of the free movement of fish to all habitats required during their life cycle. Particularly relevant during key migration periods but also at other times*	Movement rates may be reduced and the timing may change but dams do not block movement and studies have shown fish of various stages passing beaver dams (Bouwes et al., 2016; Bylak & Kukuła, 2018; Lokteff et al., 2013; Malison & Halley, 2020)	

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				Scale of impact may be greater for species that have a limited ability to overcome in-stream obstacles, like lamprey and cyprinids		
Changes in water quality downstream	~~*Reduction in the amount of fine material deposited on the stream or riverbed downstream of the impoundment, may result in improvement of downstream spawning area*~~ *Trapping finer sediment and associated nutrients and contaminants improving water quality downstream, although the relatively temporary nature of beaver dams would suggest this retention of contaminants is also temporary* ~~*Accumulation of fine sediments may increase the volume of available habitat for lamprey ammocetes*~~	This is not a water quality effect, it is listed under “changes in hydrological processes” **Citations?** Data do not suggest this is temporary (see Correll et al., 2000; Devito et al., 1989; Lazar et al., 2015; Puttock et al., 2017; T.J. et al., 1987) Sediment accumulation is not a water quality effect, it is listed under “changes in		*Breaching of dam may deposit high volumes of fine sediments and contaminated materials downstream* *Potential warming of water in impounded area may raise downstream water temperature which could affect fish survival, especially of salmonids*	**Citations?** It also may not, sediment may primarily remain behind dam remnants (Curran & Cannatelli, 2014; Giriat et al., 2016; Levine & Meyer, 2014) **Citations?** Scale important, influence of groundwater upwelling also. Many studies show that beaver ponds provide quality rearing habitat (see citations in this table)	

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	Beaver activity creates conditions for removal of pollutants; ponds retain Nitrogen and Phosphorus	hydrological processes" (Correll et al., 2000; Devito et al., 1989; Lazar et al., 2015; Puttock et al., 2017; Maret et al., 1987)				
Construction of lodges, burrows and canals						
Effects of construction	~~*Indirect habitat creation/restoration initiatives as result of beaver presence*~~ ~~*Beaver used to promote opportunities for riparian and freshwater habitat creation/restoration*~~ ~~*Presence of beaver may act as an incentive for greater investment, management and monitoring. This could include those related to the restoration and management of riparian woodland*~~ Presence of lodges and food caches provide	This is a human/management response, not a beaver-fish interaction Same as above Same as above	France 1997	~~*Beaver habitats may benefit invasive non-native species such as skunk cabbage or signal crayfish, if these are present within the catchment*~~ *Beaver tunneling causing collapse of river banks and increased sediment loading* *Beaver presence may impact fish-related riparian woodland restoration activities*	This negative effect is not the result of lodges or burrows, but rather "*change of upstream habitat from flowing to Stillwater system*" and has already been included as part of potential benefit to non-natives (De Visscher et al., 2014; Harvey et al., 2019) Again, human/management related influence, not a beaver-fish interaction	

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	habitat complexity and refugia from predators					
Direct beaver-human interactions						
Beaver attacks				*People and pets attacked by aggressive beavers defending their territories* *More prominent during night fishing*	Not a beaver-fish interaction Not a beaver-fish interaction	Citations? Data? Citations? Data?
Disease transmission				*Beavers transmit Echninococcus multilocularis, which can have serious human health implications*	Not a beaver fish interaction. However, beavers certified clear of *E. multilocularis* can be reintroduced (Girling et al. 2019; Janovsky et al. 2002). This parasite also is carried by domestic animals (e.g. dogs).	

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2.2.1 Distribution of beaver in Europe
No comments

2.2.2 Distribution of beaver in the UK
In a number of places, the author uses the term "introduced" when in fact it should be "reintroduced."

The fact that beavers can been present in the wild in the River Otter in Devon since at least 2008 shows means that this population has had the opportunity to impact the system for longer than the 5 years of study in the ROBT.

Beaver dams do not function the same as major artificial barriers (i.e. hydropower dams or weirs) and do not present the same impassable and permanent barriers, thus they should not be considered the "antithesis" to the EU AMBER project. Beaver dams are in fact more leaky, they are overtopped frequently during floods or after high rains, commonly have bypass channels flowing around them and can also break (Bylak et al., 2014; Bylak & Kukuła, 2018; Malison & Halley, 2020).

2.2.3 Ecology of beavers
Statements are also made in this section of Prof Cowx's review that are not referenced with citations.

No citation is given for differences in dam building between *C. fiber* and *C. canadensis*. The author states that different landscapes and river topography are responsible for differences in dam building. Malison has observed the dam building behaviors of both beaver species (in North America and Norway). From personal observations the large degree of anthropogenic habitat modification and/or simplification (e.g. turning streams into ditches, loss of floodplains, cutting of riparian vegetation, etc) in many European lotic systems limits the ability for C. *fiber* to build large beaver complexes like *C. canadensis*. Anthropogenic stressors appear to be a much bigger problem for salmonids in European systems than beavers (Malison and Halley 2020).

If healthy riparian buffers were present, then the presence of beavers would not immediately remove all trees. Furthermore, if agri-environment schemes planted tree species well adapted to beaver foraging then riparian zones would have greater capacity to provide both a buffer and beaver forage.

"Beavers are known to establish territories close to agricultural crops such as maize to benefit from this abundant food source."

No citation is given for beavers establishing territories close to agricultural crops such as maize and no data are given to document how beavers utilize or damage agricultural crops.

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"Although beavers have a preference for foraging on soft wood trees and shrubs, one aspect that has not been well studied, which is especially relevant to wild, open populations, is what vegetation beavers feed on if their preferred vegetation species are not abundant or depleted. This can have significant effects of the landscape if the trees regenerate slowly and potentially change the river form and function, and possibly lead to increased erosion of fine sediments where riparian vegetation buffer zones are depleted. Further the change in the riparian vegetation community structure can leave the opportunity for invasive plant species, such Japanese knotweed and Himalayan balsam to colonise and dominate, causing a different array of problems (Jones et al. 2012)."

This paragraph is speculative and does not include citations. What is the evidence from other areas with abundant beavers? The only study cited, Jones et al. (2012) does not provide any data.

"Another issue that that is critical when introducing or reintroducing animals and plants is transmission of diseases and parasites or other species piggy-backing on the target species. There is a risk of one such parasite, the tapeworm Echinococcus multilocularis, being introduced into the UK with beavers (Campbell-Palmer et al. 2015)."

If beavers certified clear of *E. multilocularis* are reintroduced (as is required), and then become infected post-introduction, that means that they are not introducing the disease, but that it is already present in the landscape. Domestic animals, including dogs, can also carry this parasite and it is common in many other parts of Europe. Through strict control of dogs and other pets entering the country the UK has remained free of *E. multilocularis*. It should be expected that many fewer beavers would be imported compared to the number of pets and that they could be first certified free of the parasite.

2.2.4 Beaver dams

"Beavers are termed "ecosystem engineers". They modify habitats by building dams and lodges and creating networks of ponds and wetlands, which can influence water quality, water storage, flood risk and biodiversity (Figure 2-1). The provision of ecosystem services by beavers, and the potential positive and negative impacts of re-establishing the species have been explored in detail throughout the literature (see Pollock et al., 2015; Kemp et al., 2012 for reviews), and impacts with particular reference to fish and fisheries are summarised in Table 2-1."

As detailed above, Table 2.1 is severely lacking representation of the positive impacts of beavers on fish and fisheries. Additional reviews by Collen and Gibson (2001) and Brazier et al. (2020) provide detailed, peer-reviewed reviews of the impacts of beavers on fish and aquatic systems.

In the paragraph starting with "*One of the defining features of beavers is the presence of dams…"* the author states that *"This changes the hydromorpholical feature of rivers to form long, continuous, deep and slow flowing reaches."* No citation is provided. Though stating that most dams are smaller (but can be much larger), the author neglects to point out the variation in

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hydromorphological features. The scale and degree to which lotic habitats are transformed into lentic habitats and the influence on hydological processes depends on dam characteristics and numbers (Giriat et al., 2016; Gurnell, 1998; Woo & Waddington, 1990). Commonly, the actual lentic habitat behind dams makes up only a very small portion of the stream network (Malison & Halley 2020).

Figure 2-5 is very simple. Multiple peer-reviewed publications are more informative regarding system capacity for beavers and their dams with regard to foraging habitat and freshwater habitat suitable for damming (Graham et al., 2020; Macfarlane et al., 2017).

"It should also be recognised that dams are not the only cause of blockages to fish movements in rivers. Beavers can cause secondary blockages by forming debris dams, especially where (a) they have felled trees into water courses (a frequent occurrence) and (b) sticks from their own dams are washed downstream in spates into culverts or constrictions. These debris dams are a further significant block to fish movement."

First, beaver dams are <u>not</u> the cause of blockages to fish movements, rather man-made dams and weirs are the main blockage. Furthermore, **no citations are presented for any of the statements about fish blockage regarding beavers felling trees and causing more woody debris to enter streams and rivers.** These statements cannot be backed up by the literature.

"Beaver colonies can exist, however, without creating dams depending on river topography and hydrology, especially where the gradient and river flow prevent construction of dams. They can burrow into river banks and create lodges on larger, wider river systems where the water depth is adequate to hide the entrance. The burrows can result in the collapsing of river banks and flooding of surrounding land, typically under high flow conditions. This is of particular concern in lower lying areas with flood protection levees, where the flood protection infrastructure can be weakened. Burrowing and collapse of banks can lead to increased erosion and sediment loading, which impacts on other wildlife, such as water voles, that inhabit these areas of the river. Beavers can also create canals for movement throughout wetland areas."

Again, the review by Prof Cowx provides no references in support of these statements.

2.2.5 Effects of habitat modification by beaver activity

"The main impact of attenuating flooding conditions is dissipation of the peak flows and prolongation of the flood cycle, albeit at a moderate discharge (Puttock et al. 2017). What does not appear to have been considered when assessing the benefits of flow attenuation is when extreme rainfall events occur over protracted periods. The dams will be quickly overtopped so their benefits will be lost, and of concern is that the dams will be vulnerable to breaching under high flow conditions, with concomitant impacts (see below)."

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Beaver dams serve to attenuate flows whether it is due to spring run-off or rainfall induced high flow events. Dams are indeed quickly overtopped but this does not mean that their benefits in flow attenuation are lost, and the fact that dams are quickly overtopped (or that water flows around them) is very important in illustrating that multiple paths for fish passage exist. In contrast to Prof Cowx's statement, recent literature illustrates that **flows are still attenuated at the high flows and that dams can remain intact during these events** (Nyssen et al., 2011; Puttock et al., 2020; Westbrook et al., 2020).

The review states: "*The slowing down of flows certainly results in deposition of fine sediments in the impounded area that might otherwise silt up river beds downstream, and potentially the accumulation of nutrients and other contaminants in the deposited sediments (Puttock et al. 2018). However, this can have a contrary effect of reducing sediment delivery to the lower catchment and estuarine and coastal water, with associated reduction of nutrients to the lower catchment (Koehnken et al. 2020). The accumulation of sediment in the impounded section, whilst being beneficial for lamprey, has the opposite effect for rheophilic species, such as juvenile salmonids, bullhead and stone loach, which rely on clean gravels. The waterlogging of adjacent land can also potentially cause increased silt erosion during wet periods, especially where the wetted area is trampled or becomes exposed and releases loose soil materials. Reductions in peak flows downstream may also reduce capacity of flows to clean gravels downstream of dams, and reduced flows in general may result in a reduced wetted width and a loss of juvenile fish habitat.*"

The input of fine sediments, nutrients and contaminants to lotic systems is a result of the surrounding land uses (Ahearn et al., 2005; Zheng et al., 2020). The presence of beavers is not the driver of nutrients and pollutions into aquatic systems, rather beavers influence how those nutrients and pollutants move through aquatic systems. Extensive literature shows how the presence of beaver dams and ponds can improve water quality by retaining nitrogen and phosphorous (Devito et al., 1989; Lazar et al., 2015; Naiman et al., 1994; Puttock et al., 2017; Rosell et al., 2005; T.J. et al., 1987).

Sediment accumulation can benefit species other than juvenile salmon but where are the author's references? In contrast to the author's statement, beaver ponds have been found to be important rearing habitat for juvenile salmon in many cases, including for species typically thought to prefer faster flowing lotic habitats (i.e. *Oncorhynchus tshawytscha*; Malison et al. 2015). Furthermore beaver ponding can increase survival (Bustard & Narver, 1975; Malison et al., 2015; Quinn & Peterson, 1996), growth rates (Bustard & Narver, 1975; Malison et al., 2015; Peterson, 1982; Swales & Levings, 1989), and production (Bouwes et al., 2016; Layman & Smith, 2001; Malison et al., 2015; Nickelson, Rodgers, et al., 1992) of juvenile salmon.

The "waterlogging" of adjacent land, otherwise known as increases in floodplain connectivity, has many ecosystem level benefits (Gorczyca et al., 2018; Hood & Bayley, 2008; Hood &

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Larson, 2015; Majerova et al., 2015; Pollock et al., 2014; Puttock et al., 2017; Westbrook et al., 2006).

Regarding the reduction in stream power to clean sediments - hydrological effects differ based on dam structure and number of dams but localized increases in gradient and stream power downstream of dams enhance the streams ability for erosion and scour and stream width can increase (Gurnell, 1998; Hering et al., 2001; Woo & Waddington, 1990) and see Brazier et al. (2020).

The review states: *"Whilst the dams may trap sediments and contaminants, consideration must be given to the potential impact of release of this material should the dam break. This could be released as a slug of fine, potentially contaminated, material, with concomitant impacts of downstream habitat and biota."*

No citations support these statements. In fact, even broken dams can retain large amounts of sediment (Curran & Cannatelli, 2014; Giriat et al., 2016) and recent research shows that dams often remain intact even in high flows (Westbrook et al., 2020).

"One aspect that has received little attention is the breaching of dams during high flow events and the potential impact of the release of large volumes of sediments, or where such sediment is deposited downstream. Several studies have highlighted that dam failures could lead to infrequent, but significant, pulses of water and sediment, particularly in high energy environments (e.g. Butler & Malanson, 2005; Curran & Cannatelli, 2014; Levine & Meyer 2014). This could potentially smoother downstream spawning and nursery habitat reducing its suitability for fish recruitment. Similarly, should a dam fail, large amounts of woody debris would be moved downstream potentially accumulating at pinch points and causing flooding or other barrier issues. Other studies, however, have suggested that the amount of sediment released following dam collapse would be minimal as the damaged structure will still retain some of its retention capacity and beavers would repair the dam to prevent full washout (Giriat et al. (2010). Alternatively, the sediment would be rapidly colonized by plants thus stabilizing the system (Levine & Meyer, 2014; Curran & Cannatelli, 2014), but, as yet, there does not appear to be any empirical evidence to suggest this is the case. Most of the benefits seem to be related to dams reducing stream power and reducing incision of the downstream channel (e.g. Pollock et al. 2014)."

See above – dams will not necessarily breach during high flows (Westbrook et al., 2020). Furthermore, the scale of sediment deposition should not be ignored and as ponds have been shown to be quality rearing habitat for juvenile salmonids (see above) it can be argued that other areas with sediment could be utilized as well. Also, there is no evidence that large amounts of woody debris would be moved and potentially accumulate to cause fish blockage.

"There is some evidence to suggest that beaver impoundments can lead to increased water temperatures, which can also affect downstream water temperatures (Weber et al. 2017, Majerova et al. 2015, 2020). Whilst this may lead to an increase in primary and secondary productivity,

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particularly in the impoundment, and potentially improved growth of fish, higher water temperatures are of concern to wild fish and fisheries, especially where beaver activity overlaps with salmonid fish communities and species like grayling that are intolerant to water temperatures above 20 °C. It is possible they may be lost to the community if the temperatures remain above this threshold for a few days, as is becoming increasingly likely under prevailing climate change conditions (Orr et al. 2015). The problem of increased water temperatures is exacerbated by the increased solar irradiation of the river surface resulting from beaver activity reducing canopy cover, and ultimately results in a reduction in resilience to climate change in rivers with impaired canopy cover (O'Briain et al. 2017, 2019, 2020).”

There is also evidence that beaver impoundments may only warm slightly, possibly contributing to increased production while still providing quality salmon habitat (Malison et al., 2015) and that ponds can provide important cool water refugia at depth compared to surrounding habitats (Weber et al., 2017).

The review states: *“In addition, apart from barriers to migration, dams and impoundments can cause degradation and loss of key spawning and nursery habitats in headwater and middle reaches of rivers. The impoundments reduce the capacity of salmonids and other lithophilic (gravel spawning) species to breed. Whilst the area of the impoundment and length of river flooded may be small in relation to the total river or steam length, the fact it like overlaps with key spawning and nursery habitat could represent a significant loss to recruitment. In addition the cumulative loses created by cascades of dams can be even more critical. Although some of this loss may be offset by reduced sediment loading downstream improving habitat quality, salmonid populations are driven by density dependent mechanisms so available habitat area is a primary driver of recruitment success (Crisp 2000).”*

Apart from assuming that beaver dams are barriers to migration without providing citations, no citations have been included to show that beavers cause the loss of spawning and nursery habitats. In contrast multiple studies have found that spawning habitat is available both up and downstream of beaver dams (Bouwes et al., 2016; Bylak et al., 2014; Hägglund & Sjöberg, 1999).

Furthermore, the question of scale and overall changes to the system are not considered. No evidence has been presented to show what proportion of river networks are converted to pond habitats and how or if the overall carrying capacity for salmonids has been altered. Furthermore, if carrying capacity is found to be reduced then data are needed to demonstrate what level of escapement would need to occur to utilize all available habitat.

“Beaver foraging can have considerable impact on the landscape, altering ecological succession, species composition and plant community structure (Rosell et al. 2005), which may change the hydromorphological processes, perhaps to the detriment of any flood control benefits. In Denmark, beavers were reported to damage forestry and agricultural crops and caused minor problems with

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flooding of arable fields, gardens, meadows and forest roads (Elmeros et al. 2003). The opening of the canopy, whilst increasing potential productivity of the impounded area, can also raise water temperatures (Weber et al. 2017, Majerova et al. 2020) and lead to increased growth of instream aquatic plants, which may choke the stream and cause flooding it its own right. This problem is likely to be greatest on chalk streams and in the lower reaches of rivers. Given that 85% of global chalk streams are found in the UK and they are highly vulnerable to climate change and human activities, it is important they are protected from further changes to their form and function (Salter & Singleton-White 2019), of which beaver activity could be one."

Healthy aquatic systems require intact riparian zones. Where these negative beaver impacts occurred, how close were the arable fields, gardens, meadows and forest roads to the stream? Was there a riparian zone? Anthropogenic stressors causing problems for aquatic systems should be addressed in restoration efforts.

Also, what direct evidence supports the idea that beaver foraging will cause problems in chalk streams?

"The creation of the impoundment upstream of beaver dams has been shown to result in a shift in fish community structure towards a predominance of lentic species, especially cyprinid species such as minnow that have no direct intrinsic value to fisheries (Hägglund & Sjöberg 1999; Smith & Mather 2013). This seems to have been misinterpreted as an enhancement of species diversity. However, in reality, the species composition is only changing to reflect the change in habitat availability, and the lentic species are exploiting their preferred environment. Species diversity is not enhanced per se but maintained, although biomass may increase (Smith & Mather 2013). Worryingly, the modified environment and shifts in fish community dynamics offer an opportunity for non-native species, including plant species, to invade and dominate in the communities. Indeed, Himalayan balsam appears to be benefitting from the altered riparian zone on the River Otter."

This paragraph is very selective in its interpretation and disregards a large body of research. Peer-reviewed literature shows enhancement of species richness (Snodgrass & Meffe, 1998) and diversity (Smith & Mather, 2013). Furthermore, beaver ponds do not always result in a shift in fish community structure as beaver ponds have been shown to provide quality rearing habitat for juvenile salmonids, even resulting in increased survival (Bustard & Narver, 1975; Malison et al., 2015; Quinn & Peterson, 1996), growth rates (Bustard & Narver, 1975; Malison et al., 2015; Peterson, 1982; Swales & Levings, 1989), and production (Bouwes et al., 2016; Layman & Smith, 2001; Malison et al., 2015; Nickelson, Rodgers, et al., 1992).

What evidence supports the statement regarding non-native species, citations?

"The upstream environment can also bring benefits to fish and fisheries in terms of improved growth and production (e.g. Sigourney et al. 2006), but other studies have highlighted changes in species composition towards small fish species of little economic value, such as minnow. Virbrickas et al.

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(2015) also found salmon abundance declined downstream of beaver dams in Lithuania streams, largely because loss of recruitment from upstream."

See above referenced literature for many examples of benefits to improved growth, survival and production.

"If faster water conditions are created below the dams, this could potentially result in an increase in the complexity and quality of habitat, especially if the substrate is composed of coarser materials such as gravels, and ultimately perhaps lead to an increase in the diversity and abundance of rheophilic species. However, beaver dams generally attenuate flows so such conditions are rarely, if ever, forthcoming, and the suggestion that beaver dams may restore downstream habitat needs further study."

Just because beaver dams attenuate floods, does not mean that there is no faster flowing water below beaver dams (see review by Brazier et al 2020).

"Beaver activity also increases the amount of large wood and associated debris in the river channel, providing a complexity of habitats, and promoting productivity and diversity of other species groups, such as amphibians, reptiles and birds, as well as fish. However, large wood can cause serious flooding issues if it moves downstream and accumulates at pinch points, potentially causing impeding fish movements."

Citations for large wood blocking movement?

2.2.6 Impacts on fish movements

It is important to understand how beaver dams may act as "barriers". In many cases it is assumed that beaver dams will block the movement of fishes. Yet the situation is much more complex. A dam that seems impassable one day may obviously not be another day during a high flow event (see Malison & Halley 2020 for photos). Though beaver dams do not act as complete barriers, they can change the patterns or degree of movement (see below). It is not clear how strong of an impact these changes in movement patterns may have on populations, yet is incorrect to assume that different species and populations would all be negatively impacted by the changes.

"Perhaps one of the most contentious issues regarding beaver dams is disruption to fish migration. The literature is replete with conflicting studies. For example, Parker & Roenning (2007) is a widely quoted example showing that beaver dams pose no problems for spawning salmonids in Norwegian rivers, whilst Kesminas et al. (2006) found the impacts of beaver dams on sea trout populations in the Baltic States highly detrimental to the extent of endangering populations. The problem arises because beaver dams are ephemeral and highly dynamic. They have a limited life, typically between 2-3 year, before they are abandoned or blow out. They vary in shape and size depending on location, and these characteristics together with the hydraulic conditions experienced at each dam determine whether the structure is passable. See, for example Figure 2-6 which shows two beaver dams that

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potentially block upstream and downstream movement of fish. The presence of a rivulet on the right-hand side of the Danescroft dam does not represent free passage under all conditions and most likely the dam will obstruct upstream movement of salmonids in all but high flow levels. The right-hand photo shows a dam that has no overflowing water or rivulet that would enable fish to bypass the dams so is probably a complete barrier to fish except possibly in high flow conditions. As a consequence, there is considerable conjecture about whether beaver dams are passable by fish, either partially or fully, and whether they are open to free movement. The problem is exacerbated because most studies only seem to be addressing migratory salmonids and eel, yet many riverine fish species are migratory during some stage of their lifecycles and thus need to move up and downstream (Radinger & Wolter 2014); many of these other migratory species have lesser swimming capacities than adult migratory salmonids, which are typically the subject of impact studies (Lucas & Baras 2001)."

There is no support or citation provide for the statement that beaver dams only last 2-3 years.

What evidence does the author have to say that the dam pictured is a complete barrier to fish?

This summary does not include multiple papers and reviews that provide evidence of fish passing beaver dams (Brazier et al., 2020; Bylak et al., 2014; Bylak & Kukuła, 2018; Cutting et al., 2018; Malison & Halley, 2020; Pollock et al., 2019)

"One aspect of fish migration that is largely overlooked is the downstream movements of post-spawning adults (salmonid kelts or adult cyprinids) or dispersal of juveniles (all species) and salmonid smolts. In the main, beaver dams are considered 'leaky' so do not pose a problem, but this is not proven and the extent to which smolts can pass through or over beaver dams remains unclear. Irrespective, it is highly likely beaver dams will disrupt downstream migration during the critical life stage of fish and lead to delayed departure or even prevent diadromous species from reaching the sea. Delays can also increase predation on migrating fish from avian and terrestrial predators, especially if the fish are held up in the upstream impoundment. Delays and disruption to migration of this nature can cause considerable mortality and affect the status of the fish populations (Gauld 2013)."

The author provides no citations to support these statements. Studies have documented fishes moving past beaver dams (Bouwes et al., 2016; Bylak & Kukuła, 2018; Malison & Halley, 2020; Virbickas et al., 2015).

"*A number of tools are available to assess barrier passability (see Kemp & O'Hanley, 2010). These fall into site-specific surveying techniques and hydraulic modelling linked to fish swimming capabilities, the latter typically assessed using tagging and tracking methodologies, through to rapid assessments based on direct observations of the barrier and hydraulic features using expert judgement. Most studies on passability of beaver dams to date have declared that fish are able to pass the dams, but most rely on observations of fish bypassing the structures or assume the presence of juvenile fish of migratory species upstream of the dam indicates some fish must have passed the*

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structure. Few studies have assessed beaver dam passability quantitatively." and *"The few studies that have utilised modern fish tagging and tracking systems to determine the probability of fish being able to bypass a beaver dam present mixed results. Lokteff et al. (2013) used Passive Integrated Tag (PIT) technology to determine if native and non-native trout could bypass beaver dams in Utah streams and considered physical characteristics of the dams, such as height and upstream location, affected passability, although they also found non-native trout species (European brown trout) were less able to pass than native Oncorhynchus [salmonid] species. Malison and Halley (2020) also used PIT technology to explore the impacts of beaver dams on movements of juvenile salmon in two Norwegian rivers and concluded that "dams did not block the movement of juvenile salmonids or their ability to use upstream habitats". However, the data presented do not support this interpretation and movements of fish in beaver-free areas were considerably greater than where dams were present. Further the experimental design was not appropriate for exploring the long-distance movements of juvenile salmon as PIT loops (stationary detector arrays), were only set over <100 m of river reach, which approximates the home range of juvenile life stages. Virbrickas et al. (2015), using RFID (short radio frequency identification) tagging, found Atlantic salmon were able to pass some dams in a series of barriers, but they were not able to ascend the full cascade, thus compromising spawning and recruitment processes."*

First, beavers and salmon have cohabited and co-evolved for millennia and have previously coexisted positively (Kemp et al. 2012). Additionally, juvenile and adult salmonids and many other species have been documented moving past dams. The author's interpretation of the empirical studies noted above is very selective. Lokteff et al. (2013) demonstrated that both juvenile and adult salmonids have the ability to negotiate multiple North American beaver dams or beaver dam analogs. In strong contrast to Prof Cowx's interpretation, Malison and Halley (2020) found that beaver dams **did not block the movement** of juvenile salmonids in **three** (not two) tributaries of important salmon rivers in Norway. Almost 500 of the 759 tagged individuals were detected by PIT-tag antennae arrays. The dams did not compromise the use of upstream habitats and the greatest proportion of juvenile Atlantic salmon were found upstream of beaver ponds. Similar proportions of juvenile salmonids moved down and up the study reach once in dammed vs. control sites and similar proportions remained above and below the study reach each dammed vs. control sites. Overall, dams did not block movements (and multiple movements past dams were documented), but more repeated movements up and down control sites occurred compared to dammed sites. The movement data combined with the small scale of habitat alteration, small dam sizes, and frequent breaching/overtopping of the dams, makes it is unlikely that beaver dams negatively impact salmonid populations in these systems. The comment about long distance movements makes no sense, the study wasn't designed to detect long distance movements. It was designed to compare movement rates between tributaries with and without dams. Though Virbrickas et al. (2015) found that tagged sea trout parr were able to pass through successive beaver dams in an upstream direction, they did not detect any tagged parr above the uppermost dam. **However, there was no evidence that the spawning and recruitment process was compromised**, or that the populations were negatively

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impacted. Furthermore, only 82 individual sea trout were tagged and other trout parr we documented in every section, below, mid, and above all the beaver dams in both streams studied.

Numerous other studies not mentioned in this review have documented the movement of fishes past beaver dams. Notably, Bouwes et al (2016) documented increases in the density, survival and production of juvenile steelhead following the installation of beaver dam analogs, with no impact on upstream and downstream migrations. Using radio-telemetry techniques, Cutting et al (2018) found that average passage probability over unbreached dams was 88% for arctic grayling (though it fell below 50% for some individual dams) and that upstream passage was strongly correlated with hydrological conditions.

Though beaver dams are often cited and or perceived as being an obstacle to fish movement, the studies most commonly cited actually show that beaver dams may alter seasonal movement patterns of fishes, rather than blocking movement (Mitchell & Cunjak 2007; Schlosser & Kallemeyn 2000).

"Whilst this is technically an expensive option to assess fish passability at a beaver dam, a full study on a range of dams would remove the controversy regarding passability. Such studies have been successfully carried out to assess the passability of fish pass structures at barriers and hydropower dams (Aarestrup et al., 2003; Knaepkens et al., 2006; Noonan et al., 2012) and should be adapted to assess the passability of beaver dams. ***Thus, before any definitive conclusion can be drawn about passability of beaver dams, fully funded telemetry studies on a range dam types, including cascades of dams, should be undertaken.*** *Such studies should include migratory salmonids, resident brown trout and potamodromous species, such as barbel, chub and dace, to account for the range of fish species and life cycle guilds found in UK rivers."and "Coarse Resolution Rapid Barrier assessment methodologies, such as that devised by Kemp and O'Hanley (2010 and Kemp et al. (2017) and revised following field trials (SNIFFER, 2012), would be suitable for assessing both up and downstream movements, and are capable of evaluating passability of numerous species and sizes of fish. The assessment method uses rule-based criteria for fish morphology, behaviour, and swimming and leaping ability to estimate barrier passability. The condition of the barrier to impede migration requires visual inspection and in-field measurements. As an example, the criteria used to assign upstream barrier passability for trout are shown in Table 2-2. Barrier passability represents the fraction of fish (in the range 0 [impassable] to 1 [100% passable under all conditions]) that are able to negotiate a given barrier successfully in an upstream or downstream direction. Each barrier is assigned one of four passability levels as follows: 0 is a complete barrier to movement; 0.3 is a high impact partial barrier, passable to a small proportion of fish or passable only for short periods of time; 0.6 is a low impact partial barrier, passable to a high proportion of fish or for long periods of time; and 1 is a fully passable structure. Partial barriers, especially at beaver dams, are often created by fluctuating river discharge, which causes variation in water depth and velocity at the barrier, thereby impeding large fish at low flows or individuals with weaker swimming abilities at high flows." and "The methodology described in SNIFFER (2010) can*

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also be used for a variety of other species but has been specifically defined for adult salmon (Salmo salar), brown trout (Salmo trutta), juvenile salmonids, cyprinids, adult lamprey and juvenile eel (Anguilla anguilla). Unfortunately, this methodology has not been field tested explicitly for beaver dams under a range of hydraulic conditions to determine the ability of fish to bypass such structures. This is important because passability likely varies under different discharge levels and a simple model does not fit the complex, diversity of typographical and hydraulic conditions presented at different dams. ***There is clear need for further research to assess the barrier effects and otherwise of beaver dams on fish migration and recruitment processes."***

It is likely that there will always be controversy over the passability of beaver dams by fishes, due to the inherent variability in systems, differences in beaver dams and the perceived negative impact. But, conducting additional studies under a number of conditions for a number of species would be very helpful to better understand the issue. Studies should be designed to occur over temporal and spatial scales that can inform how any changes in movement might influence species at the population scale. Additionally, more studies on juvenile fishes should be conducted using PIT-array technologies.

In concert with such studies of dam passability, studies should be conducted to determine the watershed or catchment scale impact of beaver dams. What portion of the drainage or stream/river is being altered, are portions of the upstream habitat lost or still utilized, how much stream bed is being altered and what is the overall influence on the populations.

2.2.7 Cumulative effects of beaver activity on water courses and fish

"One issue that is often overlooked is the cumulative effect of multiple barriers and impoundments in a cascade or series of cascades in a single river system. Whilst the dams may improve water quality and reduce fine sediment movement, they also act to deprive the downstream region of coarser sediments such as gravels, which are important for the spawning of many fish species, especially salmonids, and attenuation of flows can reduce the capacity of the river discharge to clean/refresh gravels prior to spawning. In addition, multiple dams in a cascade inundate large areas of riverine habitat that are potential spawning and nursery habitats for fish species, and create multiple barriers to fish migration. These issues can be clearly seen in the extent of damming and inundation associated with the Tamar enclosed beaver population (Figure 2-7; Puttock et al. 2017). Here the river is transformed from a flowing system to wetlands with areas of open water. Not only is an extended reach of river lost to salmonid spawning and production, it is unlikely migratory adult salmonids will be able to bypass the 13 dams in the cascade, thus isolating the total upstream reach for migratory salmonids. In this case, it is not just the area of river flooded by the impoundments but the habitat from the dams to the headwaters that are lost to recruitment of migratory fishes. Caution must, however, be paid in interpreting the cumulative conditions for the Tamar site because the beavers are enclosed in a limited area so restricted in where they can build dams, and potentially the

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size and structure of dams. Beavers in open populations may build dams in markedly different locations, potentially causing a different array and scale of impacts. They may also abandon dams after a few years when moving onto new territories, thus expanding the range of impact within catchments from their dam construction activities."

The Puttock et al. (2017) paper presents no data on beaver dams as barriers, rather it is a good example of the ecosystem benefits from beaver dams including flow attenuation, improved base flows and nutrient storage. In this example, beavers were enclosed in a small area and were not able to move, dams are generally not found this close together in nature. Puttock et al. (2017) also notes the leaky nature of the dams, and observed overflow, through-flow and underflow all at the same time in the dams and this would allow passage by juvenile fishes.

"*The latter point is particularly pertinent because each dam in a cascade may pose different challenges to migrating fish as they will each have different form and structure, and different hydraulic conditions. The cumulative effect of fish trying to bypass multiple structures will ultimately lead to a decline in total numbers reaching suitable spawning and nursery habitats, upstream of the dam complex, thus impacting recruitment dynamics and stock status. This can have considerable implications for achieving EU Water Framework Directive objectives where species have been excluded from upstream reaches of rivers, thus failing to meet Good Ecological Status."*

Citations? This is all speculation. In contrast, beaver ponds have been found to be productive rearing habitat, as noted multiple times in response already.

"*An example of the cumulative impact of multiple barriers on a system is shown in Figure 2-8. Here the impacts of seven barriers in succession on the population size of an upstream migrating species are compared with different levels of passability. It can be clearly seen that the cumulative effect of compromised passabilities <0.5 at the barriers (i.e. less than 50% of the fish successfully bypassing each dam) results in extirpation of the population in the upstream areas, potentially where the fish spawn. It is thus essential to model the impact of variable passabilities at the various barriers to determine the cumulative impact. Coarse resolution rapid barrier assessment methodologies, such as the one described above (SNIFFER 2012) and adapted by the West Country Rivers Trust for the River Otter Beaver Trial (RAP: West et al. 2019), could be used to determine the cumulative impact of multiple barriers, although it will require considerable development and testing to gain confidence in the tool."* and "*The cumulative impacts of multiple dams have also been examined by Bylak and Kukuła (2018) in a western Carpathian river. Here they showed how fish species composition and size structure changed with environmental heterogeneity created by the beaver dams. It appears the fish community structures shift in relation to the changes in habitat availability towards lentic species, and lotic species abundance, typically found in in upland reaches, are reduced in abundance."*

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Figure 2-8 is hypothetical, referencing peer-reviewed literature is required to make assessments. The benefits in habitat productivity, juvenile salmonid growth, survival and production (all cited above) have all been ignored.

2.3 Ecosystem Services

"Most of the services are generated by the impounded section of river and creation of a matrix of wetland habitats that are favoured by a wide range of biota, or the benefits of the dam on the downstream reach."

The benefits of increased biodiversity etc are a result of the overall changes in the entire system, lentic and lotic reaches combined.

"Thompson et al. (2020) attempted to put monetary value on the services generated by beavers, and estimated values of US$1.6 million from recreational hunting and fishing benefits and US$133 million for habitat and biodiversity provision per year (equivalent to 133 30 US$/ha) over the entire beaver distribution range in the Northern Hemisphere (Figure 2-9) This was compared with non-consumptive recreation estimated to be equivalent to 167 US$/ha. It should be noted these values are small in comparison to the services generated from recreational fishing (£1.6 billion in in England alone [Environment Agency 2018a, b]) or other nature-based activities."

The author seems to be assuming that value from beavers and service from recreational fishing cannot occur at the same time. Furthermore, there is evidence that beaver habitat can stimulate the growth and production of fishes (see above) which could in turn increase fishing revenue.

"Disbenefits arising from beaver activities include, but are not exclusive to, loss of agricultural land, flooding of urban areas, felling of trees, foraging on agricultural crops, disruption to fish community dynamics and associated fisheries, damage to infrastructure, including flood defences, and beaver attacks (see Table 2.1)."

Again, no citations are provided and no citations are present in Table 2-1.

"*The loss of fisheries or compensating for loss of fish recruitment are also borne by small groups of stakeholders, including land/riparian owners, fishery owners and river conservation bodies, with little support from government or recovery from those who benefit from beaver presence."*

Where are the data and citations that show this loss of fish recruitment?

"To give an indication of the potential scale of economic losses from disruption to fisheries, freshwater angling in England in 2015 contributed £1.46 billion to the economy (expressed as gross value added) and supported 27,000 full-time equivalent jobs (Environment Agency 2018a). A total of 22.3 million days were spent freshwater angling in England in 2015, and total non-trip related expenditure in 2015 was estimated at around £680 million (Environment Agency 2018a, b). This

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included items such as clothing, media, tackle and club memberships. More than half of this expenditure was on tackle and equipment (56% of the total). Non-trip related expenditure supported over 10,700 FTE jobs and contributed £583 million to household incomes in 2015."

What evidence does the author have to show that this will change or that beaver reintroduction will negatively impact freshwater angling and fish populations. There is no evidence to show that beavers will negatively impact fish populations.

"Another interaction between beavers and humans is attacks on domestic pets and anglers[12][13]. Although considered rare, there are reports of such interactions and even death of a person killed from a beaver bite[14]; thus the risks are potentially high. Anglers fishing at night, especially sea trout anglers fishing in May, June and July, are at higher risk of attack than the public, because beavers are particularly protective of their new born kits at this time of year. Encounters of this nature are likely to increase as beaver numbers increase and their distribution widens into semi urban areas or beavers occupy fishing pools. These risks also apply to other groups such as canoeists, wild swimmers, and dog walkers and their dogs."

The risks of attack are very, very low. Malison and other researchers have spent uncounted hours in beaver ponds with no attacks and no risk of attack. To think that humans and pets nearby beaver habitat need worry about beaver attacks is ridiculous unless they decide to try and pick up a beaver for a picture.

2.4 Potential mitigations and management options and further R&D
*Comments were only made in this section with regard to interactions of beavers-fish, management practices/recommendations were not reviewed and "no comments" was listed

"Possible impacts from the introduction of beavers into river systems (cause-effect and problem analyses) are summarised in Figure 2-1, and discussed in Sections 2.2.3-2.2.7 and Section 2.3. The information illustrates the problems that are likely to arise but not the magnitude of such problems. This issue of quantifying the impact of beaver activity on fish and fisheries has also been neglected when the valuation of ecosystem services attributed to beavers is assessed (Section 2.3)."

The review and above-mentioned sections failed to list and discuss many of the positive impacts of beavers. To help clarify the balance between potential positive and negative impacts citations (representing the weight of evidence) have been added to the revised Table 2.1. Again, no citations were listed for many possible and likely impacts.

2.4.1 Legal status
No comments

2.4.2 Mitigation measures

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"Whilst beavers may play an important ecological role in creating and maintaining ponds and wetlands for fish and wildlife habitat, their dams can cause a number of key problems associated with disruption to fish migration and flooding of fish spawning and nursery areas. In addition, beavers can cause considerable damage to riparian trees, including destroying stands of trees along river banks. Beavers can also damage infrastructure, including burrowing into flood banks and causing them to collapse, as was see in Poland where beaver damage caused considerable flooding of a town following the collapse of a flood bank they had undermined[15]. Where these problems are deemed to be excessive, preventative measures or actions to mitigate the damage are required. These take three main forms of action: 1) controlling beaver foraging activities; 2) managing the impacts of the dam and impoundment; and 3) regulating beaver numbers and relocation."

Once again, note that the author has not conducted a comprehensive review that includes positive impacts of beavers.

2.4.3 Beaver Management Plans
No comments

3 Overview of the River Otter and its fisheries

*Comments were only made in this section with regard to interactions of beavers-fish, management practices/recommendations were not reviewed and "no comments" was listed

3.1 Catchment characteristics

"The river is also impacted by a number of major barriers to fish movement that contribute to the WFD status."

Major barriers are weirs, not beaver dams.

"Technically beaver dams can be used to attenuate floods (see section 2.2.5) and could contribute to Water Framework Directive targets, but conversely they may exacerbate issues with fish and fisheries because of disruption to migratory fish distribution and abundance, and alteration of channel form and function, especially if breached under high flow events. This is also at odds with the East Devon Catchment Action Plan 2019[21], which indicates the requirement for "Catchment-scale river and fisheries improvements to meet WFD targets and restore rivers" and states the need "To improve fish migration throughout catchment for all fish species"."

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Beavers and beaver dams would successfully help attenuate floods, increase floodplain storage and create wetland habitat (Brazier et al., 2020; Puttock et al., 2017). Beaver dams **may** cause issues with fish and fisheries, but they may not and the author does not provide any citations yet again. The need to improve fish migration refers to the large impassable barriers (weirs, in Fig 3-4), beaver dams which regularly overtop and have pathways for fish passage do not act as permanent barriers in this sense.

3.2 River Otter fish and fisheries

3.2.1 Rod fisheries

"The prime salmonid spawning areas in the River Otter are considered to be above Monkton, between Honiton and Upottery. Fish can typically reach this far upstream when the river is in spate. Currently only three of the weirs have fish passes, all in the lower reaches of the river, including a new pass on the weir at Tipton St John. Tracey Weir, to the north of Honiton, is an obstacle. 3.2.2 River Otter national fisheries surveys (Source Environment Agency, National Fish Populations Database)"

Beaver dams are not found in the mainstem of the River Otter and dams aren't predicted to be built there (Graham et al. 2020). The man-made weirs are causing this problem with longitudinal connectivity.

3..2.2 River Otter nation fisheries surveys

"No significant differences in fish community composition (PERMANOVA analysis based on Bray Curtis similarity index) were found between sites, although clusters representing the mainstem river and higher gradient streams were evident (Figure 3-7). This analysis provides evidence that sites on tributaries that have not been impacted by beaver activity could have provided suitable control sites for impact assessment. The same could be said for understanding the impact of beavers on the mainstem of the Otter where significant beaver presence is reported."

Beavers are not known to influence fish and fisheries where there are no dams (i.e. where they live in bank burrows in larger rivers; Kemp et al. 2012, Collen and Gibson 2001).

4 Review of the River Otter Beaver Trial Science and Evidence Report

*The review of the River Otter Beaver Trial Science and Evidence Report section was primarily conducted with regard to statements about interactions of beavers-fish or scientifically sound science. Comments specific to management practices/recommendations were not reviewed nor were very specific questions regarding study design.

4.1 Background

No comments

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4.2 Beaver activity

"An assessment of the number of beaver dams in the River Otter was attempted in October 2018. It was concluded that 26 dams were in place at that time, but that approximately 80 had been constructed since the start of the Trial at 55 locations on seven different land holdings. It appears that the construction of dams were largely in the narrower tributary streams rather than the mainstem of the River Otter. This is in line with the precept that beavers construct dams in higher gradient streams where suitable ponds are not available to establish a territory. One territory was established on the River Tale, where the beavers appear to have built dams to raise the water to access maize crops. They also built bank lodges nearby, which could have impacted on agricultural land causing problems with operation of agricultural machinery. As previously stated, however, the total number of dams that could be constructed on the River Otter was anything between 262 and 814 dams (; Brazier et al. 2020), and this suggests the distribution, and any impact, will likely grow in future years until the population stabilises. During this period, the propensity for dispersion into adjacent catchments is likely to increase and need to be controlled."

Use of the words "it appears" and "with the precept" suggests that the author is not familiar with beaver ecology or is trying to reduce confidence in the work. Beavers do not need to build dams in mainstem rivers because they have access to deep water, nor can they dam these habitats due to the power of the river. They need to build dams to have deep water and access food in smaller tributaries. Additionally, it could be possible for that many dams to be present eventually if one assumes that no beaver management would take place.

"The data presented in the heat maps provide an indication of the distribution of beavers in the River Otter, but appear to reflect mainly where surveys were carried out."

Statements like this make it seem like the reviewer is trying reduce the credibility of the science conducted for the ROBT, when sound scientific methods were followed and published in peer-reviewed publications (Campbell-Palmer et al., 2020).

"Studies on the distribution of beavers in the River Otter have also moved beyond reporting empirical evidence of beaver activities. Graham et al. (2020) used algorithms of likelihood of construction of dams at various locations on the Otter (and other river systems –River Tay and Coombeshead sub-catchment) to determine the density of beaver dams that can be supported within a given reach. The outputs (Figure 4-3) suggest beavers are likely to construct dams in the headwaters of streams and not so much in the larger rivers, as would be expected. The outputs agree to some extent with where beaver dams have been constructed in the Otter and show where dams are likely to be constructed in the future as beavers increase in abundance and expand their range in the catchment. Interestingly, as predicted by the simple classification tree presented in Figure 2-5, there appears to be little likelihood of dams being constructed on the mainstem River Otter. Notwithstanding, the modelling only determines the likelihood of dams being constructed and not the presence of beavers or the likelihood of them colonising specific reaches. As already observed, the main beaver activity in the River Otter is in the mainstem of

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the river and in the River Tale (Figure 4-1), where the models suggest there will be few or no dams constructed. ***It is thus important that future studies on the impact of beavers on fisheries cover areas where beavers are active not just where dams have been constructed, i.e. in the main river channels and larger tributaries.*** *This is particularly important because beavers tend to burrow into river banks where they do not build dams and thus create a different set of issues related to infrastructural damage and bank damage, including loss of other wildlife such as water voles. In this context, the trial should have modelled the areas that beavers are likely to inhabit and burrow into river banks, particularly as the population continues to grow towards the predicted 147 – 179 territories (Brazier et al. 2020), by the 2030s.* ***Any models produced also need ground-truthing against existing distribution patterns and systematically cross-checked against expanding abundance and range."***

Once again, Prof Cowx has not seemed to review all the literature. The study by Graham et al. (2020) did indeed use field data to ground truth the modeling. Also, it is very unclear why he continually suggests that the impact of beavers on fisheries where no dams are present need be studied when there is no evidence in the literature that this is an issue.

4.3 Fish and Fisheries Assessment

"Subsequent surveys carried out on the River Tale, used a control / impact survey design. Two control reaches were surveyed, respectively, upstream and downstream (and not in close proximity) to the beaver dam. Impacted sites were the impounded section and immediately downstream of the beaver dam (2017 and 2019 only). Reaches were surveyed using a multiple-pass electric fishing strategy between stop nets. ***Different lengths of river were surveyed in the different years*** *(50-m reaches in 2016, 25-m reaches in 2017 and 30-m reaches in 2019). It should be noted the minimum length of survey site recommended by the EA Fisheries Monitoring Programme Guidance is 30 m, thus the 2017 surveys are inconsistent with this criteria. Further,* ***the location of the sites surveyed, including the control sites, were not consistent between years****, although this was, in part, due to shifts in location of the dam under study between years (Figure 4-2). The area fished immediately upstream of the dam (impounded area) appears to be approximately 120 m upstream of the beaver dam in the headwater of the impoundment, where it was probably possible to sample by wading, and not the impounded area proper, which would likely be deep water that cannot be easily surveyed by electric fishing without using a boat. This zone is likely a transition zone between river lotic and lentic environment and the fish populations/community structure are not representative of the beaver pond per se. Electric fishing efficiency for the quantitative three-catch sampling for brown trout in the wadeable sections surveyed was between about 0.5 and 0.8 and is consistent with the 0.6 recommended in the EA guidelines for electric fishing, except for the downstream control site in 2017 when the efficiency was inexplicably low at 0.17. Electric fishing efficiency for other species was generally must lower and reflects species-specific sampling characteristics, especially for cryptic benthic species, such as bullhead and stone loach, which are notoriously difficult to survey accurately, and usually have a low capture efficiency."*

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Community composition and species presence data can be compared for different lengths of reaches, as can fish densities, this is not an issue. Why would the author highlight the fact that the location of the sites surveyed changed and were not consistent between years when this was in response to the dam moving locations? Would the author rather expect the surveys to be conducted in the same location and not in the appropriate habitats as based on the location of the dam? Again, this seems to be an effort to reduce credibility of the scientific effort. This is further exemplified by the fact that the author makes multiple assumptions with the text "appears to be", "where is was probably possible", and "is likely". There is no evidence to say that the area just upstream of a beaver dam must be sampled by using a boat, it may have been wadable.

"In addition, the surveys on the River Tale were carried out in different months of the year: October in 2016, July in 2017 and August in 2019. This can have considerable impact on the efficiency of the electric fishing for small-sized individual fish, especially young-of-the-year fish, that are not of a sufficient size to be captured effectively until later in the year (typically late August until early October is the best time to sample juvenile salmonids). Comparison of the size of fish between years will also be problematic given most of the growth of fish in English rivers occurs in the spring and summer months (Cowx 2001), and the different timings of the surveys do not necessarily account for movements between habitats."

No, even small young-of-the-young can be sampled by electrofishing early in the season.

"Interestingly, the ROBT Science and Evidence report (Brazier et al. 2020) presented the increase is abundance of fish in the beaver pool in 2019 as a positive, but they used total number of fish caught at the site as a direct measure of abundance for comparison with other sites (Figure 4-6). Such data do not take into account fishing effort or area of river sampled, and when standardised as relative densities (fish per 100 m2), the numbers were considerably lower (Figure 4-5). In addition, the majority of fish caught in the beaver pool in 2019 was minnows, which is a shoaling species. It is likely the survey encountered a large shoal of minnows to account for this contribution, although Vowles (2019) suggested the increased abundance may have been the result of more large woody debris accumulating in the pool upstream of the dam in 2019. Minnows are better adapted to slower flowing, pool conditions and this may also account for this increase in abundance. This example highlights the need for long-term sampling using standardised capture and reporting methodologies, and use of replicate surveys in multiple dam reaches."

The author has no evidence to suggest that "a large shoal of minnows" was encountered.

"Further, abundance of fish in the upstream impoundment cannot be considered representative of improvement in fisheries. These habitats flood spawning and nursery areas and allow the proliferation of fish species that prefer lentic habitat such as minnow. Other rheophilic species such as bullhead (a species of concern under the EU Habitats Directive) and stone loach also declined. Whilst it is recognised that other species of conservation concern, such as lamprey,

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may be benefit, they are not typically found in great abundance in higher gradient rivers where the beaver dams are built."

Once again, negative impact statements are made without citations. See Section 2 comments for the importance of beaver ponds as rearing habitats for juvenile salmonids (with citations).

"Biomass of fish was generally higher in the most upstream [control] site except in 2019 when the highest relative abundance was found in the beaver pool (Figure 4-5). This was largely the result of larger trout occupying the pool, the large catch of minnows and an increase in the contribution of lamprey making use of the silty habitat. Note, interpretation of larger fish in the impoundment being equated to better growth can only be proven from growth studies based on scales from the fish. Biomass of fish in the most downstream [control] site was less than the upstream sites in 2016 and 2017, despite the abundance [densities] being similar. This apparent anomaly was because few trout were caught at the downstream site in 2016 and the trout caught at the downstream site in 2017 were smaller (mean 70 ± 22 mm FL) than upstream (130 ± 78 mm FL), which may indicate the downstream site was a nursery area for the species. Abundance and biomass of fish species in the site downstream of the dam, representing a site recovering from a dam break, were similar to the upstream control site suggesting the river may recover rapidly after dams have been removed or washed away."

Or, instead of scales, individuals can be tagged in said habitat, recaptured repeatedly and measured/weighed, as is commonly done. Higher growth rates for fishes (including salmonids) have been documented in beaver ponds many times (see references in Section 2).

"During the walk-over surveys, eight beaver dams were observed between the confluence with the Otter and Colaton Raleigh on the Stowford Brook, and it was concluded these structures may impact returning sea trout, other salmonids, brown trout and minor fish species such as bullhead and stone loach from accessing their spawning grounds. ***This type of survey is critical to understanding both the ongoing impact of beaver dams on the spawning and recruitment of migratory fish species and should have been carried out for the entire catchment and validated against EA fisheries survey data. This is a major limitation of the fisheries assessment in the ROBT evidence report*** *(Brazier et al. 2020)."*

The dams **may** impact returning fish but there is no data to support **if** they will. Also, what about all the manmade weirs?

"Overall, surveys to assess the impact of beavers on extant fish populations and communities were based on one semi-quantitative survey on the main River Otter in 2015 and quantitative surveys at four sites representing controls and impacted reaches up and downstream of a single dam on the River Tale in three different years (2016, 2017 and 2019). Further, no evaluation or conclusion on the likely impact of the expanding beaver population on fish population and community dynamics towards 2030, particularly the impact of barriers and impoundments on fish migration and

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recruitment, is provided. ***Given the ROBT was set up to assess the impact of beavers on fish and fisheries and serve as a reference study*** *for deciding whether a) beavers should be allowed to remain 'wild' in the River Otter and b) to support the decision to allow further releases of beavers into the wild in England,* ***the sampling framework falls well short of that expected for a robust impact assessment.*** *At the very least, a number of dams representing different locations, construction design, environmental and habitat conditions and several cascades of dams should have been surveyed in a consistent manner over a number of years. This is particularly relevant given there are 28 known dams ranging height from 15 to 180 cm in at least 13 areas of activity (Brazier et al. 2020, Table1.2), but with a potential 147 – 179 territories and 262 and 814 dams (; Brazier et al. 2020) that could be occupied and constructed, respectively, by 2030. The upstream-downstream control-impact strategy used in the study is considered suitable but should have been supplemented by control sites in different tributaries that have not been impacted by beavers to date. This is feasible given the similarity in fish community structure between tributaries in the Otter catchment (Figure 3-7)."*

Commonly in ecological studies, what is possible in the field does not match idealized experimental design. More studies as more dams are built would be useful.

4.3.2 Barriers to fish migration
In general, the author brings up many points that have already been addressed in Section 2 above regarding the passability of beaver dams by fish. Notably, the author does not take into account lateral and overtopping bypass channels, the fact that dams are "leaky" allowing small fish to pass through and that a wide array of literature shows that fish can move past dams (see Section 2). The author again fails to provide citations to support statements.

4.3.3 Alteration of habitat
The author again repeats much here regarding spawning habitat and dams breaking in high flows that is not supported by citations and that has already been addressed in Section 2 above.

4.3.4 Disease
No comments besides that domestic animals also carry E. multilocularis and that it should be able to be controlled.

4.3.5 Mitigation measures
Figure 4-8 does not illustrate an option for fish passage, the pipe simply reduces water levels year round and the dam would still be overtopped during high flow events. In general more statements were made without associated citations or data to back them up.

4.3.6 Attitudes to beavers
No comments.

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4.3.7 Economic characterization
No comments.

4.3.8 Conflicts
No comments.

4.3.9 River Otter Beaver Management Strategy Framework
No comments.

5 Conclusions and recommendations

"It is widely recognised that beaver is a keystone conservation species that once inhabited large areas of Europe, but was driven to extinction in many countries through hunting hundreds of years ago, including in the UK. There is now considerable traction to reintroduce beavers across the UK; and over the past 15 years, they have been reintroduced into a range of locations, mostly in controlled environments (Halley et al. 2020). To support this initiative, there is considerable emphasis in the literature and media on the positive benefits that beavers can bring to aquatic ecosystems and biodiversity. These include opening up dense riparian tree canopies, improving (temporarily at least) water quality, attenuating floods, and providing habitat heterogeneity through the creation of impounded areas that promote opportunities for enhancing aquatic biodiversity (see Sections 2.2, 2.3). However, the reintroduction of beavers can also cause a number of potential problems, such as disruption to fish migration and fish recruitment processes, shifts in fish species composition and abundance, damage to trees, loss of agricultural production and damage to banks and other infrastructure, with concomitant impacts on biodiversity and potential conflict with other catchment uses and resource sustainability (see Section 2.2, 2.3). These impacts have been less well documented and publicised."

In contrary to this conclusion the most evidence, presented in multiple peer-reviewed publications shows that the positive benefits of beavers outweigh the negative benefits (Brazier et al., 2020; Collen & Gibson, 2001; Kemp et al., 2012). Unfortunately the review by Prof Cowx was not comprehensive and did not include much of the literature regarding the positive influences of beavers on fishes and linked aquatic-terrestrial ecosystems.

Prof Cowx argues: ***"the science behind the reintroductions and justifications for further open site reintroductions remain a source of considerable debate and conjecture."***

However, citations and data are not presented for many of the statements in his review regarding the negative impacts of beavers. In fact, the peer-reviewed literature shows that the positive benefits outweigh the negative (see above).

Furthermore he states "*For example, the Scottish Government (2017) concluded that: "Based on experience of mitigation techniques and practice from elsewhere in Europe and North America and from some trial work in Scotland, there is sufficient evidence that the majority of the adverse effects*

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identified can be satisfactorily and straightforwardly mitigated to avoid significant effects." With respect to fish, the report concluded "beavers are likely to impact on fish species, mainly from changing the structure of the riparian woodland through foraging activity and changing the riverine habitat from running water to still water through damming activity. There will be both positive and negative effects on the variety of Scottish fish species from these activities. There are effective mitigation measures available to address adverse effects." However, in the report there were several caveats to this conclusion, including: "The identification of cumulative and long and short term effects is complex when dealing with the interactions of a wild animal and its environment." The report importantly recognised ***the 3-5 year timeframe of the impact study was insufficient to understand the full implications of reintroducing beavers into open catchments.*** *This clarification is at odds with the previous statement that adverse impacts can be mitigated because the full impacts remain a huge unknown and evidence from Europe suggests these impacts escalate as the beaver populations become established and reach carrying capacity for the inhabited waterbody (see Sections 2.2.5, 2.2.6, 2.2.7)"*

The combination of positive impacts of beavers and the ability to mitigate potential negative impacts while managing beavers on the landscapes supports reintroductions moving forward.

"The same limitations described above persist with the River Otter Beaver Trial. The population has a long way to develop, perhaps another 25 years, before it reaches its carrying capacity, and the impact on the catchment landscape, hydrogeomorphology and interactions with fish and fisheries are yet to be fully understood. There is clear need for predictive modelling on both the River Otter [initially] and other catchments where the beaver has been reintroduced or proposed for reintroduction, as well as different catchment types where beavers might recolonise. Of particular importance is understanding the differences encountered when beavers occupy headwaters of spate rivers and vulnerable habitats like chalk streams. This is needed to fully assess any potential impacts on aquatic ecosystem functioning, resultant ecological impacts, including on fish and fisheries, and potential impacts on other sectoral uses and demands of the target catchments."

The ROBT was conducted for a longer time period than most short-term studies and additional experiments and monitoring are ongoing to continue collecting data. The vast amount of research of beaver-fish and fisheries interactions should not be ignored, though additional experiments will provide even more useful information.

"Surprisingly, the illegal release of beaver on Tayside in Scotland has been accepted by the Scottish Government because "it is perceived to be politically impossible to be officially testing beaver reintroduction in Knapdale while culling them on Tayside". ***The unofficial release of beaver in the River Otter was also approved in August 2020 following the beaver trial, although it is questioned whether the weight of evidence of the impacts of beavers in the Otter catchment or elsewhere has been fully evaluated, and whether the concerns of the wider array of stakeholders have been fully considered****.*

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- *limited studies took place, and these did not fully assess actual and potential impacts;*
- *there was no baseline, or 'control' study, against which to measure change;*
- *the beaver population did not reach its potential max density (estimated 150+ territories);*
- *after just 5 years from first studying the population, long-term impacts have yet to emerge"*

The ROBT was a catchment-scale effort, the amount of work done was ambitious and done using sound scientific methods.

"Further, because a river is wide and deep and does not have a dam structure does not mean that beavers are not present. Here beavers use pool characteristics and burrow into the banks potentially causing problems with flood mitigation measures and downstream sediment loading: the antithesis of the benefits portrayed. Studies should have focussed on the potential impact of beavers on fish and fisheries under these open water conditions where dams are not constructed as much as, if not more than, around dam sites."

There is no evidence to suggest that beavers will influence fish and fisheries where no dams are present on larger rivers and the author does not provide any citations in support of this idea.

"One of the defining features of the presence of beavers is the construction of dams, although beavers also occupy territories without constructing dams and creating burrows into banks where the eater depth is greater than one metre. It appears there are number of established characteristics of the river topography to determine whether beavers will construct dams across the river channel. This characteristics have now been modelled and thus could be used to predict potential impacts on fisheries, and this has been done at the catchment scale for the River and a few other systems. The efficacy of the modelling, however, needs ground-truthing, and this is only possible when the beaver population in a catchment has reached its capacity and occupies all suitable habitat."

Did the author read Graham et al 2020? This peer-reviewed paper used field data on 258 km of river channel to ground truth the models in question above.

"Irrespective, ROBT has not provided a robust assessment of the impact of beaver dams on fish migration. Instead the interpretation is based on several videos showing adult sea trout attempting to bypass one barrier under what appear to be optimal hydraulic conditions, when the flows are high and create an overflow side channel. Occasional observations of fish bypassing beaver dams are not considered a true representation that all fish can pass, and this issue needs to be more robustly assessed using telemetry or tagging studies under a range of hydraulic conditions at the dam, especially at the time the fish need to migrate upstream or downstream, as well as for a range of species and sizes of fish. Further, the coarse resolution rapid barrier assessment tool (RAP) developed by the West Country Rivers Trust for the River Otter Beaver Trial (West et al. 2019) is currently limited in scope and needs to be field tested for

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validity with a range of dams in different water courses and with a range of migratory species, not just adult salmonids, before any confidence can be placed in its application and resulting outputs. ***As a consequence, there is clear need for further research to assess the barrier effects and otherwise of beaver dams on fish migration and recruitment processes before any definitive conclusions can be drawn about passability of beaver dams. This will require fully funded studies, including telemetry studies, on a range dam types, including cascades of dams, and for a full range of species.*** *Whilst telemetry studies are technically an expensive option to assess fish passability at beaver dams, a full study on a range of dams would remove the controversy and ambiguity regarding passability. This is largely because the hydraulic characteristics of the dams, and thus ability to bypass the structures, change with discharge, and a simple model does not fit the complex diversity of conditions presented at different dams."*

Specialists from the University of Southampton collected multiple years of electrofishing data for the ROBT in addition to the videos noted in this section of the review. While additional research should be conducted, the literature showing that beaver dams can be passed by fishes should not be ignored. Furthermore, the author is ignoring the primary issues that have been identified for the "poor" ecological status of the Lower Otter, Middle Otter and Wolf relative to fish. The main issue is man-made barriers to fish (ROBT: Science and Evidence Report). Additional issues include elevated phosphates and phytobenthos and poor nutrient management, in addition to sewage discharge (ROBT: Science and Evidence Report), all issues that beavers ponds could help mitigate by improving water quality.

"This issue is particularly important because there are many field-based observations and media reports that suggest the conflicts arising from beaver introductions are greater than reported in the ROBT Evidence reports, and that these issues are disproportionately greater as the abundance of beavers increases in catchments towards the system's carrying capacity. ***There is a fundamental requirement for a multi-sectoral review of the issues and an impact/resolution matrix*** *(similar to that produced by Ecke et al. 2019)* ***needs to be prepared, based on empirical findings from validated studies, to support management decisions on the reintroduction of beavers under different scenarios (wild open versus enclosed), which accounts for variability on catchment topography and ecosystem functioning, as well as fish community structure and dynamics."***

The ROBT Evidence reports show a number of conflicts that arose, the author does not provide any citations for the additional observations noted here.

"What is evident throughout the literature and media are complex human-human and human-wildlife conflicts, and the somewhat opposed views of stakeholders that potentially can be impacted by beaver reintroductions and those promoting beaver reintroductions. Such interactions are common throughout the world with other human-wildlife conflicts (Marshall et al. 2007; Redpath et al. 2013, 2015) and often arise because of polarised debates and little attempt to understand the opposing stakeholders' motives and drivers (Meffe 2002). Similar conflicts arise with other wildlife species and fisheries, e.g. cormorants (e.g. Cowx 2013), or between fisheries and infrastructural development, e.g. small-scale hydropower development (e.g. Anderson et al. 2013). With respect to

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beaver-fish interactions, much of the literature and media presents the positive benefits brought by beavers, which cannot be ignored, but there seems to be an imbalance against the considerable evidence of actual and potential impacts, especially as beaver populations expand their ranges and increase in abundance. There is a clear need for ***an independent panel with a balanced membership representing all sectors of society and expertise****, as highlighted above,* ***to discuss, in an open and frank manner, the issues arising from the complex interactions between beavers and fish and fisheries, and other sectors.*** *The science and evidence on which any decisions are to be based should be openly shared and transparent so the voices of all can be heard and represented in any final decisions made. Auster et al (2019) argued for a similar approach and the English Beaver Strategy Working Group30 has been set up to this effect, but this group has yet to endorse a strategy for moving forward as there remain many issues to resolve.* ***Decision support tools,*** *such as that produced by Ecke et al. (2019),* ***which attempt to balance the beneficial and detrimental effects of beaver dams, will help focus on the problems that need to be addressed and help find solutions for potential conflict. It is also recommended that independent reviews of the interactions between beavers and other sectors of society, e.g. agriculture, silviculture or nature conservation, are carried out to fully understand and quantify potential areas of conflict, and find a way forward to allow beavers to be introduced into the UK landscape in a socially, environmentally and economically regulated manner that addresses the concerns of all stakeholders."***

Peer reviewed publications on conflict are available (Auster et al., 2020). Additionally, it is not common to repeatedly refer to "media" in scientific writing. The author states that "with respect to beaver-fish interactions, much of the literature and media presents the positive benefits brought by beavers…" yet his review ignores most of the positive benefits.

"In conclusion, based on the review of potential interactions between beavers and fish and fisheries, and on the current science and evidence available, further reintroductions of beavers into the wild should not take place until the recommendations made herein have been fulfilled. Once these knowledge gaps have been filled and management issues resolved, it may be possible to find solutions that would allow further controlled introductions of beaver, where their location, activities and numbers can be managed to curtail any damage to fish and fisheries or other economic or social sectors."

In conclusion, the review of potential interactions between beavers and fish and fisheries was flawed and unbalanced, not including literature on many of the positive impacts of beavers. Furthermore, many of the claims in the review for negative impacts were not supported by any citations of peer-reviewed literature. There is no evidence to prove that any damage to fish or fisheries has occurred, not does the review show that it will occur. A comprehensive review of the literature shows that the benefits of beaver outweigh the costs.

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6 Literature

As noted numerous times, the review by Prof Cowx was missing many citations relevant to the positive impacts of beavers, a number of which have been cited in this review and are included in the References listed below.

References

Ahearn, D. S., Sheibley, R. W., Dahlgren, R. A., Anderson, M., Johnson, J., & Tate, K. W. (2005). Land use and land cover influence on water quality in the last free-flowing river draining the western Sierra Nevada, California. *Journal of Hydrology*, *313*(3–4), 234–247. https://doi.org/10.1016/j.jhydrol.2005.02.038

Auster, Roger E., Barr, S. W., & Brazier, R. E. (2020). Improving engagement in managing reintroduction conflicts: learning from beaver reintroduction. *Journal of Environmental Planning and Management*, *0*(0), 1–22. https://doi.org/10.1080/09640568.2020.1837089

Auster, Roger Edward, Puttock, A., & Brazier, R. (2020). Unravelling perceptions of Eurasian beaver reintroduction in Great Britain. *Area*, *52*(2), 364–375. https://doi.org/10.1111/area.12576

Beedle, D. (1991). *Physical Dimensions and Hydrologic Effects of Beaver Ponds on Kuiu Island* (Issue June).

Benke, A.C., Ward, G. M., & Richardson, T. D. (1999). Beaver-impounded wetlands of the Southeastern Coastal Plain: Habitat-specific composition and dynamics of invertebrates. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (pp. 217–245). John Wiley and Sons.

Benke, Arthur C., Van Arsdall, T. C., Gillespie, D. M., & Parrish, F. K. (1984). Invertebrate Productivity in a Subtropical Blackwater River: The Importance of Habitat and Life History. *Ecological Monographs*, *54*(1), 25–63. https://doi.org/10.2307/1942455

Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., Wheaton, J. M., & Pollock, M. M. (2016). *Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (Oncorhynchus mykiss)*. https://doi.org/10.1038/srep28581

Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. L. (2020). Beaver: Nature's ecosystem engineers. *Wiley Interdisciplinary Reviews: Water*, *8*(1), 1–29. https://doi.org/10.1002/wat2.1494

Bryant, M. D. (1983). *The role of beaver dams as coho salmon habitat in southeast Alaska streams. Pages 183-192 in J. M. Walton, and D.B. Houston, editors. Proceedings of the Olympic Wild Fish Conference. Fisheries Technology Program, Peninsula College, Port*

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Burchsted, D., Daniels, M., Thorson, R., & Vokoun, J. (2010). The river dicontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience*, *60*(11), 908–922.

Bush, B. M., & Wissinger, S. A. (2016). Invertebrates in Beaver-Created Wetlands and Ponds. In D. Batzer & D. Boix (Eds.), *Invertebrates in Freshwater Wetlands: An International Perspective on Their Ecology* (pp. 411–449). Springer International Publishing. https://doi.org/10.1007/978-3-319-24978-0

Bustard, D. R., & Narver, D. W. (1975). Aspects of the winter ecology of juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). *Journal of the Fisheries Research Board of Canada*, *32*, 667–680.

Bylak, A., & Kukuła, K. (2018). Living with an engineer: fish metacommunities in dynamic patchy environments. *Marine and Freshwater Research*, *69*(6), 883. https://doi.org/10.1071/MF17255

Bylak, A., Kukuła, K., & Mitka, J. (2014). Beaver impact on stream fish life histories: the role of landscape and local attributes. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(11). https://doi.org/10.1139/cjfas-2014-0105

Campbell-Palmer, R., Puttock, A., Wilson, K. A., Leow-Dyke, A., Graham, H. A., Gaywood, M. J., & Brazier, R. E. (2020). Using field sign surveys to estimate spatial distribution and territory dynamics following reintroduction of the Eurasian beaver to British river catchments. *River Research and Applications*, *November*, 1–15. https://doi.org/10.1002/rra.3755

Chisholm, I. M., Hubert, W. A., & Wesche, T. A. (1987). Winter Stream Conditions and Use of Habitat by Brook Trout in High-Elevation Wyoming Streams. *Transactions of the American Fisheries Society*, *116*(2), 176–184. https://doi.org/10.1577/1548-8659(1987)116<176:wscauo>2.0.co;2

Collen, P., & Gibson, R. J. (2001). The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. *Reviews in Fish Biology and Fisheries*, *10*, 439–461.

Cook, D. B. (1940). Beaver-trout relationships. *Journal of Mammalogy*, *21*, 397–401.

Correll, D. L., Jordan, T. E., & Weller, D. E. (2000). Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry*, *49*(3), 217–239. https://doi.org/10.1023/A:1006330501887

Cunjak, Richard A. (1996). Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(SUPPL. 1), 267–

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282. https://doi.org/10.1139/cjfas-53-s1-267

Cunjak, Richard Anthony, Caissie, D., El-Jabi, N., Conlon, J. H., Pollock, T., Giberson, D. J., & Komadina-Douthwright, S. (1993). *The Catamaran Brook (New Brunswick) habitat research project : biological, physical and chemical conditions (1990-1992): Canadian technical report of fisheries and aquatic sciences, 1914*. 81-. https://islandscholar.ca/islandora/object/ir%3Air-batch6-1038/

Curran, J. C., & Cannatelli, K. M. (2014). The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. *Earth Surface Processes and Landforms*, *39*(9). https://doi.org/10.1002/esp.3576

Cutting, K. A., Ferguson, J. M., Anderson, M. L., Cook, K., Davis, S. C., & Levine, R. (2018). Linking beaver dam affected flow dynamics to upstream passage of Arctic grayling. *Ecology and Evolution*, *October*, 1–13. https://doi.org/10.1002/ece3.4728

Czerniawski, R., & Sługocki, Ł. (2018). A comparison of the effect of beaver and human-made impoundments on stream zooplankton. *Ecohydrology*, *11*(5). https://doi.org/10.1002/eco.1963

Dalbeck, L., Hachtel, M., & Campbell-Palmer, R. (2020). A review of the influence of beaver castor fiber on amphibian assemblages in the floodplains of European temperate streams and rivers. *Herpetological Journal*, *30*(3), 135–146. https://doi.org/10.33256/HJ30.3.135146

Dalbeck, L., Janssen, J., & Luise Völsgen, S. (2014). Beavers (Castor fiber) increase habitat availability, heterogeneity and connectivity for common frogs (Rana temporaria). *Amphibia Reptilia*, *35*(3). https://doi.org/10.1163/15685381-00002956

De Visscher, M., Nyssen, J., Pontzeele, J., Billi, P., & Frankl, A. (2014). Spatio-temporal sedimentation patterns in beaver ponds along the Chevral river, Ardennes, Belgium. *Hydrological Processes*, *28*(4). https://doi.org/10.1002/hyp.9702

Devito, K. J., Dillon, P. J., & Lazerte, B. D. (1989). Phosphorus and nitrogen retention in five Precambrian shield wetlands. *Biogeochemistry*, *8*(3), 185–204. https://doi.org/10.1007/BF00002888

Enders, E. C., Boisclair, D., & Roy, A. G. (2003). The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 1149–1160.

Fox, M. G., & Keast, A. (1990). Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. *Canadian Journal of Zoology*, *68*(12), 2489–2498. https://doi.org/10.1139/z90-348

France, R. L. (1997). The importance of beaver lodges in structuring littoral communities in

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boreal headwater lakes. *Canadian Journal of Zoology*, *75*(Novak 1976), 1009–1013.

Gard, R. (1961). Effects of beaver on trout in Sagehen Creek, California. *Journal of Wildlife Management*, *25*, 221–242.

Giriat, D., Gorczyca, E., & Sobucki, M. (2016). Beaver ponds' impact on fluvial processes (Beskid Niski Mts., SE Poland). *Science of the Total Environment*, *544*. https://doi.org/10.1016/j.scitotenv.2015.11.103

Gorczyca, E., Krzemień, K., Sobucki, M., & Jarzyna, K. (2018). Can beaver impact promote river renaturalization? The example of the Raba River, southern Poland. *Science of the Total Environment*, *615*. https://doi.org/10.1016/j.scitotenv.2017.09.245

Gorshkov, D. (2003). Is it possible to use beaver building activity to reduce lake sedimentation? *Lutra*, *46*(2), 189–196.

Graham, H. A., Puttock, A., Macfarlane, W. W., Wheaton, J. M., Gilbert, J. T., Campbell-Palmer, R., Elliott, M., Gaywood, M. J., Anderson, K., & Brazier, R. E. (2020). Modelling Eurasian beaver foraging habitat and dam suitability, for predicting the location and number of dams throughout catchments in Great Britain. *European Journal of Wildlife Research*, *66*(3). https://doi.org/10.1007/s10344-020-01379-w

Grasse, J. E. (1951). Beaver ecology and management in the Rockies. *Journal of Forestry*, *49*, 3–6. https://doi.org/10.5849/jof.2017-001

Grasse, J. E. (1979). Some trout-raising alternatives...irrigation ditches and beaver ponds. *Salmoni*, *3*, 12–15.

Gurnell, A. M. (1998). The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, *22*(2), 167–189.

Gurnell, A. M., Piégay, H., Swanson, F. J., & Gregory, S. V. (2002). Large wood and fluvial processes. *Freshwater Biology*, *47*(4), 601–619. https://doi.org/10.1046/j.1365-2427.2002.00916.x

Hägglund, Å., & Sjöberg, G. (1999). Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management*, *115*(2–3), 259–266. https://doi.org/10.1016/S0378-1127(98)00404-6

Halley, D. J., Jones, A. C. L., Chesworth, S., Hall, C., Gow, D., Parry, R. J., & Walsh, J. (2009). *The reintroduction of the Eurasian beaver Castor fiber to Wales: an ecological feasibility study / Ail-gyflwyniad yr afanc Ewropeaidd Castor fiber i Gymru. Astudiaeth dichonoldeb ecolegol.* NINA Report 457.

Harvey, G. L., Henshaw, A. J., Brasington, J., & England, J. (2019). Burrowing Invasive Species: An Unquantified Erosion Risk at the Aquatic-Terrestrial Interface. *Reviews of Geophysics*, *57*(3), 1018–1036. https://doi.org/10.1029/2018RG000635

Harvey, G. L., Henshaw, A. J., Parker, C., & Sayer, C. D. (2018). Re-introduction of structurally complex wood jams promotes channel and habitat recovery from overwidening: Implications for river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(2), 395–407. https://doi.org/10.1002/aqc.2824

Hering, D., Gerhard, M., Kiel, E., Ehlert, T., & Pottgiesser, T. (2001). Review study on near-natural conditions of Central European Mountains streams, with particular reference to Debris and Beaver dams: Results of the “REG meeting” 2000. *Limnologica*, *31*(2), 81–92. https://doi.org/10.1016/S0075-9511(01)80001-3

Hood, G. A., & Bayley, S. E. (2008). Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, *141*(2), 556–567. https://doi.org/10.1016/j.biocon.2007.12.003

Hood, G. A., & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. *Freshwater Biology*, *60*(1). https://doi.org/10.1111/fwb.12487

Huey, W. S., & Wolfrum, W. H. (1956). Beaver-trout relations in New Mexico. *Progressive Fish Culturist*, *18*, 70–74.

Hughes, B. B., Beas-Luna, R., Barner, A. K., Brewitt, K., Brumbaugh, D. R., Cerny-Chipman, E. B., Close, S. L., Coblentz, K. E., De Nesnera, K. L., Drobnitch, S. T., Figurski, J. D., Focht, B., Friedman, M., Freiwald, J., Heady, K. K., Heady, W. N., Hettinger, A., Johnson, A., Karr, K. A., … Carr, M. H. (2017). Long-Term studies contribute disproportionately to ecology and policy. *BioScience*, *67*(3), 271–278. https://doi.org/10.1093/biosci/biw185

Jakober, M. J., McMahon, T. E., Thurow, R. F., & Clancy, C. G. (1998). Role of Stream Ice on Fall and Winter Movements and Habitat Use by Bull Trout and Cutthroat Trout in Montana Headwater Streams. *Transactions of the American Fisheries Society*, *127*(2), 223–235. https://doi.org/10.1577/1548-8659(1998)127<0223:rosiof>2.0.co;2

Jones, A. L., Halley, D. J., Gow, D., Branscombe, J., & Aykroyd, T. (2012). *Welsh Beaver Assessment Iniative Report: An investigation into the feasibility of reintroduction European Beaver (Castor fiber) to Wales*.

Jones, K., Gilvear, D., Willby, N., & Gaywood, M. (2009). Willow (Salix spp.) and aspen (Populus tremula) regrowth after felling by the Eurasian beaver (Castor fiber): implications for riparian woodland conservation in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*, 75–89. https://doi.org/10.1002/aqc

Kemp, P. S., Worthington, T. A., Langford, T. E. L., Tree, A. R. J., & Gaywood, M. J. (2012). Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries*, *13*(2), 158–181.

Knudsen, & J., G. (1962). Relationship of beaver to forests, trout and wildlife in Wisconsin.

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http://flbs.umt.edu

Wisconsin Department of Natural Resources Technical Bulletin, *25*, 1–50.

Law, A., Gaywood, M. J., Jones, K. C., Ramsay, P., & Willby, N. J. (2017). Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Science of the Total Environment*, *605–606*. https://doi.org/10.1016/j.scitotenv.2017.06.173

Law, A., Levanoni, O., Foster, G., Ecke, F., & Willby, N. J. (2019). Are beavers a solution to the freshwater biodiversity crisis? *Diversity and Distributions*, *25*(11). https://doi.org/10.1111/ddi.12978

Law, A., Mclea, O., And, N., & Illby, N. J. W. (2016). *Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams*. https://doi.org/10.1111/fwb.12721

Layman, C. A., & Smith, D. E. (2001). Sampling bias of minnow traps in shallow aquatic habitats on the eastern shore of Virginia. *Wetlands*, *21*(1), 145–154.

Lazar, J. G., Addy, K., Gold, A. J., Groffman, P. M., McKinney, R. A., & Kellogg, D. Q. (2015). Beaver Ponds: Resurgent Nitrogen Sinks for Rural Watersheds in the Northeastern United States. *Journal of Environmental Quality*, *44*(5), 1684–1693. https://doi.org/10.2134/jeq2014.12.0540

Leidholt Bruner, K., Hibbs, D. E., & McComb, W. C. (1992). Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. *Northwest Science*, *66*, 218–223.

Levine, R., & Meyer, G. A. (2014). Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. *Geomorphology*, *205*. https://doi.org/10.1016/j.geomorph.2013.04.035

Levine, R., & Meyer, G. A. (2019). Beaver-generated disturbance extends beyond active dam sites to enhance stream morphodynamics and riparian plant recruitment. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-44381-2

Lindstrom, J. W., & Hubert, W. A. (2004). Ice Processes Affect Habitat Use and Movements of Adult Cutthroat Trout and Brook Trout in a Wyoming Foothills Stream. *North American Journal of Fisheries Management*, *24*(4), 1341–1352. https://doi.org/10.1577/m03-223.1

Lokteff, R. L., Roper, B. B., & Wheaton, J. M. (2013). Do Beaver Dams Impede the Movement of Trout? *Transactions of the American Fisheries Society*, *142*(4), 1114–1125. https://doi.org/10.1080/00028487.2013.797497

Macfarlane, W. W., Wheaton, J. M., Bouwes, N., Jensen, M. L., Gilbert, J. T., Hough-Snee, N., & Shivik, J. A. (2017). Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*, *277*. https://doi.org/10.1016/j.geomorph.2015.11.019

Majerova, M., Neilson, B. T., Schmadel, N. M., Wheaton, J. M., & Snow, C. J. (2015). Impacts

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of beaver dams on hydrologic and temperature regimes in a mountain stream. *Hydrology and Earth System Sciences*, *12*, 839–878.

Malison, R. ., & Halley, D. J. (2020). Ecology and movement of juvenile salmonids in beaver-influenced and beaver-free tributaries in the Trøndelag province of Norway. *Ecology of Freshwater Fish*. https://onlinelibrary.wiley.com/doi/full/10.1111/eff.12539

Malison, R. L., Eby, L. A., & Stanford, J. A. (2015). Juvenile salmonid growth, survival, and production in a large river floodplain modified by beavers (Castor canadensis). *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(11). https://doi.org/10.1139/cjfas-2015-0147

Malison, R. L., Lorang, M. S., Whited, D. C., & Stanford, J. A. (2014). Beavers (Castor canadensis) influence habitat for juvenile salmon in a large Alaskan river floodplain. *Freshwater Biology*, *59*(6). https://doi.org/10.1111/fwb.12343

Malison, R. L., & Stanford, J. A. (2016). Do beaver dams reduce connectivity and salmon productivity in expansive river floodplains? *PeerJ*, *4:e2403*. https://doi.org/10.7717/peerj.2403

McDowell, D. M., & Naiman, R. J. (1986). Structure and function of a benthic invertebrate stream community as influenced by beaver (Castor canadensis). *Oecologia*, *68*, 481–489.

Means, C. D. O. (2018). *Stream Temperature Variability in Headwater Beaver Dam Complexes in Relation to Hydrologic and Environmental Factors*. http://libproxy.lib.unc.edu/login?url=https://search.proquest.com/docview/2128024619?accountid=14244%0Ahttp://vb3lk7eb4t.search.serialssolutions.com/?genre=dissertations+%26+theses&atitle=&author=Means%2C+Catherine+Doris+O%27Connor&volume=&issue=&spage=&d

Miller, B. A., & Sadro, S. (2003). Residence Time and Seasonal Movements of Juvenile Coho Salmon in the Ecotone and Lower Estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society*, *132*(3), 546–559. https://doi.org/10.1577/1548-8659(2003)132<0546:rtasmo>2.0.co;2

Morzillo, A. T., & Needham, M. D. (2015). Landowner Incentives and Normative Tolerances for Managing Beaver Impacts. *Human Dimensions of Wildlife*, *20*(6), 514–530. https://doi.org/10.1080/10871209.2015.1083062

Murphy, M. L., Heifetz, J., Thedinga, J. F., Johnson, S. W., & Koski, K. V. (1989). Habitat utilization by juvenile Pacific salmon (Oncorhynchus) in the glacial Taku River, southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 1677–1685.

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (Castor canadensis). *Ecology*, *67*(5), 1254–1269.

Naiman, R. J., Pinay, G., Johnston, C. A., & Pastor, J. (1994). Beaver influences on the long-

32125 Bio Station Lane Polson, Montana, U.S.A. 59860
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http://flbs.umt.edu

term biogeochemical characteristics of boreal forest drainage networks. *Ecology*, *75*(4), 905–921.

Neff, D. J. (1957). Ecological Effects of Beaver Habitat Abandonment in the Colorado Rockies. *The Journal of Wildlife Management1*, *21*(1), 80–84.

Nickelson, T. E., Nicholas, J. W., McGie, A. M., Lindsay, R. B., Bottorn, D. L., Kaiser, R. J., & Jacobs, S. E. (1992). *Status of anadromous salmonids in Oregon coastal basins. Coravallis (OR): Oregon Department of Fish and Wildlife*.

Nickelson, T. E., Rodgers, J. D., Johnson, S. L., & Solazzi, M. F. (1992). Seasonal changes in habitat use by juvenile coho salmon (Oncorhynchus kisutch) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 783–789.

Nummi, P., Liao, W., Huet, O., Scarpulla, E., & Sundell, J. (2019). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Global Ecology and Conservation*, *20*. https://doi.org/10.1016/j.gecco.2019.e00701

Nyssen, J., Pontzeele, J., & Billi, P. (2011). Effect of beaver dams on the hydrology of small mountain streams: Example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. *Journal Of Hydrology*, *402*, 92–102.

Orr, M. R., Weber, N. P., Noone, W. N., Mooney, M. G., Oakes, T. M., & Broughton, H. M. (2020). Short-Term Stream and Riparian Responses to Beaver Dam Analogs on a Low-Gradient Channel Lacking Woody Riparian Vegetation. *Northwest Science*, *93*(3–4), 171–184. https://doi.org/10.3955/046.093.0302

Osipov, V. V., Bashinskiy, I. V., & Podshivalina, V. N. (2018). Influence of the Activity of the Eurasian Beaver Castor fiber (Castoridae, Mammalia) on the Ecosystem Biodiversity of Small Rivers in the Forest–Steppe Zone. *Biology Bulletin*, *45*(10), 1139–1148. https://doi.org/10.1134/S1062359018100205

Peterson, N. P. (1982). Population characteristics of juvenile Coho Salmon (Oncorhynchus kisutch) overwintering in riverine ponds. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 1303–1307.

Pollock, M M, Beechie, T. J., & Jordan, C. E. (2007). Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms*, *32*, 1174–1185.

Pollock, Michael M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. In *BioScience* (Vol. 64, Issue 4). https://doi.org/10.1093/biosci/biu036

Pollock, Michael Moritz, Witmore, S., & Yokel, E. (2019). A field experiment to assess passage of juvenile salmonids across beaver dams during low flow conditions in a tributary to the

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Klamath River, California, USA. *BioRxiv*. https://doi.org/10.1101/856252

Puttock, A., Graham, H. A., Ashe, J., Luscombe, D. J., & Brazier, R. E. (2020). Beaver dams attenuate flow: A multi-site study. *Hydrological Processes*, *October 2020*, 1–18. https://doi.org/10.1002/hyp.14017

Puttock, A., Graham, H. A., Carless, D., & Brazier, R. E. (2018). Sediment and nutrient storage in a beaver engineered wetland. *Earth Surface Processes and Landforms*, *43*(11). https://doi.org/10.1002/esp.4398

Puttock, A., Graham, H. A., Cunliffe, A. M., Elliott, M., & Brazier, R. E. (2017). Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of the Total Environment*, *576*. https://doi.org/10.1016/j.scitotenv.2016.10.122

Quinn, T. P., & Peterson, N. P. (1996). The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile choh salmon (Oncorhynchus kisutch) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1555–1564.

Rosell, F., Bozser, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. *Mammal Review*, *35*(3&4), 248–276.

Scruton, D. A., Anderson, T. C., & King, L. W. (1998). Pamehac Brook: A case study of the restoration of a Newfoundland, Canada, river impacted by flow diversion for pulpwood transportation. *Aquatic Conservation-Marine And Freshwater Ecosystems*, *8*, 145–157.

Sigourney, D. B., Letcher, B. H., & Cunjak, R. A. (2006). Influence of beaver activity on summer growth and condition of age-2 Atlantic salmon parr. *Transactions of the American Fisheries Society*, *135*, 1068–1075.

Smith, J. M., & Mather, M. E. (2013). Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology*, *58*(7), 1523–1538. https://doi.org/10.1111/fwb.12153

Snodgrass, J. W., & Meffe, G. K. (1998). Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. *Ecology*, *79*(3), 928–942.

Stringer, A. P., & Gaywood, M. J. (2016). The impacts of beavers Castor spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, *46*, 270–283.

Swales, S., & Levings, C. D. (1989). Role of off-channel ponds in the life cycles of coho salmon (Oncorhynchus kisutch) and other juvenile salmonids in the Coldwater River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 232–242.

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P (406) 982-3301 F (406) 982-3201
http://flbs.umt.edu

T.J., M., M., P., & T.E., F. (1987). The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming. *Water Research*, *21*(3), 263–268.

Taylor, B. R., Macinnis, C., & Floyd, T. A. (2010). Influence Of Rainfall And Beaver Dams On Upstream Movement Of Spawning Atlantic Salmon In A Restored Brook In Nova Scotia, Canada. *River Research and Applications*, *26*(2), 183–193.

Thompson, M. S. A., Brooks, S. J., Sayer, C. D., Woodward, G., Axmacher, J. C., Perkins, D. M., & Gray, C. (2018). Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, *55*(2), 895–904. https://doi.org/10.1111/1365-2664.13013

Virbickas, T., Stakenas, S., & Steponenas, A. (2015). Impact of beaver dams on abundance and distribution of anadromous salmonids in two lowland streams in Lithuania. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0123107

Wathen, G., Allgeier, J. E., Bouwes, N., Pollock, M. M., & Jordan, C. E. (2018). Beaver activity increases habitat complexity and spatial partitioning by steelhead trout. In *Canadian Journal of Fisheries and Aquatic Sciences*. https://mc06.manuscriptcentral.com/cjfas-pubshttps://mc06.manuscriptcentral.com/cjfas-pubs

Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., Wirtz, J., & Jordan, C. E. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS ONE*, *12*(5). https://doi.org/10.1371/journal.pone.0176313

Westbrook, C J, Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, *42*(6).

Westbrook, Cherie J., Ronnquist, A., & Bedard-Haughn, A. (2020). Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm. *Hydrological Processes*, *34*(18), 3726–3737. https://doi.org/10.1002/hyp.13828

Willby, N. J., Law, A., Levanoni, O., Foster, G., & Ecke, F. (2018). Rewilding wetlands: Beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761), 1–8. https://doi.org/10.1098/rstb.2017.0444

Wissinger, S. A., & Gallagher, L. J. (1999). Beaver pond wetlands in western Pennsylvania: Modes of colonization and succession after drought. In D. P. Batzer, R. B. Rader, & S. A. Wissinger (Eds.), *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (pp. 333–362). John Wiley and Sons Inc.

Woo, M. K., & Waddington, J. M. (1990). Effects of beaver dams on sub-arctic wetland hydrology. *Arctic*, *43*, 223–230.

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P (406) 982-3301 F (406) 982-3201
http://flbs.umt.edu

Zheng, W., Wang, S., Tan, K., & Lei, Y. (2020). Nitrate accumulation and leaching potential is controlled by land-use and extreme precipitation in a headwater catchment in the North China Plain. *Science of the Total Environment*, *707*, 136168. https://doi.org/10.1016/j.scitotenv.2019.136168