Beavers & Fish: What does the science tell us about challenges and opportunities?

Dr. Rachel L. Malison

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Beaver Conference: Restoring Beavers to the British Landscape
What factors drive and control the structure and function of freshwater systems?

- linkages within and among lotic systems
- encompassing scales from genes to ecosystems
- systems level approaches
My perspective – research background

MS in Biology – Effects of Wildfire

PhD in Systems Ecology – Beavers and Salmon in AK

Marie Curie Fellowship in Norway
Outline

• Habitat modifications by beavers
• Benefits of beavers to aquatic ecosystems
• Beaver – fish interactions
  • Positive
  • Negative
• Important factors to consider with regard to beavers and fish
  • Scale, habitat connectivity & stream size
  • Temporal variability
  • Considering cumulative and system level effects
Habitat modifications
· Water flux
· Sediment flux
· Heat flux
· Nutrient and carbon cycles, availability
· Strong changes from lotic to lentic environments
· Understand habitat structure and function to interpret effects on fish

Naiman et al. 1988; Pollock et al. 1995; Collen & Gibson 2001; Rosell et al. 2005
Habitat modification: dam characteristics

- Vary in shape and size
- Some long lasting
- Some are ephemeral and highly dynamic
- Numbers change over time
- Located near or far from the river
- Influence fish in various ways
Habitat modification: flow attenuation

Other studies:
Giriat et al. 2016
Gurnell et al. 1998
Hood & Bayley 2008
Woo & Waddington 1990
Nyssen et al. 2011
Westbrook et al. 2020
Puttock et al. 2017
Puttock et al. 2020

- Influences sediment dynamics
- Sustain baseflows and summer habitat
A global review of beaver dam impacts

Fig. 1. Distribution of beaver home ranges (A) and studies examined across biomes by category; B) morphology, C) hydrology, D) water chemistry, E) aquatic biota, F) habitat. Home range distribution data was attained from the International Union for Conservation of Nature (https://www.iucnredlist.org/).

Grudzinski et al. 2022
Benefits of beavers to aquatic ecosystems
Habitat availability, heterogeneity, & connectivity for many species: Dalbeck et al 2014; Hood & Larson 2015; Stringer & Gaywood 2016; Anderson et al. 2015; Rosell et al 2005; Wathen et al. 2018


Many beaver-produced ecosystem services: water purification, moderation of extreme events, habitat and biodiversity provision, greenhouse gas sequestration, recreational hunting and fishing, water supply, and non-consumptive recreation (Thompson et al. 2021); climate resiliency
Beaver-Fish Interactions
Beaver-Fish Interactions


naturebob.com

gallery.nanfa.org

Cailean Moore
Beaver-Fish Interactions

- Salmon and beavers co-evolved and have previously coexisted
  - Collen & Gibson 2001
  - Kemp et al., 2012
  - Brazier et al 2020

Positive interactions generally outweigh negative interactions:

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

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

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

<table>
<thead>
<tr>
<th>Negative impacts</th>
<th>Number</th>
<th>% of total citations</th>
<th>Data driven (%)</th>
<th>Speculative (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barriers to fish movement</td>
<td>51</td>
<td>42.9</td>
<td>21.6</td>
<td>78.4</td>
</tr>
<tr>
<td>Reduced spawning habitat</td>
<td>20</td>
<td>16.8</td>
<td>40.0</td>
<td>60.0</td>
</tr>
<tr>
<td>Altered temperature regime</td>
<td>11</td>
<td>9.2</td>
<td>9.1</td>
<td>90.9</td>
</tr>
<tr>
<td>Reduced oxygen levels</td>
<td>12</td>
<td>10.1</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Reduced habitat quality</td>
<td>2</td>
<td>1.7</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Altered flow regimes</td>
<td>4</td>
<td>3.4</td>
<td>75.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Loss of cover</td>
<td>5</td>
<td>4.2</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Reduced productivity</td>
<td>9</td>
<td>7.6</td>
<td>33.3</td>
<td>66.7</td>
</tr>
<tr>
<td>Retarded growth</td>
<td>2</td>
<td>1.7</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Abandonment of beaver settlements</td>
<td>1</td>
<td>0.8</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Reduced water quality</td>
<td>6</td>
<td>1.7</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Total</td>
<td>119</td>
<td>100</td>
<td>28.6</td>
<td>71.4</td>
</tr>
</tbody>
</table>
Positive Interactions

- Slower current velocities, larger extent of edges, increased food, more cover
- Increased nutrients, temperature refugia

Leidholt-Bruner et al. 1992
Malison et al. 2014
Positive Interactions

Higher growth rates
- Bustard & Narver 1975
- Malison et al. 2015
- Swales & Levings 1989
- Sigourney et al. 2006
- Needham et al. 2021

Increased production
- Bouwes et al. 2016
- Nickelson, Rodgers et al 1992
- Pollock et al. 2004

Needham et al. 2021

Pollock et al. 2004

Fig. 6. Differences in mass (g) of (A) post-YOY trout (FL 61-121 mm) and (B) YOY parr (FL 31-60 mm) between the modified and control streams. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).
Positive Interactions

Increased species richness:

- Snodgrass & Meffe 1998

<table>
<thead>
<tr>
<th>Scientific name, common name, (abbreviation)</th>
<th>All sites</th>
<th>Streams</th>
<th>Active ponds</th>
<th>Abandoned ponds</th>
<th>Recovering streams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Notropis lutipinnis, yellowfin shiner (lut)</td>
<td>935 (0.16, 1)</td>
<td>538 (0.60, 1)</td>
<td>91 (0.04, 8)</td>
<td>145 (0.08, 4)</td>
<td>161 (0.23, 1)</td>
</tr>
<tr>
<td>Gambusia holbrooki, mosquito fish (hol)</td>
<td>892 (0.16, 2)</td>
<td>5 (0.01, 15)</td>
<td>406 (0.17, 1)</td>
<td>481 (0.27, 1)</td>
<td>0</td>
</tr>
<tr>
<td>Lepomis marginatus, dollar sunfish (mar)</td>
<td>671 (0.12, 3)</td>
<td>23 (0.03, 6)</td>
<td>308 (0.17, 2)</td>
<td>216 (0.12, 2)</td>
<td>34 (0.05, 8)</td>
</tr>
<tr>
<td>Notropis cyanoguttatus, dusky shiner (cum)</td>
<td>620 (0.11, 4)</td>
<td>0</td>
<td>238 (0.10, 3)</td>
<td>257 (0.15, 2)</td>
<td>125 (0.18, 2)</td>
</tr>
<tr>
<td>Erimyzon sugetta, lake chub sucker (suc)</td>
<td>256 (0.05, 5)</td>
<td>13 (0.01, 11)</td>
<td>128 (0.05, 6)</td>
<td>133 (0.08, 5)</td>
<td>22 (0.03, 9)</td>
</tr>
<tr>
<td>Notropis chalybeus, iron colored shiner (nich)</td>
<td>257 (0.05, 6)</td>
<td>0</td>
<td>186 (0.08, 4)</td>
<td>70 (0.04, 6)</td>
<td>1 (&lt;0.01, 29)</td>
</tr>
<tr>
<td>Erimyzon oblongus, creek chub sucker (obl)</td>
<td>255 (0.04, 7)</td>
<td>55 (0.06, 3)</td>
<td>91 (0.04, 9)</td>
<td>66 (0.04, 7)</td>
<td>43 (0.06, 5)</td>
</tr>
<tr>
<td>Aphelodon axyurus, pirate perch (say)</td>
<td>239 (0.04, 8)</td>
<td>61 (0.07, 2)</td>
<td>108 (0.05, 7)</td>
<td>53 (0.03, 8)</td>
<td>17 (0.02, 10)</td>
</tr>
<tr>
<td>Erimyzon cyanoguttatus, black handed sunfish (ech)</td>
<td>164 (0.03, 9)</td>
<td>1 (&lt;0.01, 24)</td>
<td>163 (0.07, 5)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Erimyzon auritus, redbreast sunfish (aur)</td>
<td>155 (0.03, 10)</td>
<td>12 (0.01, 12)</td>
<td>62 (0.03, 12)</td>
<td>25 (0.01, 16)</td>
<td>56 (0.08, 3)</td>
</tr>
<tr>
<td>Esox americanus, redfin pickerel (ame)</td>
<td>144 (0.03, 11)</td>
<td>23 (0.03, 7)</td>
<td>84 (0.04, 10)</td>
<td>26 (0.01, 15)</td>
<td>11 (0.07, 14)</td>
</tr>
<tr>
<td>Erimyzon cyanoguttatus, blue spotted sunfish (glu)</td>
<td>114 (0.02, 12)</td>
<td>0</td>
<td>84 (0.04, 11)</td>
<td>30 (0.02, 12)</td>
<td>0</td>
</tr>
<tr>
<td>Fundulus lineatus, lined topminnow (lin)</td>
<td>560 (0.11, 1)</td>
<td>1 (&lt;0.01, 25)</td>
<td>55 (0.02, 14)</td>
<td>44 (0.02, 9)</td>
<td>5 (&lt;0.01, 21)</td>
</tr>
<tr>
<td>Lepomis punctatus, spotted sunfish (pun)</td>
<td>98 (0.02, 14)</td>
<td>5 (0.01, 16)</td>
<td>26 (0.01, 18)</td>
<td>27 (0.02, 14)</td>
<td>40 (0.06, 6)</td>
</tr>
<tr>
<td>Notropis leucopleurus, bluehead chub (lep)</td>
<td>96 (0.02, 15)</td>
<td>51 (0.06, 4)</td>
<td>2 (&lt;0.01, 27)</td>
<td>4 (&lt;0.01, 25)</td>
<td>39 (0.05, 7)</td>
</tr>
<tr>
<td>Etheostoma serraforum, sawcheek darter (ser)</td>
<td>87 (0.02, 16)</td>
<td>0</td>
<td>31 (0.01, 17)</td>
<td>6 (&lt;0.01, 23)</td>
<td>50 (0.07, 4)</td>
</tr>
<tr>
<td>Notrogenes crysoleucus, golden shiner (cry)</td>
<td>87 (0.02, 17)</td>
<td>15 (0.02, 10)</td>
<td>36 (0.02, 16)</td>
<td>33 (0.02, 11)</td>
<td>3 (&lt;0.01, 24)</td>
</tr>
<tr>
<td>Lepomis gulosus, warmouth (gul)</td>
<td>77 (0.01, 18)</td>
<td>2 (&lt;0.01, 19)</td>
<td>45 (0.02, 15)</td>
<td>27 (0.02, 13)</td>
<td>3 (&lt;0.01, 25)</td>
</tr>
<tr>
<td>Centrarchus macropterus, flier (mac)</td>
<td>74 (0.01, 19)</td>
<td>0</td>
<td>57 (0.02, 13)</td>
<td>11 (0.01, 18)</td>
<td>6 (0.01, 19)</td>
</tr>
</tbody>
</table>
Positive Interactions

Importance of winter rearing habitat
- Bustard & Narver 1975
- Chisholm et al 1987
- Cunjak 1996
- Jakober et al 1998
- Lindstrom & Hubert 2004
- Miller & Sadro 2003
- Nickelson et al 1992ab

CHISHOLM ET AL.

Lindstrom & Hubert 2004
Positive Interactions

Importance of winter rearing habitat
Positive Interactions

Other positive interactions:
- Increased invertebrate productivity
- Changes in community structure

Table 1. Perceived positive and negative effects of beaver activity on fish as identified by Kemp et al. (2012).

<table>
<thead>
<tr>
<th>Positive effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heightened habitat availability–complexity</td>
</tr>
<tr>
<td>Improved overwintering habitat</td>
</tr>
<tr>
<td>Enhanced rearing habitat</td>
</tr>
<tr>
<td>Provision of cover</td>
</tr>
<tr>
<td>Enriched diversity–species richness</td>
</tr>
<tr>
<td>Enriched abundance–productivity</td>
</tr>
<tr>
<td>• Provision of habitat under low flows</td>
</tr>
<tr>
<td>• Provision of low flow refuge</td>
</tr>
<tr>
<td>• Establishment of temperature refuge</td>
</tr>
<tr>
<td>• Boosted water quality</td>
</tr>
<tr>
<td>• Sediment trap</td>
</tr>
<tr>
<td>Enriched invertebrate productivity</td>
</tr>
<tr>
<td>Increased growth rates – fish condition</td>
</tr>
<tr>
<td>Establishment of fishing areas</td>
</tr>
</tbody>
</table>

Needham et al. 2021

Malison et al. 2014
Negative Interactions: Dams as barriers

Table 1. Comparison of beaver and run-of-the river human dams as an example of human-built replacement of one type of preexisting discontinuity along the river corridor.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Run-of-the-river human dam</th>
<th>Intact beaver dam</th>
</tr>
</thead>
<tbody>
<tr>
<td>Permeability</td>
<td>Impermeable</td>
<td>Leaky or somewhat permeable</td>
</tr>
<tr>
<td>Structure longevity</td>
<td>100 to 1000 years</td>
<td>10 to 100 years</td>
</tr>
<tr>
<td>Number of spillways or downstream channels</td>
<td>One</td>
<td>One or more</td>
</tr>
<tr>
<td>Crest geometry</td>
<td>Simple, usually linear</td>
<td>Complex, irregular</td>
</tr>
<tr>
<td>Hydraulic cross section at the spillway crest</td>
<td>Uniformly fast and shallow</td>
<td>Variable, with concentrations of faster and deeper water, often with multiple spillways; flow may be entirely through the dam</td>
</tr>
<tr>
<td>Low-flow water passage</td>
<td>Little to no release</td>
<td>Water continues to leak through dam</td>
</tr>
<tr>
<td>Upstream water level variability</td>
<td>Little to none</td>
<td>Variable over the year</td>
</tr>
<tr>
<td>Upstream littoral zone</td>
<td>Narrow</td>
<td>Wide</td>
</tr>
</tbody>
</table>

Note: Run-of-the-river dams are the most common existing and removed dam type in the United States (Poff and Hart 2002). Source: Müller-Schwarze and Sun 2003, Burchsted et al. 2009.
Negative Interactions: Dams as barriers

Sometimes dams block fish migration:
- Kemp et al., 2012
  - Many examples are anecdotal/speculative
Negative Interactions: Dams as barriers

Not impassable:
- Taylor et al 2010 – spawning salmon passage varied with rainfall
- Bouwes et al 2016 – no impact of BDAs on migration of juvenile steelhead
- Bylak & Kukula 2018 – no tagging, community differences, trout present above and below dams
- Bylak et al 2014 – all dams passable, varied with flow
- Lokteff et al 2013 – PIT tags, Utah, both juvenile & adult salmonids over multiple dams
- Malison & Halley 2020 – reduced frequency of movement of juvenile trout and salmon, trout and salmon present upstream
- Parker & Roenning 2007 – not a problem for spawning salmonids in Norway
- Cutting et al 2018 – 88% average passage probability for arctic grayling, correlated with hydrological conditions
- Virbickas et al 2015 – RFID tagging, Atlantic salmon passed some dams, no redds past furthest upstream dams
- Schlosser & Kallemeyn 2000 – seasonal movement altered
- Puttock et al 2017 – overflow, through-flow, underflow allowing passage
Negative Interactions: Dams as barriers

Not impassable:

- Malison et al 2015 – 1000’s of juvenile salmonid reared in ponds and many left prior to winter, others moved during summer
- Wathen et al 2018 – beaver complexes provided important rearing habitat for steelhead
- Mitchell & Cunjak 2007 – species above & below dams, but limited spawning habitat
Negative Interactions: Dams as barriers

Not impassable:
- Pollock et al 2022 – movement & hydrologic conditions, up to 91% of coho moved upstream past BDAs
Negative Interactions: Dams as barriers

Summary:
• Dams were not impassable but movement was often modified

More research:
• Both adult and juvenile fish
• More species (with varying life histories)
• Using telemetry and PIT-arrays
• Greater temporal and spatial scales
  • Seasonality
  • Multiple dams
• Longer-term studies of population dynamics
• Linked with hydrological measures and measurements of when dams are overtopped or bypassed
Negative Interactions: Hypoxia, Sedimentation

Winter fish kills:
- Fox & Keast 1990 – pumpkinseed populations

Low oxygen:
- Snodgrass & Meffe 1998
- Burchsted et al 2010 (based on Snodgrass & Meffe 1998)
- But other studies – no decline, site dependent
- Bylak & Kukla 2018 – highest DO in a beaver pond

Inundated spawning sites:
- Knudsen 1962
- Swanston 1991
- Halley & Lamberg 2001 - Norway
- Muller-Schwarze & Sun 2010 – trout, California
- Taylor et al. 2010 – Nova Scotia
Do Eurasian beavers negatively impact Atlantic salmon and sea trout populations in Norway?
Study Area – Stjørdalselva and Orkla

Distance from fjord
- Pair 1: 11.8-12.3 km
- Pair 2: 17.7-20.3 km

- 7.4-13.7 km
Study Design

Movement

3 beaver influenced tributaries

3 beaver free tributaries

Above Pond

Pond

Below Pond

Main River

Upstream

Downstream
Fish sampling
Figure 6  (a) Mean (±1SE) overall movement rates and (b) mean (±1SE) movement rates for each portion of the study reach.
Figure 6 (a) Mean (±1SE) overall movement rates and (b) mean (±1SE) movement rates for each portion of the study reach.
Summary

- **Movement:**
  - Juvenile salmonids moved through the ponds
  - Dams did not block movement
  - But repeated movements past dams were reduced and movement patterns were altered
  - Juvenile salmonids were present below and above the beaver ponds

- **Habitat use:**
  - Juvenile salmon were not captured in the ponds...
Detailed Movement Study

Above Pond

Pond

Below Pond

Orkla Beaver

A1 A2 A3 A4

A1 A2 A3 A4

A1 A2 A3 A4

Orkla Beaver

Ongoing...

Stj. North Beaver
Potential negative impact of beavers in Norway?

- Movement not blocked
- Very few dams
- Dams flood and break often
- Trout and salmon present below and above beaver dams
  - A lot of beaver activity where salmon can’t access already

- Very low compared to human land use changes
Importance of Scale, Habitat Connectivity and Stream Size
A case study from Alaska

Hauer et al. 2016

River Floodplains
Beavers in the Kwethluk River Floodplain

Salmonids per m²

<table>
<thead>
<tr>
<th>Location</th>
<th>Salmonids per m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main shoreline</td>
<td>0.5</td>
</tr>
<tr>
<td>Spring brooks</td>
<td>2.0</td>
</tr>
</tbody>
</table>
Production

- Growth & Condition
  - Diet
  - Food availability
  - Habitat Type
    - Beavers

- Population Size/Densities
  - Survival
  - Movement
Floodplain Modification By Beavers
Floodplain Modification By Beavers
Floodplain Modification By Beavers
Floodplain Modification By Beavers

- Main Channel Connected
- Beaver Free Springbrooks
- Beaver Springbrooks
- Early successional
- Mid successional
- Late successional
Beavers (Castor canadensis) influence habitat for juvenile salmon in a large Alaskan river floodplain

RACHEL L. MALISON, MARK S. LORANG, DIANE C. WHITED AND JACK A. STANFORD
Flathead Lake Biological Station, The University of Montana, Polson, MT, U.S.A.

- 87.5% of the off-channel habitat was dammed
- Movement between early-successional beaver ponds and spring brooks was facilitated by flooding

Survival and densities were highest in spring brooks
Biomass produced highest from early-successional ponds (habitat size and growth)
Do beaver dams reduce habitat connectivity and salmon productivity in expansive river floodplains?

Rachel L. Malison\textsuperscript{1,4}, Kirill V. Kuzishchin\textsuperscript{1,5} and Jack A. Stanford\textsuperscript{1}

\textsuperscript{1}Flathead Lake Biological Station, University of Montana, Polson, MT, United States
\textsuperscript{2}Ichthyology Department, Moscow State University, Moscow, Russian Federation
\textsuperscript{3}Current affiliation: Norwegian Institute for Nature Research, Trondheim, Norway
Scale, Connectivity
Stream Size

What is the watershed or catchment scale effect on the fish population?
Temporal variability
Dams regularly overtop or there are bypass channels (Collen & Gibson 2001)
How does the life history of the fish species align with high flows?

Fig. 4. Changes, within a few months, in ‘dam 4’ on the Cheval. In summer (23/08/2009), the dam was nearly watertight; on 17/11/2009 there was overflow with beginning breaching; gapflow (arrow) on 26/03/2010. On 04/08/2010 the gap was again fully closed.
Cumulative and systems level effects
Human altered landscapes
Conclusions
Conclusions

- Beavers and salmon have co-evolved
- Systems are dynamic, connectivity exists
- Positive interactions of beavers and fish generally outweigh the negative
- System characteristics and context matters
- It’s complicated and hard to generalize
- Each reintroduction should be carefully considered at the systems level
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