Meta-Analysis of Beaver Dam Impacts on Pacific Salmon Reveals Variable Outcomes Across Species–Life Stage Combinations

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Abstract

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Beaver-based habitats (BBH) in streams are rapidly growing in number as beaver populations expand and are an increasingly common tool used in riverine restoration projects aiming to improve degraded freshwater Pacific salmonid habitat. Though the prevalence of BBH has increased through time, there has yet to be an investigation of how BBH affects Pacific salmonids generally. This study used both quantitative and qualitative data from 225 published reports to quantify unique species-life stage combinations of Pacific salmonid responses to BBH compared to reference sites without BBH via meta-analysis techniques. Our results revealed novel patterns of Pacific salmonid species-life stage specific responses to BBH, but in some cases these patterns were different between the quantitative and qualitative results. The egg and juvenile life stages of most Pacific salmonid species exhibit a positive response to BBH, while resident adult trout and spawner life stages had a more complex, mixed response to BBH across species. We discuss the implications of these results for future applications of BBH in restoration and enhancement, and identify opportunities to further untangle the complex relationship between BBH and Pacific salmonids.

Acknowledgements

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Table of Contents

Introduction

Population declines in Pacific salmon originally became a noted concern by the U.S. government in 1875 when the first appointed U.S. Commissioner of Fisheries recognized overfishing, damming, and habitat degradation as threats to these fish (Lichatowich, 2001). Many population level declines are attributed to the loss and degradation of freshwater habitat (Nehlsen et al., 1991). All salmonid species native to the Pacific Northwest belong to the *Oncorhynchus* genus: the five salmon species Chinook (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) and the trout species cutthroat trout (*O. clarkii*) and rainbow trout/steelhead (*O. mykiss*) (Smith and Stearley, 1989; Ford, 2022). With the exception of pink salmon, all species of Pacific salmonids have faced such substantial decline to the point that each species has evolutionary significant populations (ESUs) in the contiguous United States that are listed under the Endangered Species Act (Nehlsen et al., 1991). Considerable effort and funding are focused on recovering these ESU's with the hope of 'de-listing' them, despite incomplete understanding of the factors that led to their declines.

Beavers *(Castor canadensis)* in the Pacific Northwest have also experienced low populations relative to pre-European settlement, with fur trapping leading to their near extirpation by the late 1800s, coinciding with the decline of the region's salmonids (Johnson and Chance, 1974). Since the early 1900s, beaver populations have been steadily increasing throughout North America due to reduced trapping pressure and fewer predators (Naiman et al., 1988). As beaver populations increased, so has the frequency of conflict with landowners via impacts on infrastructure. Many of the wetlands that beavers created and maintained prior to European settlement, that were utilized by salmon, trout, and other diverse organisims, were drained for farming and establishment of permanent infrastructure for expanding urbanization (Müller-Schwarze, 2011).

In the past few decades, the recognition of beavers as a keystone species that has a disproportionate influence on target stream and salmonid restoration and conservation measures has been well documented in the published literature (Lapointe, 2012; Larsen et al., 2021; Pollock et al., 2003). This recognition has been translated to beaver relocation and beaver dam structural and functional mimicry by water managers as tools with ever-growing use in stream restoration projects and urban wildlife management (Wathen et al., 2019; Bailey et al., 2018). Natural beaver dams and beaver dam mimicry by people are collectively referred to as beaver-based habitats (BBH) in this study. The number of BBH restoration projects has been exponentially increasing the past three decades, particularly in the western U.S. and Canada. A commonly cited goal of these projects is to recover threatened salmonid populations by improving the quality of freshwater habitat. Prior to 2000, only five such projects were reported, while from 2011-2016, 58 BBH restoration projects were reported (Pilliod et al., 2018). Of these BBH restoration projects, most of them relocated beavers to stream reaches identified as in need of restoration, often with the goal of improving salmonid habitat conditions, as is the case with the Tulalip Beaver Project in Washington State (Alves et al., 2019).

In locations where severely degraded streams cannot yet support beavers or do not allow beaver relocation, restoration practitioners employ beaver dam analogs (BDAs), human-made structures that aim to mimic the structure and function of actual beaver dams (Pollock et al., 2023). Proponents of salmonid restoration projects using BBH argue that the benefits for salmonids are multifaceted: beaver dams slow down water to provide refugia during high flows, retain water in streams during dry months, and increase total floodplain area adjacent to streams (Pollock et al., 2003). Skeptics argue that beavers do more harm than good for salmonids by creating migration barriers, warming water, and decreasing dissolved oxygen levels (Kemp et al., 2012), or are simply ineffective in changing salmon habitat (Petro et al., 2015).

Despite the growing and current widespread use of BBH in salmonid stream habitat restoration projects, the overall effect of beaver dam structures on salmonids remains a contentious topic, with no clear consensus of the impact that these restoration projects have on targeted fish populations over time (Pilliod et al., 2018). Benefits from BBH, including both actual beaver dams and BDAs, for Pacific salmonids are often assumed using standard proxy parameters for salmonids such as dissolved oxygen (DO) and temperature thresholds rather than direct measurements of fish responses. These indirect measures do not always reflect actual fish response to beaver dams, since DO and temperature vary spatiotemporally in micro-habitats around beaver ponds (Stevenson et al., 2022). Pacific salmonid ecological needs also spatiotemporally shift during their lifetime: within each life stage, and the seasonality and duration of freshwater use varies greatly between species (summarized in Table 1).

Since salmonids and beavers have coexisted for millions of years, it is reasonable to assume that beaver dams have been influencing these fishes over ecologically and evolutionarily relevant time scales (Montgomery, 2000; Xenikoudakis et al., 2020). This overlap implies strong coevolution of Pacific salmonids and beavers, since beavers generate much of the habitat complexity of freshwater streams that Pacific salmonids depend upon (Bruner et al., 1989; Malison et al., 2014). Stream habitat complexity has allowed Pacific salmonids to develop diverse life history pathways, which better enables species-wide persistence through time due to highly variable hydrologic and climatic regimes these fishes face (Moore et al., 2010; Schindler et al., 2015). The last two centuries of industrialization have interrupted this relationship, with waterways and hydrologic regimes extensively altered from their historic states (Wohl, 2005).

With exacerbated warming at Earth's poles, beaver populations are also expanding into previously unoccupied regions in the arctic, which will undoubtedly induce bio-physical changes to the stream systems there that will affect the fish species community compositions currently found in these regions (Tape et al., 2018).

Species	Life Stage			
	Egg/Alevin	Juvenile	Adult	Spawner
Pink	Late Winter (8-16 weeks)	Early Spring , Estuary/Ocean	Early Spring, Ocean (2 years)	Late Summer – Early Fall
Chum	Late Winter- Early Spring (8-16 weeks)	Late Winter- Spring, Estuary/Ocean	Spring, Ocean (3-5 years)	Fall-Winter (Summer-Fall in Yukon and Amur Rivers)
Chinook	Whole Year (12 weeks)	Whole Year, increasing freshwater residency as you move North (<1 month - >1 year)	Whole year, Ocean (1-6 years)	Whole Year
Coho	Winter (6-7 weeks)	Winter, Streams (1-3 years)	Spring, Estuary (<1-2 years)	Summer-Winter
Sockeye/Kokanee	Late Winter – Spring (8-20 weeks)	Summer, Lakes/Streams(1-3 Years)	Sockeye - Summer, Ocean (1-3 years) Kokanee -Summer, Lake (1-3 years)	Early Summer – Late Fall
Rainbow Trout / Steelhead	Spring - Early Summer (4-6 weeks)	Summer, Lakes/Streams (1-4 years)	Rainbow Trout: Summer, Freshwater (1-5 years) Steelhead: Summer, Ocean/Freshwater (1-5 years)	Late Winter-Spring (summer run steelhead spend another year in freshwater to mature, winter run do not)
Freshwater Cutthroat Trout / Coastal Cutthroat	Freshwater: Spring-Fall Coastal: Spring (6-7 weeks)	Freshwater: Late Spring – Late Fall, Lakes/Streams (2-5 years) Coastal: Late Spring - Summer , Streams/Estuary (2-6 years)	Freshwater: (1-10 years) Coastal (1-8 years): Summer - Estuary/Ocean Winter – Lakes/Streams	Freshwater: Spring - Summer Coastal: Winter - Early Spring

Table 1. Life cycle seasonal timing, duration, and habitat types for each species of Pacific salmonid. The species are ordered roughly from those that use freshwater the least (only for egg incubation, out-migrating juveniles, and adults returning to spawn, called spawners) to those that use freshwater ecosystems over the course of their full lifespans (resident rainbow and cutthroat trout that remain in freshwater systems their entire lives). The potential for beaver dams to influence Pacific salmonid species is expected to roughly follow this order as well, since beaver dams primarily exist in freshwater systems, with some instances of beaver dams in estuarine environments (Hood, 2012). Habitat use variability within species' ESUs stocks were not part of this high-level summary, and why such broad ranges exist for some species like Chinook seen in this table. *Freshwater cutthroat trout is now considered a clade of three separate species (Ford, 2022a)

To synthesize our understanding of the net impact of BBH on Pacific salmonids in today's anthropogenically altered and climatically impacted hydrologic systems, we performed a meta-analysis of studies that measured or observed direct responses of *Oncorhynchus* spp. to BBH. Previous meta-analyses have investigated the impact of beaver activity on many other genera of stream fishes in addition to *Oncorhynchus* spp., but these studies mostly used proxy parameters (temperature, dissolved oxygen, etc.) and generalized beaver impacts across the entire lifespan of salmonid species (Collen et al., 2000; Kemp et al., 2012). Due to the unique habitat requirements of salmonids within the *Oncorhynchus* genus, and within each species' life stage, we saw a need for a comprehensive investigation of the direct effects of BBH on each unique Pacific salmonid species-life stage combination (Hoar, 1958).

Based on the unique ecological timing and habitat types each species' life stages are specialized in (as seen in Table 1), we developed the following hypotheses:

1) We hypothesized that BBH would have the greatest positive direct effect on Pacific salmonid species with the greatest freshwater residence time. We anticipated this effect for species with freshwater-focused life history strategies (LHS) because the more time salmonids reside in freshwater streams, the more BBH impacts can accumulate.

2) We expected that BBH would have a net negative effect on eggs of all Pacific salmonid species due to siltation and reduced dissolved oxygen levels.

3) We expected that BBH would have a net positive effect on the individual growth rates and densities of juvenile stream-rearing Pacific salmonid species. A positive response was anticipated because BBH provides juveniles refugia from extreme flows and predators, as well as increases available rearing habitat area (Pollock et al., 2011).

4) We expected that BBH would have a positive effect on freshwater-resident adult rainbow trout and cutthroat trout by increasing survivorship during low flow summer periods.

5) We expected that BBH would have a net negative effect on returning spawners of all Pacific salmonid species, with this effect greatest in species like pink and chum salmon with weaker jumping capabilities (Powers et al., 1985). We anticipated that this negative effect would be driven mostly driven by dam height and the downstream impact on streambed morphology blocking spawner access to upstream spawning sites.

Methods

Selection of Studies

We performed a meta-analysis according to the methods outlined by Koricheva et al. (2013), limiting our scope to *Oncorhynchus* spp. (Pacific salmonids) and *Castor canadensis* (North American Beaver). The lead author searched Google Scholar, Web of Science, and University of Washington Libraries databases through the software program *Publish or Perish* using the search string: ("beaver*" OR "Castor canadensis" AND "Oncorhynchus" OR "salmon" AND "dam*"). The software program *Publish or Perish* was used to aggregate the resulting search into a database for screening (Harzing, 2007). No year limitation was applied and all study formats (articles, books, reports, etc.) were included in the initial search conducted, including pre-released publications ahead of print with publication dates in 2024. All geographic locations where Pacific salmon and North American beaver co-occur were included in the review, with the majority coming from North America (Figure 1).

The initial search yielded 5,707 results. Since rainbow and cutthroat trout belonged to the genus *Salmo* prior to 1989 (Smith and Stearley, 1989), an additional search was conducted to include publications prior to 1989 mentioning rainbow or cutthroat trout. This second search was conducted using the same method as the first search except for limiting year to 1990 or prior, and using the keywords: “beaver*” OR “Castor canadensis” AND "rainbow trout" OR "cutthroat trout" AND “dam*”. This search was compared against the initial search results to eliminate duplicates and ultimately resulted in an additional 819 publications. For simplicity, and because the cutthroat trout clade versus species distinction only recently happened after the aggregation of relevant studies for this meta-analysis, the cutthroat trout clade will be labeled as a singular species in this paper (Page et al., 2023). We also pooled steelhead with rainbow trout as one species, and pooled kokanee with the sockeye salmon species grouping. To aggregate any additional relevant publications, we used “snowballing”, which involved adding publications that were cited in the initial publication database generated that were missing and seemed likely to be relevant. This process added an additional 17 publications to the initial database total, resulting in 6,543 total publications to screen. The lead author did an initial high-level screening of the aggregated publications’ text by searching for both “beaver” and “salmon” or “trout” to eliminate publications that were not directly assessing beaver-salmonid interactions. This first screening narrowed the number of studies down to 2,531. A second in-depth screening further excluded any studies irrelevant for use in this analysis, and were deemed irrelevant for the following reasons: the study was about BBH effects on species other than Pacific salmonids, the study involved only speculative or modeled responses of salmonids to beavers, the study only referenced reported beaver-salmonid relationships of studies already included in our analysis, the study measured proxy variables instead of direct salmon response variables, the study assessed salmonid responses to BBH without a reference or treatment site, the study excluded BBH from their measurements, or the study was a meta-analysis.

The 225 publications that remained were sorted as either quantitative or qualitative studies based on the type of data they reported. Quantitative studies reported a numerical mean salmon response for beaver and reference sites. Qualitative studies only reported observed, but not quantitatively measured, evidence of a difference between beaver and reference sites. There were 88 quantitative studies with 227 unique measured effects. Numeric data from the quantitative studies were simplified to fit the qualitative observational response outcomes so they could also be included in our qualitative effects review. Given the addition of the quantitative responses in the qualitative study database as well, the final number of qualitative studies included in our study is 225, with 500 unique salmon responses reported. A visual summary of the screening process is shown in Figure A1 in the appendix.

Extraction of Data

Qualitative studies included the type and direction of effect of beaver dams on *Oncorhynchus* spp. on at least one of the life stages. Possible directional effects included the following: positive, negative, mixed, or neutral. A positive effect meant that the beaver site resulted in a more favorable response from salmonids than the reference site, and a negative effect was the inverse relationship. A mixed response meant that both positive and negative effects were observed such that a directional effect could not be explicitly determined. A neutral response meant there was no difference in salmonid response observed between the beaver and reference site. The type of responses recorded from the studies included: abundance, biomass, density, growth, survival, movement, disease, egg oxygenation, population growth, and production. The qualitative database was organized into rows, with each row representing a unique combination of response type, salmonid species, and salmonid life stage. Additional study metrics recorded in each row included: study name, first author, publication year, latitude, longitude, ecoregion, and percent human impact. The ecoregion delineation used was from a WWF report delineating global ecoregions, and was identified for each study by searching the study's location on Esri ArcGIS Online (Olson et al., 2001). Percent human impact was defined as the estimated relative human influence for a given location, using metrics developed by Columbia University's Wildlife Conservation Society and Center for International Earth Science Information Network (WCS, and CIESIN, 2005)

For publications containing comparative quantitative data on direct salmonid responses between BBH and beaver-free reference sites, these paired data were extracted and recorded in the quantitative database. Each row of the quantitative database also represented a unique combination of response type, species, and life stage. The same study metrics as the qualitative database were extracted for the quantitative studies as well. Additional metrics recorded for the quantitative studies included: dam type, dam stage, response units, and the mean, variance, and number of sites for both the beaver and reference sites. Dam type refers to whether a study only had natural beaver dams in the treatment sites (beaver), only BDAs in the treatment sites (BDA), or if both natural beaver dams and BDAs were in the treatment sites (mixed). Two studies included in this analysis only used BDAs, a few studies involved mixed beaver dam structure types, but most studies had natural beaver dams as their treatment sites. The dam stage refers to the amount of time the beaver dam was recorded as persisting in the stream when the study's measured effects were recorded. Dam stage was categorized into the following options: early (less than two years), mid (two to five years), late (five years or more), all (each of the previous stages were observed or no stage was indicated in the study). The length of time for each grouping was determined from studies showing how, as beaver dams age, specific biogeochemical processes shift at certain temporal thresholds (Ecke et al., 2017; Meentemeyer et al., 1999; Murray et al., 2021). The mean and variance values were directly pulled from the study's tables or text when available. Otherwise, mean and variance from the study's supplemental raw data values were manually calculated, or extracted from figures using WebPlotDigitizer 4.8 (Rohatgi, 2024). Response units refer to the way in which the study measured their specific responses; for example, some studies measured growth as mean daily percent growth calculated over a repeated sampling period, and others as a single mean fork length where the measurements were taken once. When possible, response units were transformed to be the same units so that they were more easily comparable across studies, i.e., density was transformed to be fish/m^2.

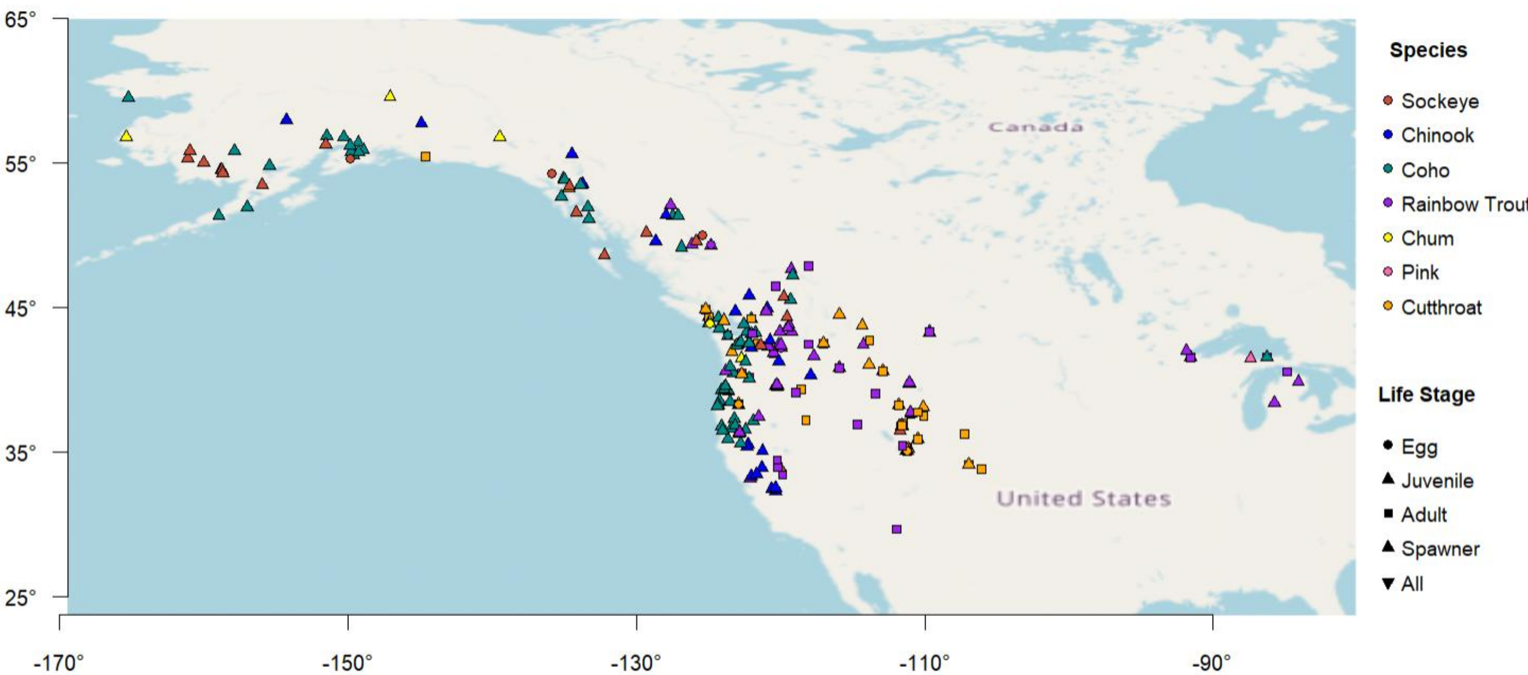

Figure 1: Map of the 216 study locations for the 225 studies included in analysis. This shows that the majority of studies are concentrated in Western North America. Species are shown by color and life stages by shape. The inland western sites are represented by juvenile and adult rainbow trout and cutthroat trout. A small number of studies came from the great lakes region where some Pacific salmonid species were introduced to, and now have established populations there.

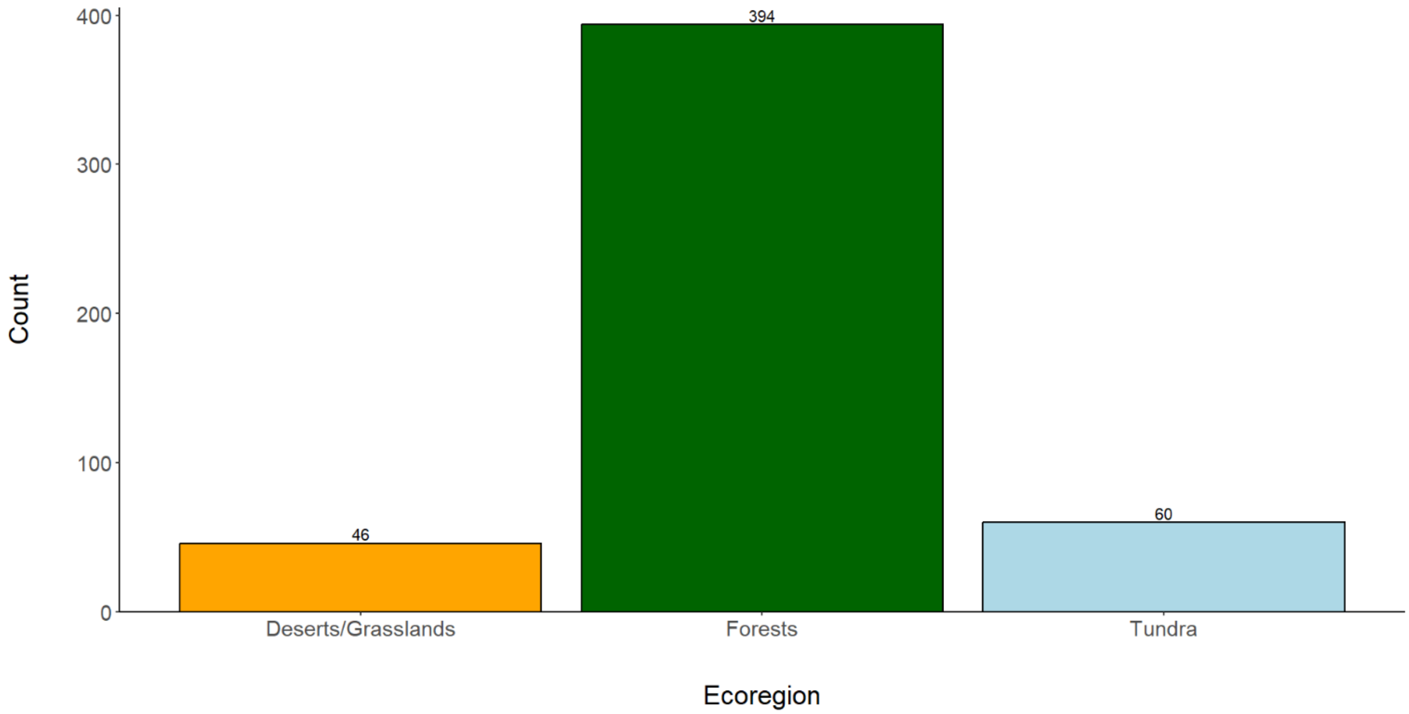

Figure 2: The number of WWF based ecoregion types represented from studies. Ecoregions are an aggregation of the following categories: the Desserts/Grasslands category includes ecoregions originally labeled as Desserts and Shrublands (23), Grasslands (22), or Mediterranean (1), and the Forests category includes ecoregions originally labeled as Boreal Forests (22), Coniferous Forests (327), Temperate Coniferous Forests (23), and Broadleaf Forests (22), and the tundra category was not changed.

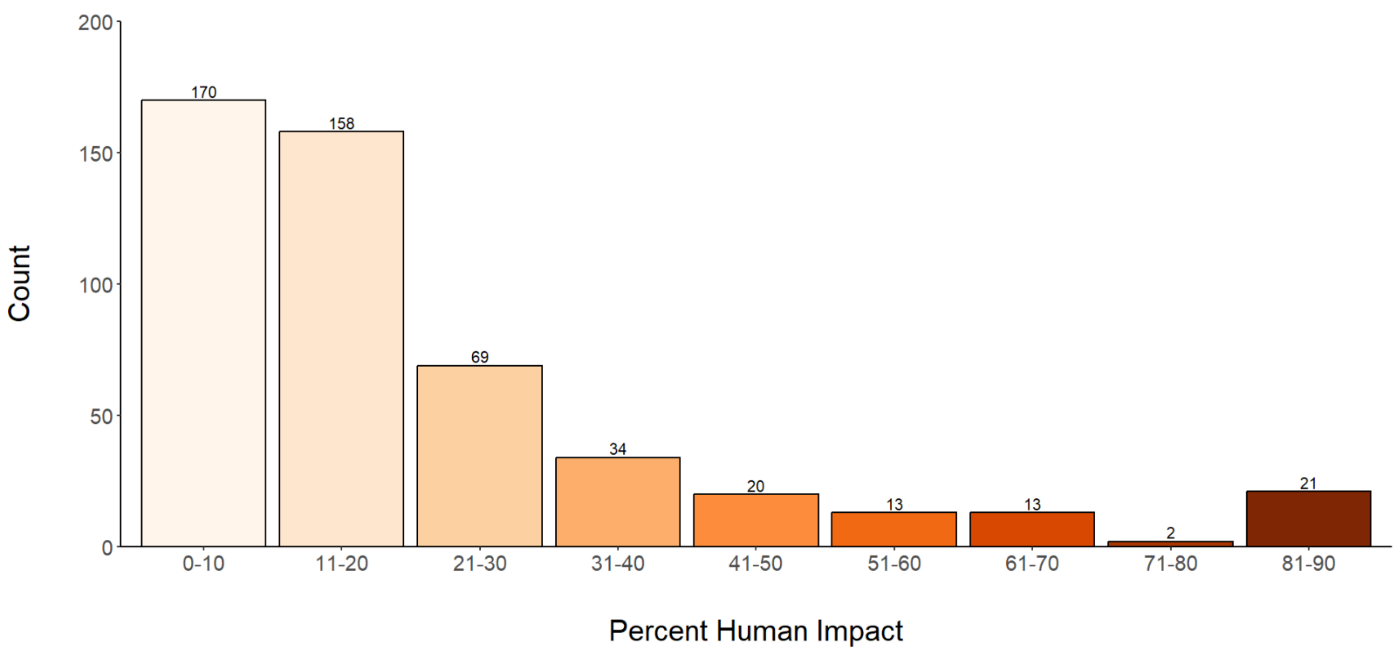

Figure 3: The human percent impact for each study and the number of studies for each impact level. Most studies took place in areas with very low human impact levels.

Statistical Analysis

We first compared differences between mean salmonid responses at beaver and reference sites to assess the average direction and magnitude of effect outcomes for each response type. The remaining quantitative analyses were conducted in *RStudio* using the *metafor* package for the 227 quantitative data points collected from 88 studies (Viechtbauer, 2010). Since data collected from the quantitative studies have a wide range of response unit values, to standardize the wide range of study variance intervals, the log ratio of means (also known as response ratio, RR) was used to calculate effect sizes for our data points (Lajeunesse, 2011; Hedges, 1999).

The log ratio of mean effect size of BBH on Pacific salmonids versus reference sites can be described by the following formula:

$$\log{(RR)} = \log{(\frac{X_B}{X_C})}$$

where X_B is the mean value from a given study's salmon response data point taken at beaver sites, and X_C is the mean value from the same study's salmon response data point taken at the reference site.

Individual mixed-effects regression models were developed to assess the strength of evidence of the hypotheses described above, for life stage and species responses to BBH, with study as a random effect. We used two separate, individual models instead of a single, combined model due to an issue with many studies only reporting their means and not reporting variance (Table A1). Regression models need a variance parameter to be able to incorporate means into an overall net effect, so this meant that of our 227 quantitative data points collected for quantitative analysis, only 73 were able to be integrated into our regression models.

In the models, RR that had lower variances and larger sample sizes were given higher weight (Viechtbauer, 2010). We assessed whether our models fit the data well by visual inspection using Q-Q plots of residuals, and were able to confirm that model errors reasonably followed a normal distribution (Figures A2 and A3), with the life stage model exhibiting slightly more deviation from normal distribution than the species model. Publication bias testing was conducted to see if non-significant results were underrepresented in the literature using Egger's regression tests and visually inspected using a funnel plot (Koricheva et al., 2013). No biases were found for our quantitative datasets ($t_{71} = -0.433$, $p = 0.666$), and most studies exhibited high precision since the data points are clustered around the low standard error area at the top of the funnel plot (Figure A4).

The next phase of the analysis involved vote-counting for the qualitative data (Bushman and Wang, 2009). Possible qualitative net mean effects recorded for each study were: positive, negative, neutral, or mixed. The quantitative data were able to be fit into the qualitative database as well since their response ratios were able to be simplified into the qualitative mean effect classification system.

Results

Quantitative Results

The raw mean quantitative data showed a clear positive response for juvenile Pacific salmonids and freshwater resident adult trout to BBH that is supported by many studies, while the egg and spawner life stages show more mixed responses, with few studies that exist on these life stages' response to BBH (Figure 4). The most abundant types of responses measured are clearly growth, abundance, and density. The most abundant life stage studied is the juvenile life stage, with a strong number of adult life stage studies as well.

The life stage regression model analyzed the individual egg, juvenile, adult, and spawner life stage RRs, with their mean and variance RRs shown in Figure 5. Juvenile salmonid response was as predicted, as there was a significant and positive response found for juvenile salmonid response to the BBH sites (effect size = 1.37, n = 49, z = 4.92, P = <0.0001). Surprisingly, given the mostly positive observed raw mean effects seen in Figure 4, residential adult trout response in the regression model were found to be significantly negative (effect size = -1.79, n = 21, z = -5.20, P = <0.0001). Also contrasting the raw mean responses observed in Figure 4 was the egg regression model response, which showed a significant positive response (effect size = 1.80, n = 2, z = 2.16, P = 0.031). The spawner life stage also had a positive response, but it was not found to be statistically significant (effect size = 1.50, n = 1, z = 1.80, P = 0.072).

The species regression model analyzed the individual Chinook salmon, coho salmon, cutthroat trout, rainbow trout/Steelhead, and sockeye salmon species RRs (Figure 6). Chum salmon did not have sufficient quantitative data to be able to be used in the species meta-regression model since the quantitative studies on this species failed to report their studies' variance (Table A1).

There were no quantitative pink salmon data to include in the model either. Cutthroat trout expressed the most positive and significant response to BBH (effect size = 2.00, n = 17, $z = 5.43$, $P = <0.0001$). Interestingly the other trout species, Rainbow Trout/Steelhead, expressed the only statistically significant negative response to BBH (effect size = -1.58, n = 19, $z = -4.28$, $P = <0.0001$). Coho exhibited a positive response to BBH that approached statistical significance (effect size = 0.69, n = 24, $z = 1.68$, $P = 0.094$), while Chinook (effect size = 0.62, n = 7, $z = 1.21$, $P = 0.225$) and sockeye exhibited no clear response to BBH (effect size = 0.06, n = 6, $z = 0.10$, $P = 0.924$).

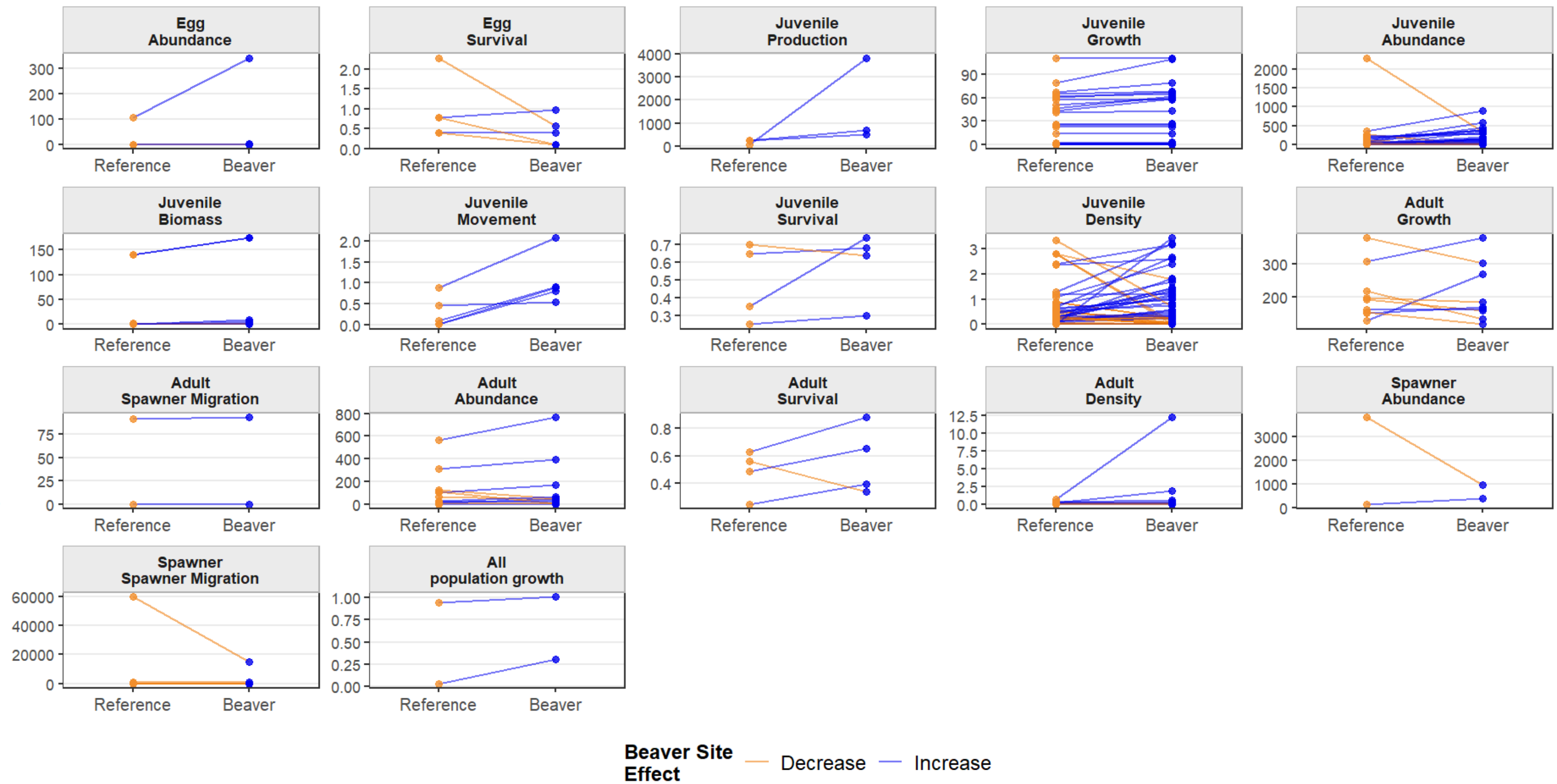

Figure 4. Point and line plots showing study-specific salmon direction and magnitude of response to beaver-free reference sites (reference) and BBH (Beaver) for life stage specific response types. The dots are raw means from the reference and beaver sites, and the lines show whether the beaver sites resulted in an increase (blue) or decrease (orange) of that given response, and the magnitude of the response is defined by the angle of the line connecting each study's paired mean points.

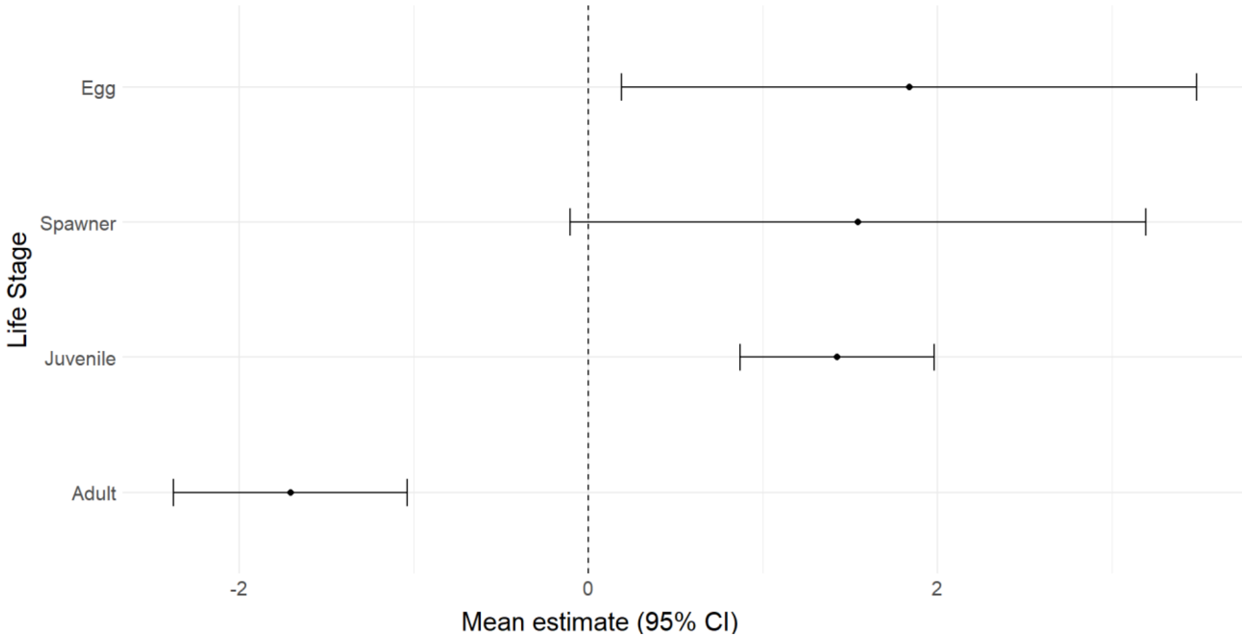

Figure 5: Mean and 95% CI outcomes for the life stage regression model. We used 95% confidence intervals (CIs) for this figure and Figure 6 to visually show the model outputs since they are sensitive to sample size and simplify interpretation (Zar, 1996). Mean effects below zero are considered a net negative response value, and above zero are a net positive response value. Variances that do not overlap with zero indicate the mean effects are also found to be statistically significant.

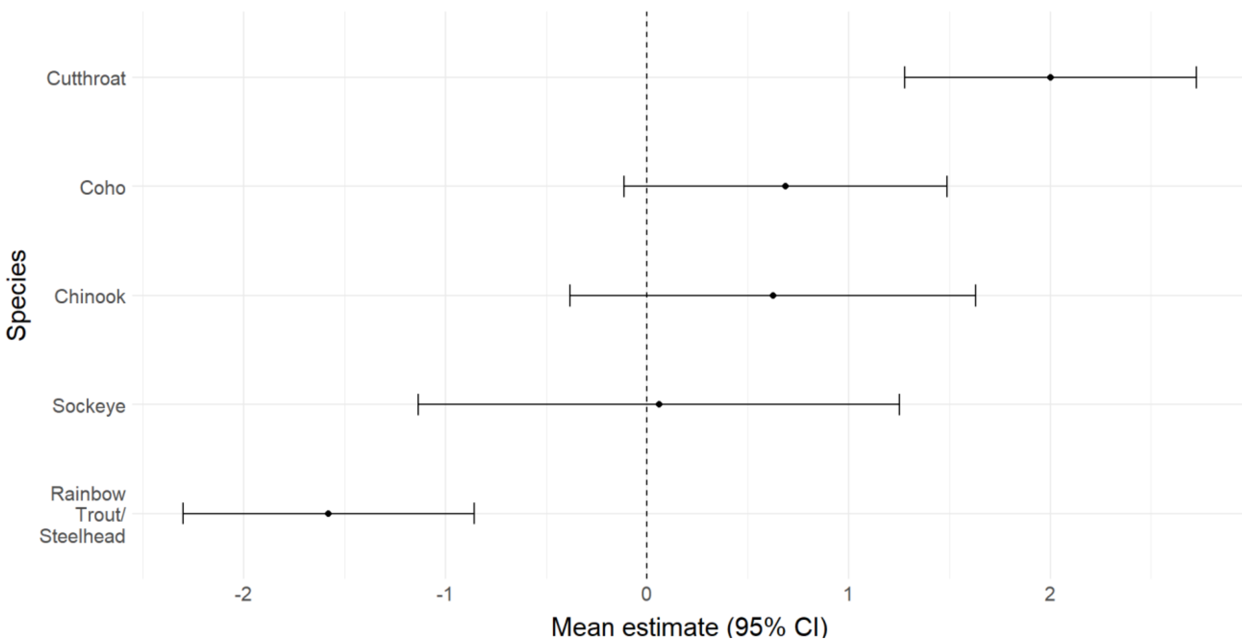

Figure 6: Mean and 95% CI outcomes for the species regression model. Mean effects below zero are considered a net negative response value, and above zero are a net positive response value. Variances that do not overlap with zero indicate the mean effects are also found to be statistically significant.

Qualitative Results

The qualitative results show a net positive response of Pacific salmonids to BBH across all response types and species-life stage combinations measured, but only marginally (Figure 6). The number of studies reporting a positive effect was only 21% higher than the number reporting a negative effect. A significant number of studies reported a neutral BBH response from salmonids as well, which was driven primarily by the spawner life stage. Only a fraction of studies found mixed salmonid responses to BBH.

The qualitative net effect of BBH on salmonids is even less clear when broken down by species and life stage, with new patterns emerging at this resolution (Figure 7). Over half of all the qualitative studies focused on juvenile salmonids, with spawners being the next most reported life stage. Less than 10 studies per species examined how BBH affects the egg life stage, indicating that this life stage's response to BBH is very data limited, both quantitatively and qualitatively. The species most represented from the literature (from highest to lowest) were: coho salmon, cutthroat trout, and Chinook salmon. There were very few studies on Pink and Chum salmon responses to BBH, and pink salmon in particular only had two studies with reported observed effects for the spawner life stage.

Our quantitative results from the regression model for life stage specific responses showed that the egg and juvenile life stages of Pacific salmonids have a significant positive response, but resident adult trout have a significant negative response. The qualitative data contrasted with the resident adult quantitative model mean effect as well as the rainbow trout/steelhead model mean effect, indicating that there were key qualitative data points for the adult rainbow trout/steelhead species-life stage combination that were unable to be included in the quantitative models.

A few key trends from the qualitative results are apparent, and mostly consistent with the quantitative results as well. Juvenile coho salmon show an overwhelmingly positive relationship with BBH. Juvenile cutthroat trout and sockeye salmon show a net positive relationship as well. Juvenile rainbow trout exhibited a mostly positive response to BBH too, but Chinook salmon had the most complex response to BBH, showing both positive and negative responses for the juvenile life stage. The few studies for juvenile chum salmon showed that they have a mostly negative response to BBH. Adult cutthroat trout had an overwhelmingly net positive response to BBH, while rainbow trout adults showed a far more complex, mixed mean response. All species exhibited a net negative or neutral response to BBH for the spawner life stage. Cutthroat trout spawners by far had the highest percentage of positive responses to BBH (50%), but this effect was still well below the 60% threshold set in Table 2 to indicate a directional response. The few egg life stage studies we were able to find showed that coho and sockeye salmon eggs have a net positive relationship with BBH, but the trout species egg life stage responses showed a more complex relationship.

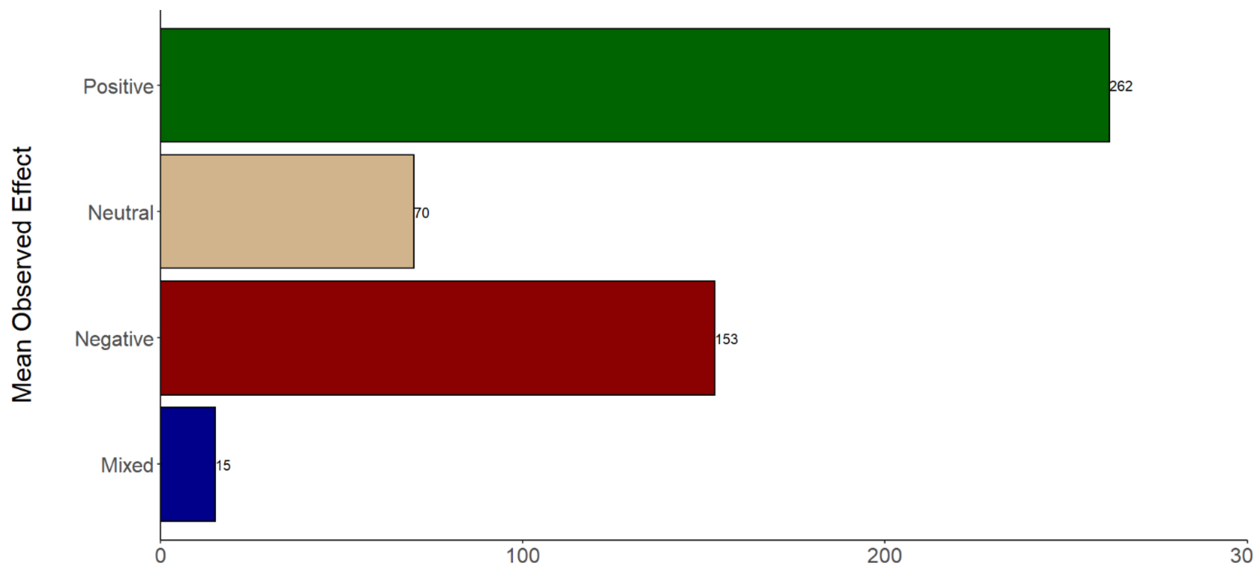

Figure 7: The number of directional effect outcomes from the aggregated qualitative study data points.

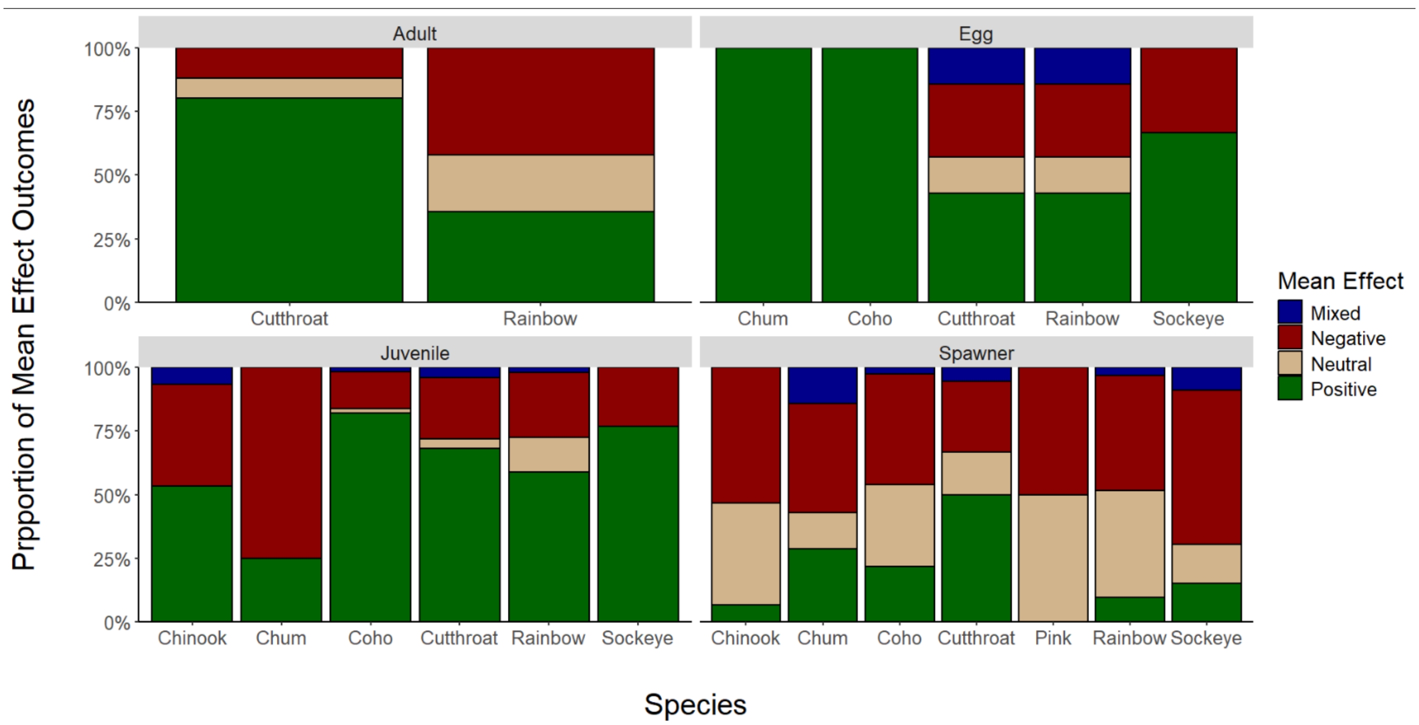

Figure 8: The proportion of each type of mean effect outcome per species-life stage combination. The spawner life stage was the only life stage to have data for every Pacific salmonid species.

Beaver Dam Impacts on Salmonids at Different Life Stages, and Degree of Support and Type of Sources Supporting Each Impact

Species	Life Stage			
	Egg/Alevin (25)	Juvenile (235)	Adult (82)	Spawner (158)
Pink (2)	siltation, flow refuge, abundance, survivorship, DO, temperature threshold[3]	migration Blockage[3]	NA	habitat area, flow refuge, survival, abundance[3], migration[1] (2)
Chum (12)	siltation, flow refuge, survivorship, DO, temperature threshold[3], abundance[1] (1)	prey, habitat, refuge, condition, survivorship, DO, temperature threshold[3], abundance[1] (4)	NA	habitat area, flow refuge, survival, abundance[3] (3), migration[1] (4)
Chinook (60)	siltation, flow refuge, abundance, survivorship, DO, temperature threshold[3]	prey, habitat, refuge, survivorship, population, DO, temperature threshold[2], condition (2) , abundance[1] (28)	NA	habitat area, survival, flow refuge[3], abundance (2), migration[1] (28)
Coho (153)	siltation, flow refuge, survivorship, DO, temperature threshold[3], abundance[1] (4)	prey, habitat, refuge, DO, temperature threshold[2], survivorship (3), population (5), movement (9), condition (13), abundance[1] (81)	NA	habitat area, survival, flow refuge[3], abundance (8), migration[1] (29)
Sockeye/Kokanee (52)	flow refuge, DO, temperature threshold[3], siltation (1), survivorship (3), abundance[1] (2)	prey, habitat, refuge, DO, survivorship, population, movement, temperature threshold[1], condition (5), abundance[1] (8)	NA	habitat area, flow refuge[3], survival (1), abundance (2), migration[1] (30)
Rainbow Trout / Steelhead (120)	siltation, flow refuge, DO, temperature threshold[3], survivorship (2), abundance[1] (5)	prey, habitat, refuge, DO, temperature threshold[1], survivorship (5), population (3), movement (3), condition (6), abundance[1] (34)	prey, habitat, refuge, DO, temperature threshold, survival, competition[2], population (3), movement (7), condition (3), abundance[1] (21)	habitat area, survival, flow refuge[3], abundance (4), migration[1] (27)
Freshwater Cutthroat/ Coastal Cutthroat Trout (101)	siltation, flow refuge, DO, temperature threshold[3], survivorship (2), abundance[1] (5)	prey, habitat, refuge, DO, temperature threshold[1], survivorship (4), population (2), movement (1), condition (1), abundance[1] (17)	prey, habitat, refuge, DO, temperature threshold, competition[2], survival (4), population (3), movement (8), condition (11), abundance[1] (25)	habitat area, survival, flow refuge[3], abundance (9), migration[1] (9)

Positive (>80%)
Positive (60-79%)
Negative (>80%)
Negative (60-79%)
Mixed (<60% for all)
No Literature
NA

[1]Primary Sources (research articles and reports)

[2]Secondary Sources (restoration guidelines and frameworks)

[3]Tertiary Sources (hypothesized impacts from this study's author knowledge of ecological systems)

*all impacts listed before superscript belong to that superscript category

Impact pathways for each species/life stage combination listed in each box, number in parentheses is the number of studies from the literature (primary sources) regarding that given impact for that specific species/life stage combination

Table 2: Net effect results from all qualitative study mean effects, separated into species and life stage combinations, and where gaps in the literature remain. The effects without the number of studies in parentheses next to them are BBH effects to those specific species life stages discussed in the literature or restoration reports, but was not a direct measured response data point we could numerically include in this study. These effects without data points to support them are therefore key gaps that remain in the knowledge base of BBH for those specific species' life stages.

Discussion

This meta-analysis tested whether Pacific salmonid species-life stage combinations vary in their response to BBH and revealed both quantitatively and qualitatively that there is significant variability among species-life stage combinations. Most of the quantitative model net effect outcomes had similar patterns as the qualitative data net effect summaries shown in Table 2. The exception to this was for the quantitative adult life stage model output and the rainbow trout model output, indicating that the qualitative data for adult rainbow trout/steelhead differs substantially from the quantitative data for this species-life stage combination. There were some salmonid species-life stage combinations that exhibited a clear net positive response to BBH based on both quantitative and qualitative net effect outcomes: coho salmon and cutthroat trout juvenile life stages consistently exhibited net positive responses. The other species-life stage combinations' net effects show high variability based on both the quantitative and qualitative net effect outputs. Few studies examined the relationship between pink salmon and BBH, but this species is not typically a focus of freshwater habitat restoration projects since they do not have any evolutionary specific units (ESUs) listed under the ESA (Ford, 2022). The variability in net effect outcomes between different species-life stage combinations examined by this study shows a need for BBH restoration projects to be specific in the target species and life stages they hope to benefit. Since some species and life stages do not have net positive responses to BBH, these types of habitats are not going to be beneficial for restoration projects targeting recovery of species and life stages found to have more complex relationships to BBH. For instance, the extensive BBH restoration projects have been found to increase the number of juvenile Coho in Puget Sound streams, but juvenile Chinook numbers in these streams have not rebounded.

Hypothesis 1

Our first hypothesis that beavers would have the strongest positive effect on Pacific salmon and trout with increasingly freshwater-focused LHS was only partially supported by this study's results. The range of freshwater-focused LHS between Pacific salmonid species is primarily driven by the juvenile life stage's degree of freshwater rearing. Rainbow trout/steelhead, cutthroat trout, and sockeye salmon species-level LHS freshwater use ranges the most since they all have possible resident freshwater LHS. Cutthroat trout had the strongest quantitative and qualitative positive net effects from BBH, and the subset of cutthroat trout populations with a freshwater-only LHS showed an even stronger net positive response to BBH. Juvenile coho salmon, which have a 1-1.5 year freshwater rearing period, showed a strong net positive response to BBH as well.

Resident freshwater rainbow trout were found to have a much more complex, mixed net effect from BBH though, which shows that increasing freshwater LHS does not necessarily mean there will also be an increasingly positive response to BBH. Chinook salmon, which exhibit a broad continuum between short-term (as little as less than a full month) and long-term (up to 2 years) stream-rearing juvenile LHS, consistently had a more complex net effect response to BBH (Quinn, 2018). This is likely due to the fact that Chinook salmon have one of the broadest spatio-temporal ranges of LHS across all life stages of the Pacific salmonids. Chinook salmon can be in freshwater environments any time of the year in the egg, juvenile, and spawner life stages; even the adult life stage has great variation in oceanic residency, distribution, and migration patterns as well (Bourret et al., 2016; Healey, 1991). Sockeye salmon responses tended to be fairly mixed as well, where their egg and juvenile life stages had a mostly qualitative net positive response to BBH, but their spawner life stage has a mostly negative qualitative response. Sockeye salmon also had the smallest directional quantitative net effect for the species model, indicating that the egg and juvenile positive responses were canceling out to zero with the negative effects for the spawner life stage. Sockeye salmonuse both rivers and lakes for freshwater rearing as juveniles, so this could explain some of the complexity with their response outcomes. Since they have a freshwater-only LHS as kokanee salmon, this is likely adding additional variability to the response outcomes for this species. Different levels of freshwater use between single species' populations were not part of our analyses because very few studies reported species-level LHS variation but is a likely driver of the mixed effects seen for the rainbow trout/steelhead, Chinook salmon, and sockeye salmon species.

As expected, few studies existed for the least freshwater dependent species, pink and chum salmon. Chum salmon qualitative responses for the juvenile and spawner life stages were mostly negative, and one egg life stage study skewed that species-life stage combination to be net positive. For the two studies that did exist for pink salmon's spawner life stage, one study reported a net negative effect, and the other was a neutral effect.

Hypothesis 2

We observed a positive net effect outcome for the egg life stage, which was unexpected given we predicted a negative net effect outcome. We had expected BBH-associated siltation and reduced DO would be primary response drivers for this life stage, and result in a net negative egg response to BBH. Instead we observed a mostly positive effect from both our quantitative and qualitative analyses. The fact that both the quantitative and qualitative species-level net effects for the egg life stage had the most consistent responses to BBH of all the life stages makes sense since there is the smallest variability in habitat needs for this life stage when comparing both intraspecific and interspecific differences found in Pacific salmonid species (Quinn, 2018). All salmonid eggs require an incubation period in streambed gravel with cool, well-oxygenated, stable water flow within the redd area. Small variation between species exists for incubation timeframes, and the size of gravel required for each species is strongly correlated with average species' spawner sizes (Kondolf et al., 1993).

The net positive response to BBH from the egg life stage was primarily driven by higher egg survivorship and abundance when compared to reference sites. These unexpected positive measured effects for the egg life stage from BBH indicate that siltation and reduced DO concerns, which are widely shared across the salmonid conservation community, are less of an issue than previously thought within the context of BBH. Though the positive response from salmonid eggs was not expected, some of the studies used in our meta-analysis study noted that their BBH sites prevented eggs from desiccating during extreme low flow events because of increased stream hyporheic flow exchange and instream water retention during drought years (Braithwaite et al., 2011; Munding-Becker et al., 2022; White et al., 2008).

Hypothesis 3

Our expectation that juvenile salmon would exhibit a mostly positive response to BBH was largely confirmed. Quantitatively this relationship was well supported, but the qualitative studies broken out to specific species-level responses showed mixed responses. The qualitative species-level juvenile life stage responses interestingly followed the same species-level trends of freshwater LHS ranges shown in Table 1, and differences in freshwater use between species as discussed previously for hypothesis 1. This pattern makes sense, since the juvenile life stage of Pacific salmonids greatly differs in their use of freshwater habitats based on different juvenile LHS among and within species-specific populations.

Juvenile coho, which qualitatively and quantitatively had the strongest positive net effect response to BBH, prefer slower velocity and deeper streambed morphology rearing habitats like the ponds BBH helps create and maintain (Bustard et al., 2011; Murphy et al., 2011). Sockeye salmon and cutthroat trout juveniles also had a qualitatively net positive response to BBH, but their response was not as strong as that of coho salmon juveniles. Juvenile cutthroat trout and sockeye salmon have a broader range of freshwater habitat rearing preferences than coho, so their positive response being less extreme than that of coho salmon juveniles is consistent with their ecology. Freshwater pools, riffles, and glides are all habitats utilized by juvenile cutthroat trout for rearing, but they prefer pool habitats that are often formed from BBH (Jakober et al., 1998). Juvenile cutthroat trout are not strong competitors with other salmonid species, and so are easily pushed out of or exist in low densities in their preferred stream habitats when other salmonid species are present (Glova, 1987). Sockeye salmon juveniles use stream floodplain side channels, lakes, and estuaries as primary rearing habitat, and so BBH can be beneficial to stream-type rearing juvenile sockeye salmon (Tappenbeck et al., 2008). Juvenile Chinook salmon and rainbow trout/steelhead had qualitatively mixed net effect responses to BBH. Chinook salmon have a wide range LHS for juvenile rearing that is likely a large contributing factor to the mixed effect response outcome for BBH (Bourret et al., 2016). Rainbow trout/steelhead juveniles tend to show a preference for rearing in stream glides as juveniles but are generalist than have been found to successfully rear in BBH as well (Bouwes et al., 2016; Hegna et al., 2013). The negative response from juvenile chum salmon was expected given they do not utilize BBH for juvenile rearing. Chum juvenile salmon rear at most a few weeks in their natal freshwater streams, but the majority of their juvenile rearing is in estuarine environments (Quinn, 2018). Even in rare cases where BBH exist in estuary environments, chum salmon prefer other areas for rearing (Hood, 2012). No data were available for juvenile pink salmon responses to BBH, but either a neutral or negative effect from migratory blockage effects from BBH would be expected since they do not spend any time rearing in freshwater habitats.

The primary response types driving the positive juvenile responses were increased density, abundance, and growth of fish in BBH sites versus reference sites. This strongly indicates that BBH improves juvenile salmonid rearing conditions and increases the amount of rearing habitat available for stream rearing juvenile salmonids.

Hypothesis 4

Adult rainbow trout/steelhead did not show a net positive response to BBH, while cutthroat trout did. Interestingly, both adult rainbow trout/steelhead and cutthroat trout stream-rearing adult LHS prefer deep pools formed by woody debris (Hegna et al., 2013; Young, 1996). Since both trout exhibit a wide range of LHS as adults, it is likely the existing studies on these species included in this analysis were biased in the LHS represented of each trout species. Based on the recorded responses, there were likely more stream-type adult cutthroat trout studies than other cutthroat trout LHS, and fewer stream-type adult rainbow trout/steelhead studies.

Both rainbow and cutthroat trout do show an overwhelmingly net positive response to BBH across all life stages when looking specifically at stream summer drought conditions in arid stream regions. Under these extreme hydrologic conditions, BBH resulted in a positive response by creating refugia habitat for fish during exceptionally low flows and elevated maximum daily water temperature levels (Silver et al., 2020; Talabere, 2002). The beaver sites contained water, and specifically water that was not surpassing lethal limits for these species, compared to the beaver-free sites during extreme summer drought conditions. These specific results were therefore consistent with our predictions for this hypothesis.

Hypothesis 5

We were quite surprised by the spawner life stage responses to BBH, as an overwhelmingly negative response was anticipated due to migratory blockages being the primary response type expected for this life stage. There were many more positive or neutral responses for the spawner life stage than was expected, with only sockeye salmon showing a species-specific level qualitative negative net response. All the other Pacific salmonid species had net neutral qualitative responses.

The positive effects were primarily driven by increased spawning habitat area and increased spawning habitat quality created behind beaver dams that were accessible, despite the impoundments (Bennett et al., 2014; ; Sarita and Pachena Watershed Renewal: Sarita River Chinook and Chum Salmon Redd Superimposition Assessment, 2018). The overwhelming majority of negative responses were driven by fully blocked upstream access to spawning habitat by beaver dams. The only other hypothesis that contrasted with our predictions of a net negative effect was the egg life stage. Since spawners typically die in close proximity to where they lay their eggs, these life stages' response outcomes to BBH are more closely correlated to one another than the juvenile and adult life stages that move independent of previous or subsequent life stages.

Study Caveats and Considerations

Our study identified new patterns in Pacific salmonid species-life stage specific responses to BBH, but like all meta-analyses, was limited by data type and availability. A potentially confounding factor not taken into account was the behavior of salmonids with one another and other species at different life stages in freshwater environments. While beaver dams impact Pacific salmonids through physical controls, the fishes impact one another through behavioral traits unique to each species. Coho salmon in particular are territorial as juveniles (Quinn, 2018). They have been observed to reduce the abundance of other salmonid species like cutthroat trout in beaver ponds by chasing them out of the preferred ponded pool habitat (Glova, 1987). This means though a beaver pond may be suitable rearing habitat for other juvenile salmonid species, the presence of coho salmon can affect how much access other species have to beaver pond rearing habitat. Some species, like Chinook salmon and rainbow trout/steelhead, are more sensitive to other habitat parameters besides BBH that make their relationship with BBH not as clear as the other Pacific salmonid species. Parameters such as velocity, substrate, depth range, and proximity to main-stem channels are all site characteristics identified as highly influential for juvenile Chinook salmon rearing (O'Neal et al., 2024). BBH indirectly affect many of these parameters too, but beaver ponds themselves are generally not a primary determinant of the quality of juvenile Chinook salmon rearing habitat.

One key data gap found in our study is the lack of measured population-level responses of salmonids to increasing BBH stream reaches. Though our analysis shows that the number of studies that measure the effect of BBH on Pacific salmon has been increasing steadily for the past century (Figure A5), there were only a few studies measuring population-level responses over that same timeframe. Knowing how BBH influences Pacific salmonid populations over time is imperative for adaptively managing BBH restoration projects within the context of recovery of threatened Pacific salmonid species. Only one study was found to have data on cutthroat trout population-level responses to beaver sites versus reference sites (McCaffery, 2009). This study showed that cutthroat exhibited 40 % higher survival rates and population growth rates 5 – 20 % higher than in non-beaver streams, even with the presence of competing invasive fish species.

As BBH restoration continues to be increasingly employed through time, more ecosystem-scale monitoring studies are needed to document the long-term effects of beaver recolonization on streams. These streams have drastically changed in structure and function since beaver populations were last present in them over 100 years ago, and some are currently too degraded in their present state to be able to support beaver populations, thus requiring BDA structures as a first step for beaver reestablishment in these streams. There are studies that have documented how beavers are generally expected to change riverscape hydrology, geomorphology, and biotic community compositions, but each stream's unique conditions can dramatically shift any of these parameters (Lapointe, 2012; Larsen et al., 2021; Pollock et al., 2003).

Though the indirect impacts beavers have on Pacific salmonids through changes in habitat connectivity, flow, temperature, prey and predator dynamics, dissolved oxygen, and nutrient fluxes were not analyzed in our meta-analysis, it is evident from other meta-analyses that variation in these indirect effects caused by beaver activity are highly impactful stream variables for Pacific salmonids (Kemp et al. 2012; Collen and Gibson 2000; Pollock et al. 2003; Ecke et al. 2017). These studies also showed complex patterns between beaver impounded habitats and indirect measures; some of the main outcomes are described as follows: beaver dams can increase habitat connectivity by raising water levels and stream bed morphology to reconnect incised streams to their floodplains. However, beaver dams can also create disconnection as very large dams can become impenetrable to fish movement. Lower initial baseflows due to shifting hydrologic regimes and withdrawals for human use can make beaver dams initially act as impassable barriers to fish. But over time, as beaver dams replenish aquifers, baseflows eventually increase benefiting fish. Beaver dams also create flow and temperature refugia during extreme drought conditions and winter floods, while becoming uninhabitable in other waterways which are temperature compromised. While beaver ponds often have reduced DO levels, water below dams is often more oxygenated due to the increasing hyporheic exchange the pond creates (Wang et al., 2018). Depending on the species, beaver ponds can facilitate better conditions for native salmonids competing with or being preyed upon by invasive species, but in other cases are found to create habitat that supports invasive species. Beaverponds vary from being sources or sinks of nutrients depending on the dam age that can have important effects on basal food web structure. These varying responses show how complex the relationship is between beavers and the landscapes they exist in, and how other organisms like salmonids respond.

Clear population-level studies measuring the responses of each Pacific salmonid species and studies linking secondary responses to BBH are needed to refine the application of BBH restoration projects. Understanding the long-term effects of BBH at the ecosystem scale and connecting those effects to population-level salmonid responses, will allow this restoration approach to be used most effectively at addressing population-level recovery of at-risk Pacific salmonid stocks. Long-term monitoring of population-level responses to BBH is also needed to be able to understand how salmonid populations will respond to these changes over time in streams with differing hydrologic and geomorphic processes.

Implications

Our analysis highlights the importance of considering targeted Pacific salmonid species-life stage combinations of freshwater restoration projects that use BBH. A one-size-fits-all approach to BBH does not consider the varying ways different Pacific salmonid species-life stage combinations respond to BBH. To improve the effectiveness of BBH, these differences need to be addressed when outlining the project goals for a restoration project. Though a common issue with restoration work is a lack of funding for monitoring following restoration action, this is an essential part of these projects. Monitoring reveals how successful a project is in accomplishing its initial goals and provides a pathway to improving future restoration work by identifying components that need to be optimized to improve restoration action outcomes. Increased monitoring of BBH will especially aid in optimizing project designs that more effectively target priority species-life stage salmonids and their identified priority responses to restoration work. For instance, the use of BDAs to help recruit beavers into streams targeted for restoration is a proven effective initial step in stream restoration, but BDAs alone are not as effective at improving conditions for Pacific salmonids as natural beaver dams (Bouwes et al., 2016). This relationship was revealed through targeted monitoring efforts and shows how crucial monitoring is for strengthening the effectiveness of restoration work. More stream restoration work is underway now than at any other point in history, so improving project designs is timely (Pilliod et al., 2018).

Conclusions

As climate change has a disproportionate effect on freshwater resources globally, the role beavers play in mitigating these effects for at-risk Pacific salmonid species needs to be taken into account within the context of the climate conditions of each unique steam and watershed (Herbold et al., 2018; Siegel et al., 2019; Sukanya et al., 2023). The historic role beaver dams played in shaping the landscapes and waterways of North America by impounding water, increasing riparian and wetland area, increasing hyporheic flow, and holding back sediment clearly had and currently has a significant impact on the fishes that rely on these systems (Naiman et al., 1988). There is much opportunity for beavers to mitigate many climate change impacts by improving habitat for at-risk species and increasing surface water persistence on landscapes. These benefits are heavily dependent on the unique underlying issues for each given site though, and these issues require a suite of stream restoration actions besides BBH, especially as climate change has a greater impact on streams Pacific salmonids depend upon (Jordan et al., 2022). For example, beavers can exacerbate climate impacts on salmon in temperature-compromised systems, but they can also negate these changes by cooling water though hyporheic exchange downstream of their dam. This study is one more source of information for stream restoration practitioners to consider when developing restoration projects that incorporate BBH, so that their projects are best tailored to the specific needs of different Pacific salmonid species, life stages, and life histories. Beavers and salmon have co-evolved for millions of years, which means they likely have many other important relationships we have yet to uncover. Better understanding and revealing these hidden relationships will enable us to create effective management actions that help restore self-sustaining Pacific salmonid populations.

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Appendix

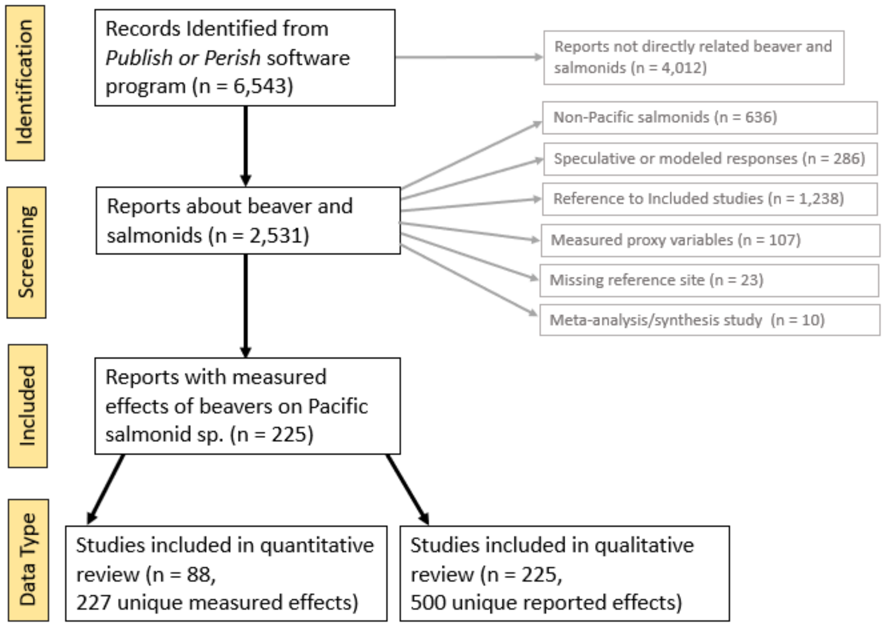

Figure A1. This study's screening process to aggregate studies with relevant data for use in analysis. N refers to the number of papers fitting this category. The initial search, secondary pre-1990 trout specific search, and snowballing searches were combined into one number under the "identification" label for simplicity

Species	Life Stage							
	Egg/Alevin		Juvenile		Adult		Spawner	
	Means	Variances	Means	Variances	Means	Variances	Means	Variances
Pink	0	0	0	0	NA	NA	0	0
Chum	0	0	6	0	NA	NA	0	0
Chinook	0	0	24	7	NA	NA	0	0
Coho	1	1	70	23	NA	NA	2	1
Sockeye	2	0	14	7	NA	NA	4	0
Rainbow Trout	4	1	40	18	16	6	1	0
Cutthroat Trout	2	1	12	3	28	16	1	0

Table A1. The number of means and variances reported from studies for specific species-life stage combinations. This shows that a large gap exists in the number of variances reported compared to the number of means reported.

Term	Estimate	SE	z	p-value	95% CI
Adult	-1.707	0.342	-4.992	0	(-2.377, -1.037)
Egg	1.839	0.841	2.188	0.029	(0.191, 3.487)
Juvenile	1.426	0.284	5.028	0	(0.87, 1.981)
Spawner	1.546	0.842	1.836	0.066	(-0.104, 3.196)

Table A2. Summary statistics for the life stage meta-regression model.

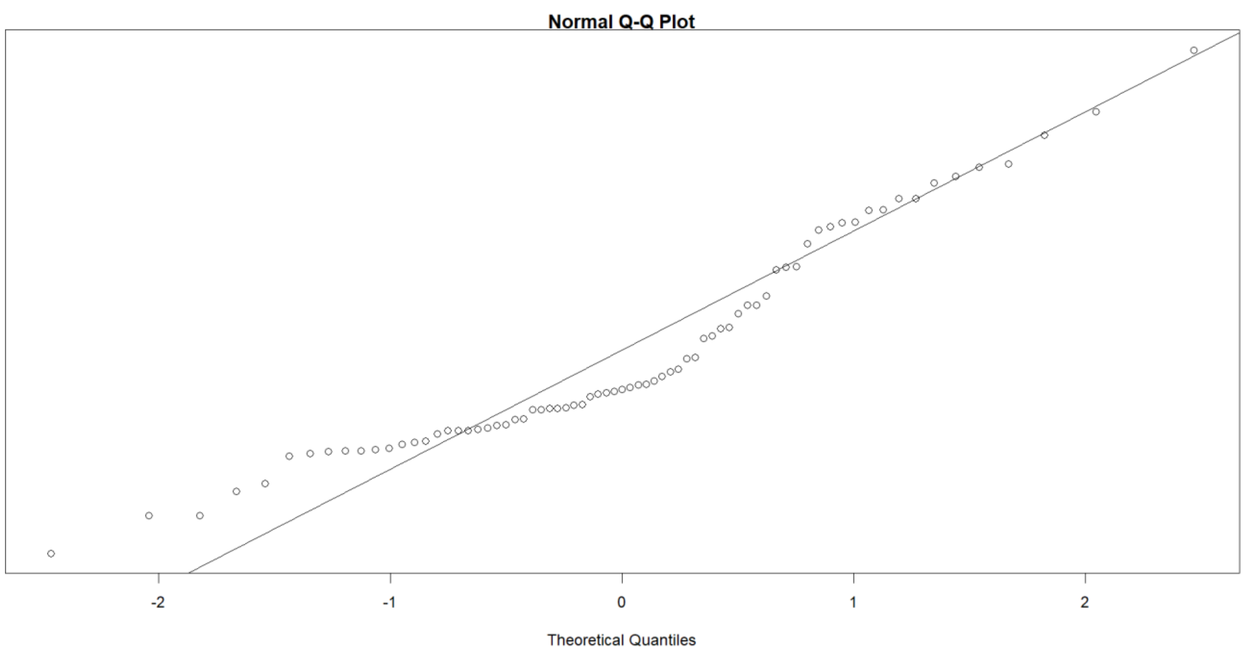

Figure A2. Q-Q- plot for the life stage regression model. The data points mostly follow normal distribution, with data to the left of the Q-Q plot slightly closer to the mean than was expected, and the data in the center was a bit further away from the mean than we would expect.

Term	Estimate	SE	z	p-value	95% CI
Chinook	0.624	0.514	1.214	0.225	(-0.383, 1.631)
Coho	0.686	0.409	1.677	0.094	(-0.116, 1.487)
Cutthroat	2.001	0.369	5.426	0	(1.278, 2.724)
Rainbow Trout/Steelhead	-1.579	0.369	-4.281	0	(-2.302, -0.856)
Sockeye	0.058	0.61	0.096	0.924	(-1.137, 1.253)

Table A3. Summary statistics for the species meta-regression model.

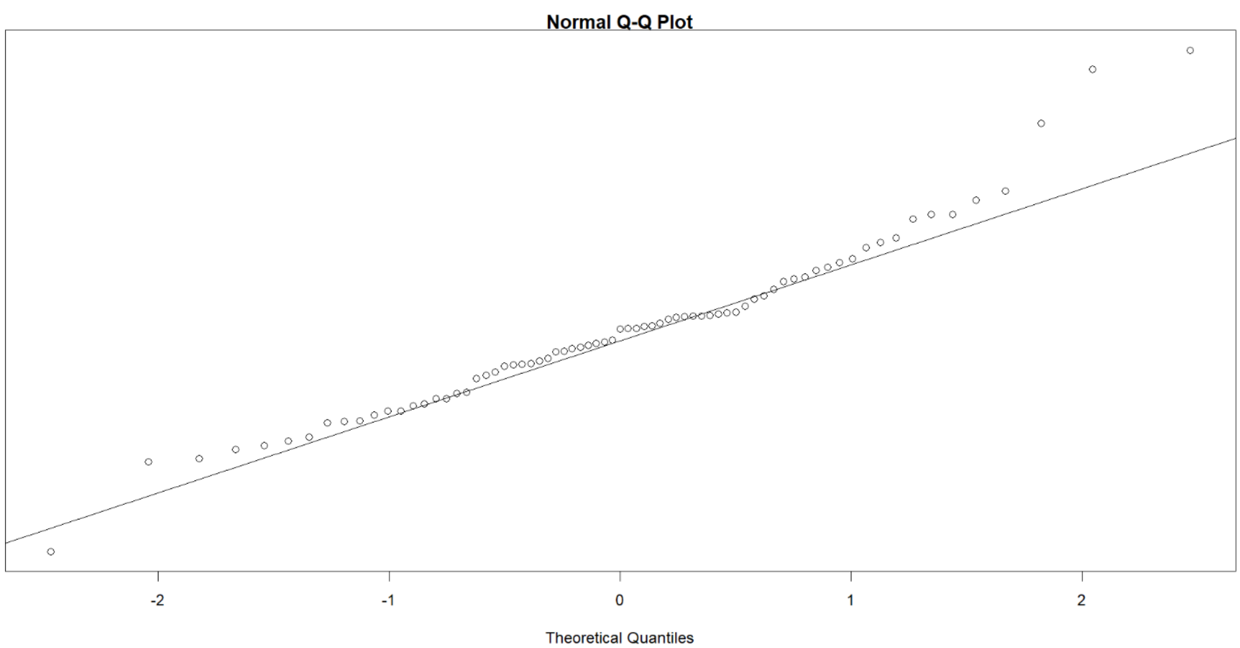

Figure A3. Q-Q- plot for the species regression model. The data points closely follow a normal distribution, with some skewing at the ends as expected, but is more pronounced for the right tail of data on the end of the Q-Q plot.

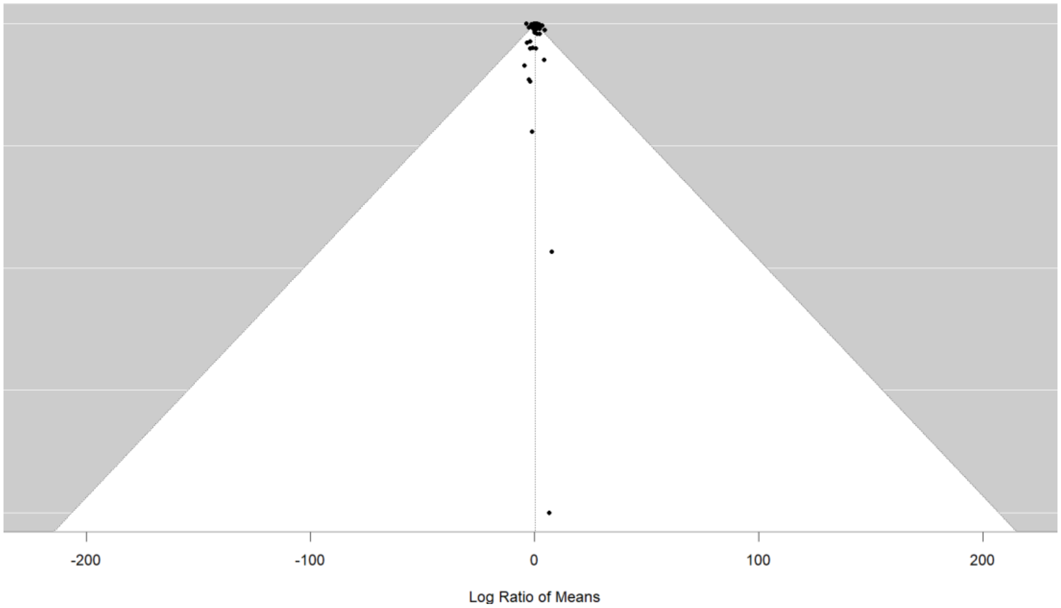

Figure A4. Funnel plot showing high precision of included data points. This is indicated by the cluster of points at the top of the plot, since study precision increases towards the top of the plot. This type of asymmetry does not raise concerns of publication bias, but instead shows that the majority of studies included for quantitative analysis exhibited high precision.

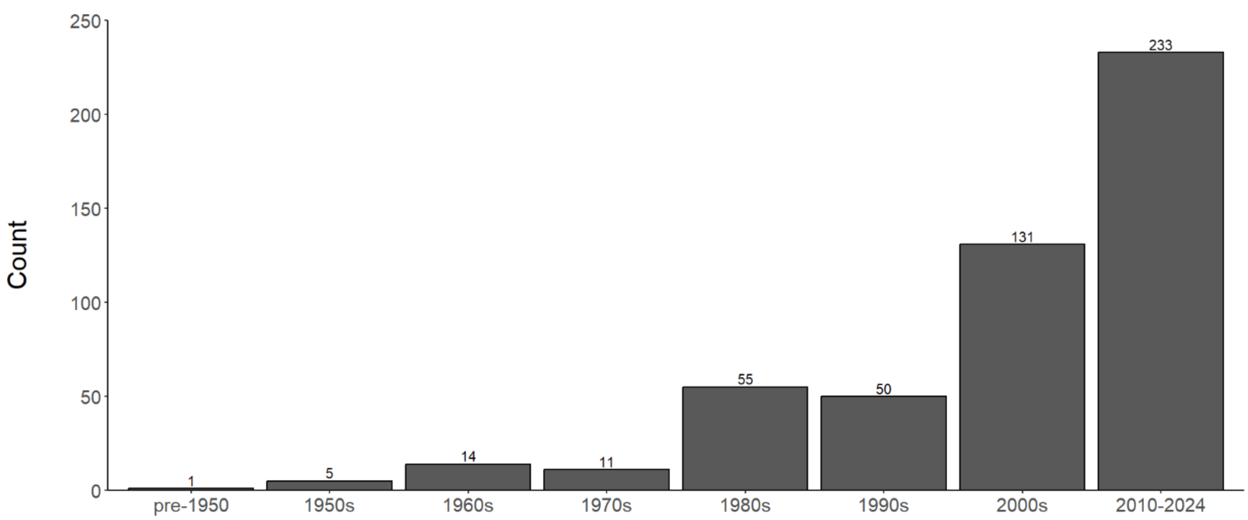

Figure A5. The change in the number of beaver-salmon studies over time. We can see from this figure that the number of studies that measure the effect of BBH on Pacific salmon has been increasing steadily for the past century.