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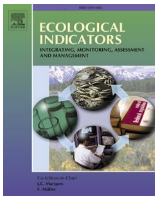

Testing for broad-scale relationships between freshwater habitat pressure indicators and Pacific salmon population trends

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ABSTRACT

Global freshwater biodiversity is declining at rates greater than in terrestrial or marine environments, largely due to habitat alteration and loss. Pacific salmon are declining throughout much of their southern range due to a combination of pressures in their marine and freshwater habitats. There is, therefore, an urgent need to understand the main drivers of decline to inform both fisheries and land-use management. Here, we draw on a suite of freshwater habitat pressure indicators to test whether we can detect relationships between them and trends in Pacific salmon spawner abundance throughout British Columbia. We related trends in spawner abundance (n = 3691 populations) to ten habitat pressure indicators that represent a snapshot in time of the level of degradation in salmon freshwater spawning habitats (e.g., Equivalent Clearcut Area, percent watershed area impacted by urban development or agriculture).

Evidence of relationships between freshwater habitat pressure indicators and trends in spawner abundance was weak at the province-wide scale, while variable in both direction and magnitude at the watershed scale likely due to the mediating effects of regional biological and physical factors. We used these empirical relationships to assess the vulnerability of individual species and regions to increasing habitat pressures. Vulnerability was highest when multiple conditions coincided: when salmon were sensitive to the habitat pressure indicator, the current level of disturbance under that indicator was moderate or low, and populations were declining but not yet at rates high enough to be deemed “threatened”. These findings highlight the need to consider the current state of the landscape and of populations when assessing where habitat protection might have the greatest benefit for biodiversity conservation. Strategic recovery planning for Pacific salmon requires multi-scale approaches that account for the diversity and complexity of relationships between habitat disturbance and population dynamics.

1. Introduction

Global freshwater biodiversity is declining at rapid rates (Dudgeon et al., 2006) and habitat degradation remains a leading cause of these declines (Dudgeon, 2019; Reid et al., 2019). With nearly one in three freshwater species threatened with extinction (WWF, 2020), there is an urgent need for conservation and recovery actions targeted at species-at-risk and their habitats. Strategic planning is required to prioritize such actions, as there are rarely sufficient resources to implement all recommended actions towards species’ recovery or the social and political will to refrain from any development that has the potential for adverse effects (Martin et al., 2018; Turcotte et al., 2021).

Indicators are useful tools for informing strategic planning processes because they can provide a measure of the magnitude and extent of habitat threats and thus help prioritize among different regions or populations. Indicators are quantifiable attributes of a system that can be assessed against critical thresholds or historical values to provide insight into the changing conditions or potential (anthropogenic) threats

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to the environment or populations (Niemi and McDonald, 2004; Niemeijer and de Groot, 2008). Habitat indicators can provide information on the current, and potential future, state of habitats and may help elucidate the causes of population declines or identify threats that could create a conservation concern for a population in the future. Habitat indicators are commonly categorized as two types: (1) pressure indicators that describe the magnitude of disturbances known or hypothesized to impact environmental conditions in a species' habitat and (2) state indicators that directly capture the current environmental conditions in that habitat (Stalberg et al., 2009; Patrício et al., 2016). Pressure indicators are generally easier to assess across broad spatial scales because they can be quantified using remotely sensed or automatically collected data or other records of human disturbance (e.g., land-use designations), whereas state indicators often require intensive fieldwork to collect information on localized habitat conditions (i.e., physical, chemical and/or biological attributes). For example, it is easier to quantify the proportion of a watershed that has been logged (a pressure indicator) than it is to quantify the total suspended sediment or water temperature (both state indicators that may be affected by deforestation) in streams throughout that watershed. Further, habitat state indicators are often influenced by multiple, interacting processes and may be highly variable in both space and time, requiring intensive and/or continuous sampling to detect relevant trends (Stalberg et al., 2009).

Broad-scale assessments of habitat status based on a suite of pressure indicators can inform land-use planning that seeks to conserve and/or restore critical freshwater habitat for species-at-risk and can also be used to assess the relative vulnerability of populations to decline as a result of historical or projected future habitat change (e.g., Hodgson et al., 2016; Berger et al., 2021). Vulnerability depends not only on a population's exposure to landscape disturbance, but also on the sensitivity of habitat conditions to landscape disturbance and the sensitivity of populations to changes to those conditions. Although data describing habitat conditions are often sparse, pressure indicators can be quantified relatively easily as described above. Determining a populations' sensitivity to pressure indicators is challenging, however, as it requires simplifying several cause-effect relationships: the effect of habitat pressures on habitat states and the response of different populations to changes in habitat state (Patrício et al., 2016). Nonetheless, strategic conservation and recovery planning requires being able to understand and predict the effects of habitat disturbances, largely due to human activities, on fish and wildlife at broad spatial scales (Minns et al., 2011).

Pacific salmon are one group of species that has experienced widespread declines throughout their range, due in part to destruction and degradation of their freshwater habitats (Nehlsen et al., 1991; Slaney et al., 1996; Beechie et al., 2013). Mechanistic understanding of land-use impacts on fish and fish habitat has been mostly informed by local, intensive, long-term field studies. For example, long-term studies on Carnation Creek, British Columbia (BC), Canada, have tracked the dynamic changes in fish populations and their habitats for over 40 years (e.g., Scrivener and Andersen, 1984; Holtby et al., 1989; Reid et al., 2020). These studies demonstrate how forest harvest practices have caused reduced complexity and stability of downstream fish habitat via bank erosion and loss of large wood input, resulting in decreased coho salmon overwintering survival (Tschaplinski and Pike, 2017). In another case study in the Upper Penticton Creek, a paired catchment experiment watershed showed the greatest reduction in summertime flows in timber harvested catchments with the longest post-harvest history (Winkler et al., 2017; Gronsdahl et al., 2019). Data from another watershed in BC's interior shows maximum summer temperatures tend to be elevated post-timber harvest compared to pre-harvest periods (Macdonald et al., 2003; Bladon et al., 2018). Past studies on pathways of effects have helped identify habitat pressure indicators that capture landscape disturbances relevant to salmon survival such as the percentage of spawning watersheds impacted by various disturbances including forestry, fires, and urban and agricultural development (e.g., Stalberg et al., 2009). However, not all studies have identified relationships between these habitat pressure indicators and population-level impacts (e.g., Bateman et al., 2016). Broad-scale, multi-species studies linking habitat pressure indicators directly to salmon population trends are lacking (Minns et al., 2011), but would help to inform landscape planning and salmon recovery actions.

Several attempts to quantify the direct relationships between habitat pressure indicators and population trends have been made, however, they have tended to focus on specific species and watersheds (Bradford and Irvine, 2000; Andrew and Wulder, 2011; Nelitz et al., 2012; Wilson et al., 2022). The lack of broad-scale studies may be, in part, because of the challenges associated with compiling high-quality spatial data of land-use impacts and population trends across large areas. However, improvements in remote sensing and online data portals have improved access to these types of data. In addition, more sophisticated analytical tools, in particular those facilitating the easy implementation of Bayesian hierarchical models, allow for appropriate structuring of model parameters to account for shared variability, spatial structure, and potential confounding factors (e.g., Wilson et al., 2022). These approaches provide greater statistical power to detect true signals in large, noisy datasets and test hypotheses for data-poor species (Kindsvater et al., 2018).

Motivated by recent advances in data availability and analytical tools, together with an increasing urgency in the salmon conservation crisis (Lackey, 2003; Anderson et al., 2015) and need for broad-scale prioritization of recovery actions, we ask the question: Can we detect relationships between freshwater habitat pressure indicators and Pacific salmon population trends at a province-wide scale? We estimated trends in spawner abundance for populations of Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon throughout BC, and related these population trends to ten habitat pressure indicators (Pacific Salmon Foundation, 2022) quantified for the spawning watersheds of those populations. The empirically derived relationships were then used to assess the relative vulnerability of salmon populations to increasing habitat pressure for each habitat pressure indicator, species, and region.

2. Methods

We used hierarchical linear models to assess the evidence for relationships between trends in Pacific salmon spawning population abundance and ten different freshwater habitat pressure indicators within spawning watersheds (henceforth "population-habitat relationships"), accounting for different spatial scales of covariation. Using the estimated model parameters, we then quantified the vulnerability of salmon populations based on the predicted population trends under increasing pressure values for each habitat pressure indicator. The methods of data compilation and treatment are described below, followed by details of the linear model and the vulnerability assessment.

2.1. Data

2.1.1. Population data

We defined populations within each species as groups of fish with unique combinations of natal rivers and spawn timing, as documented in the Fisheries and Oceans Canada's New Salmon Escapement Database System (NuSEDS; Fisheries and Oceans Canada, 2020). Population data are often aggregated to coarser scales for management and recovery planning in Canada. In particular, Conservation Units (CUs) are distinct groups of fish that have unique genetic and life-history traits, such that they are unlikely to recolonize within a human lifetime if lost (Fisheries and Oceans Canada, 2005), and are often comprised of multiple spawning populations. However, CUs can be geographically large (e.g., hundreds or even thousands of square kilometers) and thus populations within CUs may be exposed to very different levels of habitat degradation in their spawning watersheds. Thus, we chose to examine population data at the finest spatial scale possible, while recognizing the potential for dispersal of spawners among rivers (i.e., straying) and common downstream pressures to potentially obscure population-habitat relationships at this fine resolution.

The status of salmon populations was quantified as the trend in spawner abundance (i.e., escapement to the spawning grounds) through time, using publicly available spawner estimates from 1950 to 2019 (Fisheries and Oceans Canada, 2020). We filtered the data to remove records prior to when reliable reporting began (1950 or later if additional information was available; see Appendix A for details) and removed populations that had <10 spawner estimates. We also removed populations either directly enhanced by hatchery production within the last three generations ($n = 228$ populations) or near major habitat enhancement projects such as artificial spawning channels ($n = 92$ populations) because these populations may respond differently to habitat degradation in their spawning watersheds because either the populations or habitats, respectively, are artificially enhanced. Additional steps and further details of the data filtering procedure can be found in Appendix A: Table A1. The initial spawner dataset contained 7,152 populations and 306,308 annual spawner estimates, which was reduced to 3,689 populations totaling 117,812 annual spawner estimates.

For each population, we estimated the linear trend in log smoothed spawner abundance over time (D'Eon-Eggertson et al., 2015). To reduce the influence of outliers and the extreme line dominance that is observed in some populations, the raw spawner estimates were smoothed using a running geometric mean over the generation length,

$$\overline{S}_{i,t} = \left(\prod_{\tau=t-G+1}^{t} \left(S_{i,\tau}\right)^{w_{i,\tau}} \right)^{1/\sum_{\tau=t-G+1}^{t} w_{i,\tau}}, \qquad (1)$$

where $w_{i,t}$ is a weight according to the quality of the data ($w_{i,t} = 1$ is the best and $w_{i,t} < 1$ is sub-optimal; see Appendix A for details) and G is the generation length for population i. Generation length varies as a function of species and life history and depends on the characteristics of each population (Pacific Salmon Foundation, 2022). If generation length was not known for a population (e.g., due to a lack of age-at-return data), we assumed a generation length of 2 years for pink salmon, 3 years for coho salmon, 4 years for chum salmon, and 5 years for Chinook and sockeye salmon. Note that for sockeye populations in southern BC, including the Fraser River, generation length is well known and is usually 4 years. Sockeye populations that are missing data on age-at-return are from northern watersheds (e.g., Skeena, Nass) where a 5-year generation length is more common (Pacific Salmon Foundation, 2022). We fitted the linear trend to $\log(\overline{S}_{i,t} + 1)$ using weighted least squares in R, with weight equal to $w_{i,t}$ for each point (R Core Team, 2021). In both Eq. (1) and the trend estimation, the data-quality weight, $w_{i,t}$, is only relevant when data quality changes through time. While the weighting had little impact on the smoothing, it did influence the estimated trend in spawner abundance. The most common effect we saw was an increase in the influence of more recent estimates for populations that have shown recent declines, which led to trends being more negative when accounting for poor- or unknown-quality data prior to 2000 than if all data points were weighted equally. The effect of this weighting scheme on population trends is explored further in Appendix A.

2.1.2. Habitat data

We used publicly available data on land-cover alteration to quantify ten habitat pressure indicators. These pressure indicators were chosen based on hypothesized direct or indirect impacts to salmon (Table 1) and have been recommended as habitat indicators for salmon under Canada's Wild Salmon Policy (Stalberg et al., 2009) and by others (Nelitz et al., 2012; Porter et al., 2014). Spatial datasets were sourced from publicly available provincial or federal agency datasets published between 1992 and 2018 (e.g., DataBC). The compilation and treatment of

Table 1

Habitat indicators and pressure values that we used in our analysis, including the hypothesized impact on salmon. For details on data sources and temporal currency, we refer readers to Appendices 6–8 in Pacific Salmon Foundation (2022).

Indicator (pressure value)	Distribution†	Description	Hypothesized impact on salmon
Agricultural development (% watershed area)	0.37 (0.00, 4.62)	The percentage of the total watershed area that has been altered by agricultural/rural land use within the total land-cover alteration layer.	Impacts of agriculture to salmon include alteration and loss of habitat, the presence of grazing animals (particularly cattle), contamination of water by pesticides, and changes to temperature regimes. Streams channelized for agricultural purposes have less fish habitat area, significantly reduced overhead cover, wetted area, and woody bank cover and increased bank grasses compared to control streams, though measured impacts on salmonid biomass have been observed only in the most severely damaged areas (Chapman and Knudsen, 1980).
Urban development (% watershed area)	0.21 (0.00, 1.96)	The percentage of the total watershed area that has been altered by urban land use within the total land-cover alteration layer.	Urban development increases runoff, which can lead to high peak flows and flooding, reduces forest cover (leading to lower salmon abundance (Bilby and Mollot, 2008)), and is associated with water contamination (e.g., by pesticides, particularly legacy organochlorine pesticides that are persistent and bioaccumulative (Harris et al., 2008)).
Riparian disturbance (% buffer area)	14.31 (6.79, 83.62)	The percentage of a 30 m buffer zone around all streams, rivers, lakes, and wetlands within the watershed that has been altered by human activity (forest disturbance, urban land use, agricultural/rural land use, mining development, and other development).	Riparian disturbance can 1) decrease the amount of large woody debris (LWD) in the system, reducing the amount of suitable fish habitat (Reid et al., 2020), 2) increase solar radiation, resulting in higher summer water temperatures, with smaller streams being more sensitive. This could cause mortality if temperatures exceed lethal thresholds, alter the timing of life history events (e.g., hatching, spawning, out migration) as well as changes in growth rates.
	0.03 (0.00, 0.31)	The density of linear developments	Right of ways associated with linear

(continued on next page)

Table 1 (*continued*)

Indicator (pressure value)	Distribution†	Description	Hypothesized impact on salmon
Linear development (km/km^2)		within a watershed, **excluding roads** (considered separately), including railways, utility corridors, pipelines, power lines, telecom cables, right of ways, etc.	developments increases exposure of streams to solar radiation. This could result in higher summer water temperatures. This impact is likely large in small streams and declines in larger rivers. This could cause mortality if temperatures exceed lethal thresholds, alter the timing of life history events (e.g., hatching, spawning, out migration) as well as changes in growth rates.
Forestry roads (km/km^2)	0.11 (0.01, 0.66)	The density of forestry roads within a watershed from the Forest Tenure Road data.*	Unpaved surfaces increases fine sediment inputs (Macdonald et al., 2003), which can cause egg mortality, and increases turbidity, which can reduce feeding opportunities for fish and reduce growth rates. Forestry roads are associated with increased risk of landslides (e.g., Goetz et al., 2015), with severe and immediate negative effects on fish habitat.
Non-forestry roads (km/km^2)	0.90 (0.59, 3.03)	The density of non-forestry roads (e.g., highways) within a watershed from the Digital Roads Atlas (DRA).	Impervious surfaces including paved roads can increase the frequency and magnitude of peak flows, which can increase the frequency and magnitude of substrate scour and high sediment transport events causing mortality of incubating eggs and displace juveniles out of rearing habitat, modify channels (e.g., remove LWD, high sediment transport rates; Macdonald et al., (2003)), and reduce the amount of suitable fish habitat. Paved surfaces also increase solar radiation, which can result in higher summer water temperatures, particularly in small streams, with subsequent impacts on survival, growth rates, and the timing of life history events (e.g., hatching, spawning, out migration).
Stream crossings (#/km)	0.33 (0.12, 1.52)	The total number of stream crossings per km of the total length of modelled salmon habitat in a watershed. Salmon habitat is defined based on a gradient criterion filtering of the Fish Passage Model (Mount et al., 2011).	In addition to the impacts associated with roads, hung culverts can reduce access to upstream spawning and rearing habitat causing a reduction in the amount of available habitat . Right of ways associated with stream crossings increases exposure of streams to solar radiation (Herunter et al., 2003). This could result in higher summer water temperatures. This impact is likely large in small streams and declines in larger rivers. Higher water temperatures could cause mortality if temperatures exceed lethal thresholds, alter the timing of life history events (e.g., hatching, spawning, out migration) as well as changes in growth rates.
Forest disturbance* (% watershed area)	12.15 (6.11, 51.79)	The percentage of total watershed area that has been disturbed by logging and burning in the last 60 years.	Forestry and the loss of trees decreases terrestrial inputs (e.g., LWD) leading to reduced habitat complexity (e.g., pools; Fausch and Northcote 1992; Mellina and Hinch 2009) and increases temperatures due to reduced canopy cover, with impacts on life-history timing (e.g., fry emergence), abundance, and productivity of salmon (Scrivener and Andersen 1984; Thedinga et al., 1989). These impacts are not only negative; for example coho salmon productivity increased in clear-cut sites due to a hypothesized increase in food availability (Bilby and Bisson, 1992). Large fires have physical impacts (sediment, flow regimes) and biological impacts (mortality, local extinction), but the frequency and severity of fires, and the time since burning, all influence the net effect on salmonids.
Equivalent Clearcut Area (ECA) (%	10.01 (5.37, 41.84)	The percentage of total watershed area that is considered	ECA reflects the pressure on salmon habitat mainly from

(*continued on next page*)

Table 1 (*continued*)

Indicator (pressure value)	Distribution†	Description	Hypothesized impact on salmon
watershed area)		functionally and hydrologically comparable to a clear-cut forest. Landscapes that have been altered by urban, road, rail, utility, and forestry development were considered.	potential increases in peak flow, with ECA greater than 25 % leading to increases in the frequency of peak flows and shifts in the timing and magnitude of snowmelt-dominated stream flows (Winkler and Boon, 2017). These changes are predicted to have negative impacts on salmon.
Mountain pine beetle defoliation (% watershed area)	7.69 (0.12, 46.91)	The percentage total watershed area that consists of pine forests killed by mountain pine beetle.	Major mountain pine beetle infestations are associated with defoliation and deforestation which can increase runoff and erosion (Gateuille et al., 2019). The impacts of salvage logging due to pine beetle to salmon include barriers to movement, sedimentation, removal of riparian vegetation, changing stream temperature, primary productivity, decreased coarse woody debris, and altered hydrology (Bunnell et al., 2004).

*Datasets may be limited by private land ownership in some regions (e.g., southeast portion of Vancouver Island), which may result in an underestimate of forest disturbance.

†Distributions are described by the mean value and 50th and 97.5th quantiles across watersheds.

spatial habitat data are fully described in Pacific Salmon Foundation (2022).

Each habitat pressure indicator was quantified at the scale of the 1:20,000 Freshwater Atlas (FWA) assessment watersheds (i.e., 2,000 to 10,000 ha; British Columbia, 2021), which is a scale at which hillslope and channel processes are generally well linked (Carver and Gray, 2009; Pacific Salmon Foundation, 2022). Pressure values were calculated as either the percent watershed area impacted or the density of the impact within the watershed (Table 1), and represent the magnitude of **exposure** to the habitat pressure represented by each indicator. Each of the ten habitat pressure indicators represented a unique disturbance and thus the pressure values from each pair of pressure indicators were not highly correlated ($\rho < 0.7$ in all cases).

We linked each salmon population to a watershed based on the point location associated with spawner abundance estimates in the NuSEDS database, which is the downstream terminus of the waterbody (i.e., where the river or lake meets another waterbody) in which that population spawns (Fisheries and Oceans Canada, 2020). This allowed us to associate a pressure value $x_{i,j}$ for each habitat pressure indicator j and spawning population i that captured the degree of habitat degradation directly upstream of its spawning habitat. This assignment can break down for spawning populations in the mainstem of large rivers that are likely influenced by multiple upstream watersheds. However, there were relatively few of those populations in our dataset: 88 % of the 3,689 populations had stream orders less than 6 and only 20 populations had stream order 10 – all in the Lower Fraser River. Thus, these cases are unlikely to have biased our analysis.

For some indicators, a lack of publicly available information limited our ability to accurately estimate pressure values for all FWA assessment watersheds. In particular, for a number of watersheds on eastern Vancouver Island, the lower mainland, and the interior, forest disturbance could not be estimated because >50 % of the land within those watersheds was privately owned. For privately owned land, the publicly available forest disturbance data managed by the Province of BC is either incomplete or not up to date. We removed watersheds that had >50 % private land ownership, and associated populations, from the analysis (158 populations removed; Table A1).

2.2. Model

We developed a linear hierarchical model to quantify the population-habitat relationships described above:

$$y_i = \left(\beta_0 + \theta_{r_i|MAZ_i}\right) + \sum_j \left[\left(\beta_{1,s_i,j} + \theta_{FAZ_i,j} + \phi_{1,j} o_i\right) x_{i,j}\right] \quad (2)$$

where y_i is the trend in spawner abundance for population i and $x_{i,j}$ is the pressure value for habitat pressure indicator j within the spawning watershed of population i.

The intercept (β_0) accounts for impacts to population trends other than those related to habitat pressure indicators within the spawning watershed (e.g., changes within freshwater rearing and marine habitats, including changes in fishing pressure over time). We included a random effect on the intercept, $\theta_{r|MAZ}$, for “rearing ecotype”, r_i, nested within Marine Adaptive Zone (MAZs; Holtby and Ciruna, 2007). We considered seven rearing ecotypes that represent the diverse life histories of Pacific salmon that we might expect to exhibit different trends in spawner abundance: stream-type Chinook, ocean-type Chinook, coho, chum, pink, lake-type sockeye, and river-type sockeye (Table 2). The MAZs (Fig. 1a) were chosen to capture broadly similar climatic conditions that populations would be exposed to in the ocean, as well as the different regions of Pacific Fisheries Management Areas (PFMAs) that may have seen diverging trends in fishing pressure over the last half century. Declines in fishing pressure may result in observed increases in spawner abundance across populations of the same rearing ecotype and MAZ, even if there were negative impacts of changing spawning habitat for some watersheds. The random effect on the intercept accounted for potential differences in trends between these groups of populations that are unrelated to changes in spawning habitat.

The influence of habitat pressures on change in abundance over time was captured by β_1, which was allowed to vary for each combination of “spawning ecotype”, s_i, and habitat indicator, j. We considered four different spawning ecotypes (Chinook, coho, pink/chum, and sockeye) based on their habitat use and expected response of these different life-history types (Table 2). The magnitude of this slope represents the sensitivity of population trends for each spawning ecotype to increasing pressure values of the different indicators. We use the term “threat” to describe the resulting predicted decline in population trends due to the sensitivity multiplied by the pressure value (i.e., the term inside the summation in Eq. (2); Table 3).

We accounted for variability in the population-habitat relationships among Freshwater Adaptive Zones (FAZs; Fig. 1b; θ_{FAZ_i}) and according to the size of the stream that spawning occurred in (o_i). The random effect for FAZs accounted for different severities of impact depending on the characteristics of the landscape. Specifically, FAZs were delineated to capture general differences in geology, climate (e.g., coastal versus interior; degree days; water temperature), hydrology (e.g., extent of lake, alpine, and glacial influence; mean annual peak flow) and stream morphology (e.g., stream gradient; Holtby and Ciruna, 2007) that we expected may mediate the impact of habitat pressures on spawning salmon. We also included an interaction term between the habitat pressure indicator and stream order, to test the hypothesis that the

Table 2
Differentiation of ecotypes in our model was based on spatiotemporal differences in use of spawning habitats, leading to four spawning ecotypes, and rearing and marine habitats, leading to seven rearing ecotypes. These are summarized as general life histories (see Quinn (2018) for examples in diversity among populations).

Species	Years to maturity	Spawning ecotypes	Rearing ecotypes
Chinook	3–8	1) Spawn in medium to large rivers in summer to fall	1) *Stream-type*– Rear for a year or two in freshwater river before extensive offshore migration 2) *Ocean-type* – Migrate to sea within the first 3 months of life; tend to reside in coastal waters and utilize estuarine habitats; almost exclusively south of 56 degrees
Chum	3–5	2) Spawn in low-gradient streams, which tend to be the lower reaches of the respective sub-watershed in late summer to fall	3) Immediate downstream migration on hatching, rear in near-shore marine waters for one summer before migrating offshore
Pink	2		4) Immediately migrate to sea on hatching, fixed 2-year lifecycle that means odd- and even-year lineages are considered separate populations
Coho	3–5	3) Spawn most often in smaller tributaries, often further upstream reaches, in late summer to winter	5) Rear in freshwater for 18 months before migrating to sea, and generally return as 3-year-olds
Sockeye	3–6	4) Spawn in low-gradient streams, often lower reaches of streams that are up- or downstream of lakes* in late summer to fall	6) *Lake-type* – Rear in a nursery lake for at least one year 7) *River(ocean)-type* – Migrate to ocean shortly after emergence

* Because of the difficulty in quantifying freshwater habitat impacts on lakes where multiple watersheds converge, we removed 27 lakeshore-spawning sockeye populations that were not closely associated with a particular river or watershed from our analysis (Table A1).

sensitivity of populations to pressure indicators (β_1) is heightened in smaller (or larger) streams (Table 1). The Strahler stream order (Strahler, 1952), o_i, was extracted from the Freshwater Atlas of British Columbia (British Columbia, 2021) for the assessment watershed corresponding to the point location provided in NuSEDS for each population. Stream order values, which were between 1 (smallest streams near the drainage divide) and 10 (largest streams, draining into the ocean) for our data, were standardized by subtracting the most common stream order of 4 so that the estimate of β_1 corresponded to a moderate-sized stream.

2.2.1. *Fitting*

We fit the model (Eq. (2)) in a Bayesian framework that was able to easily accommodate hierarchical random effects, using JAGS via R (Plummer, 2019). In calculating the likelihood, we assumed that the residuals from Eq. (2) were normally distributed with variance to be estimated.

Populations were weighted according to their data quality, with populations that had sub-optimal data quality over the most recent 20 years having a weight less than one (see Appendix A for details). In model fitting, we divided the variance in the likelihood by the population weight. In this way, a population with high quality spawner estimates and a large weight had a smaller variance, and thus contributed more to the overall likelihood than a population with the same trend but with low quality spawner estimates and low weight.

We included relatively uninformative priors on all parameters (Appendix B: Table B1). We ran three independent MCMC chains, with 20,000 iterations for adaptation of the algorithm, 20,000 iterations for burning and the subsequent 50,000 iterations for model inference. Convergence of parameters was checked by assessing the within versus between chain variance using the Gelman and Rubin's convergence diagnostic ($\widehat{R}$; (Gelman and Rubin, 1992)), with values of $\widehat{R} < 1.1$ indicating convergence. In total, we estimated 62 fixed parameters (Table B1) from 3689 population trends and associated habitat pressure values for each pressure indicator. When reporting results, if 97.5 %, 90 %, or 82.5 % of the posterior distribution was above or below zero, we categorized the weight of evidence for a relationship as strong, moderate, or weak, respectively. This weight of evidence is analogous to the "statistical significance" of the effect, which is different from the magnitude of the relationship (i.e., the mean effect size or slope).

2.2.2. *Vulnerability assessment*

We applied our fitted model to predict the vulnerability of salmon populations within each FAZ to increases in pressure values for each of the 10 habitat indicators. For each indicator, we simulated an increase in pressure values equal to the 97.5th percentile of current pressure values across all watersheds (Table 1). For example, a watershed that currently has zero agricultural development would see an increase to 4.62 % of the watershed area, whereas a watershed that currently has 3.00 % agricultural development would see an increase to 3.00 % + 4.62 % = 7.62 %. When increasing the pressure values for one indicator, all other indicators were held at their current pressure values. Though we recognize the real potential for increases in multiple indicators at once, addressing this requires careful consideration of potential non-additive cumulative effects, which was beyond the scope of this project.

We took a randomization approach to predicting population trends under increasing pressure values, accounting for both the variability in stream order and other pressure values among watersheds within the FAZ and uncertainty in model parameters. First, we drew 10,000 samples (with replacement) from the joint posterior distribution for the model parameters. For each parameter draw n, we randomly selected a population within each FAZ and species (all populations had equal probability of being selected regardless of spawner abundance or data quality). Because we chose many more samples than there were populations in a FAZ, populations may be represented more than once among the 10,000 samples. For a given population and parameter set, we calculated the predicted trend in spawner abundance given the current pressure values. We also calculated the predicted trend given the increased pressure value described above, for each habitat indicator. This resulted in 10,000 samples of predicted population trends for each species, FAZ, habitat indicator, under current and increased pressure values.

We quantified vulnerability as the proportion of these samples that were predicted to have rates of decline in spawner abundance that would result in those populations being classified as "threatened", denoted p_{threat}, according to the assessment criteria of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2021). Specifically, we applied the COSEWIC quantitative criteria A. Decline in Total Number of Mature Individuals, which specifies a population as threatened if there is a reduction of ≥50 % in the total number of mature individuals in the last 10 years or 3 generations, whichever is longer (COSEWIC, 2021). Although our model was fitted to population trends over the entire time series (see Section 4.1.1 Population data), we compared the predicted annual change in spawner abundance from the model to this COSEWIC threshold as a proxy for whether the population would be considered threatened. Specifically, a population was considered threatened if the predicted annual change in log spawner abundance, $\widehat{y}$, was less than or equal to $\log(0.5)/\widehat{G}$, where $\widehat{G}$ is the maximum of 10 years and 3 generations and depended on the species. We summarized the change in vulnerability with increasing pressure

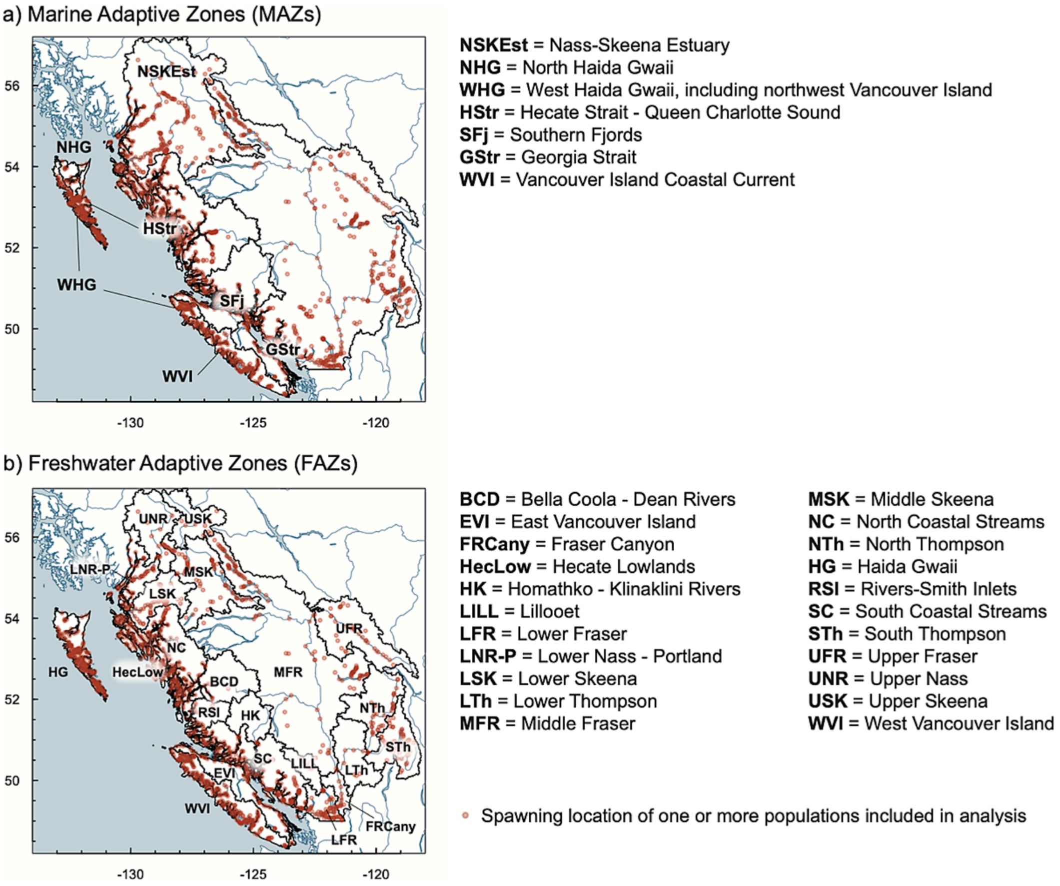

Fig. 1. a) Watersheds in this study discharge into seven marine adaptive zones (MAZs; Holtby and Ciruna, 2007). We assumed populations within each MAZ had shared variability in population trends due to, e.g., shared ocean conditions. b) Freshwater Adaptive Zones (FAZs; Holtby and Ciruna, 2007) were defined to capture general differences in freshwater habitat characteristics such as geomorphology, peak flows, stream gradient, stream temperatures, and the influence of wetlands, lakes, alpine/tundra cold water, and glaciers. We structured variability in the sensitivity of population trends to pressure indicators (i.e., the slope in Eq. (2)) by the 22 FAZs shown here.

values by calculating the change in p_{threat} between current and increased pressure values for each indicator.

Table 3
Definitions of terms and specific mathematical notation applied in model fitting (Eq. (2)) and simulations of vulnerability to further change.

Term	Definition	Notation
Exposure	The magnitude of the pressure value for a given habitat pressure indicator *j* within the spawning watershed of population *i*.	$x_{i,j}$
Sensitivity	The per-unit effect of a particular habitat disturbance on salmon population trends, quantified as the slope in Eq. (2), which was allowed to vary among life-history ecotypes, stream orders, and FAZs.	$\beta_{1,s_i,j} + \theta_{\mathrm{FAZ}_i,j} + \phi_{1,j} o_i$
Threat	The impact of a particular habitat disturbance on salmon population trends accounting for the magnitude of exposure in spawning watersheds, calculated as the product of exposure × sensitivity	$\left(\beta_{1,s_i,j} + \theta_{\mathrm{FAZ}_i,j} + \phi_{1,j} o_i\right) x_{i,j}$
Vulnerability	The predicted probability of a population reduction of ≥50 % over 10 years or 3 generations, whichever is longer (COSEWIC, 2021) given simulated increases in exposure to habitat disturbance and current baseline trends in abundance.	p_{threat}

3. Results

There was an overall negative trend in spawner abundance of −2.22 % per year ($\log(S_{t+1}/S_t) = \beta_0 = -0.022$, 95 % credible interval: −0.031, −0.014) across all species and populations. Three groups of populations stood out with strong evidence for annual rates of decline greater than 5 % per year (based on the random effect on the intercept for MAZ and rearing ecotype): lake-type sockeye in the Georgia Strait MAZ, pink salmon in the Vancouver Island Coastal Current MAZ, and stream-type Chinook in the Georgia Strait MAZ (Fig. 2).

We found that population-habitat relationships were uncertain, with habitat pressure indicators having no relationship or a weak relationship with population trends for most habitat pressure indicators and spawning ecotypes (Fig. 3). Two notable exceptions were a strong negative relationship between trends in sockeye spawner abundance and the density of non-forestry roads (Fig. 3f; $\beta_{1,s,j} = -0.042$; −0.082, −0.000013) and a strong positive relationship between trends in sockeye spawner abundance and the percent agriculture (Fig. 3a; $\beta_{1,s,j} =$ 0.011; 0.003, 0.020). (Note that there were only 35 sockeye populations that were exposed to agriculture in their spawning watersheds to inform that estimate, although there were 427 sockeye populations with 0 % agriculture in their spawning watersheds.) The relationship between the percent watershed area with mountain pine beetle defoliation and population trends was the same for all species and not different from the

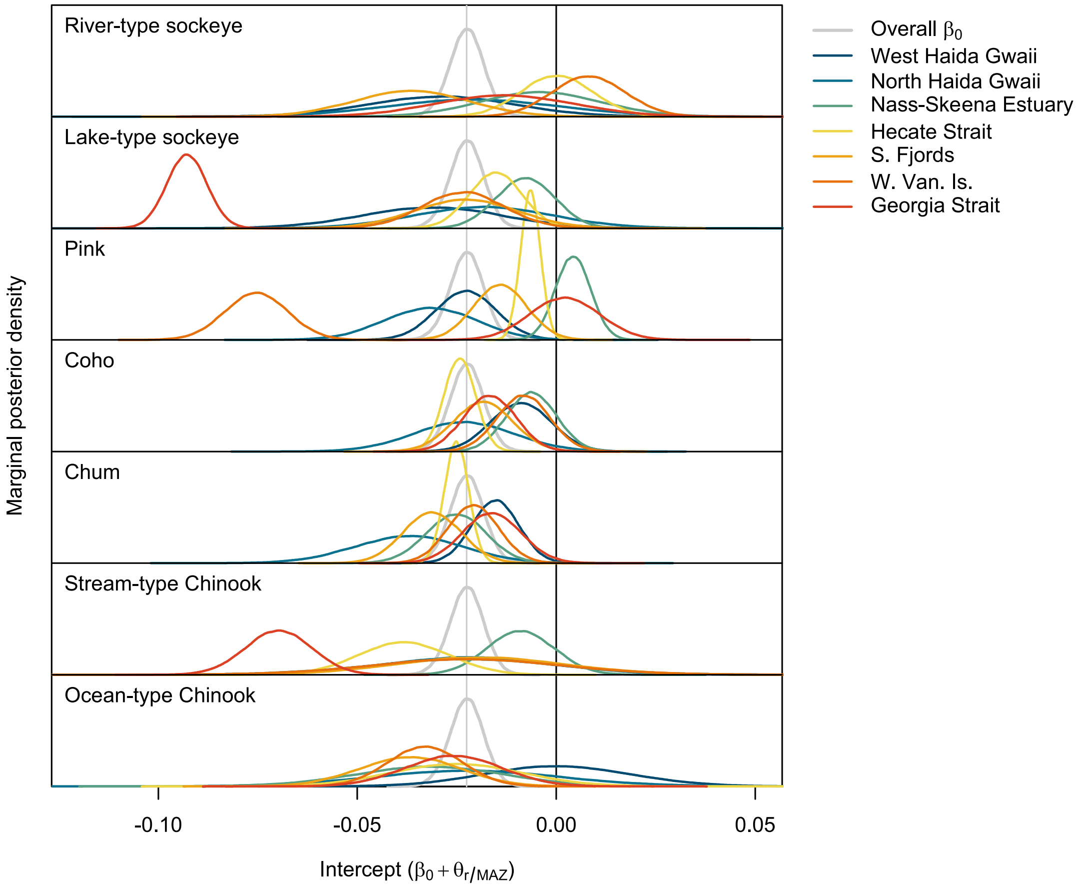

Fig. 2. The marginal posterior densities for the intercept (β_0, thick grey line), which capture the trends in spawner abundance in the absence of the freshwater habitat pressures that we considered. The coloured distributions show the random intercepts for each rearing ecotype nested within MAZ ($\beta_0 + \theta_{r|MAZ}$; see legend for MAZ names).

prior distribution (Fig. 3j), suggesting a lack of information in the data with which to estimate these parameters.

In general, we found no evidence for a mediating influence of stream order on the relationship between rates of change in spawner abundance and habitat indicators (see Appendix C).

Although there was weak to no evidence of relationships between population trends and habitat pressure indicators at broad spatial scales, when considering the random slopes, some species and FAZs stood out as particularly sensitive (Fig. 4a). We recognize the potential for spurious correlations to arise when considering the relationships between 10 different habitat pressure indicators and populations trends for 22 FAZs and 4 different spawning ecotypes, but nonetheless report the strong relationships that we found as potential candidates for further study. For example, all species present in the Middle Fraser had showed declines associated with increased urban development, despite small, weak, or even positive associations between urban development and population trends in other FAZs. Linear development had a small positive association with population trends for all spawning ecotypes (Fig. 3d), that was accentuated in the Lower Skeena, Haida Gwaii, Lillooet, East Vancouver Island, and Middle Fraser FAZs. All species in the Lillooet FAZ appeared particularly sensitive to mountain pine beetle defoliation, despite no relationship being found at the province-wide scale (Fig. 3j).

Habitat pressure values were generally lower in more northern FAZs (Fig. 4b). Average exposure within a FAZ was not necessarily the same across species because the number of populations and the watersheds that they spawn in will vary among species. For example, in the Upper Skeena, Chinook had high exposure to pine-beetle defoliation, while the other species did not (Appendix C).

For populations in southern FAZs, particularly in Lillooet, there was both exposure and sensitivity to certain habitat pressure indicators, leading to strong evidence of potential threats. In the North Thompson, the percent riparian disturbance in spawning watersheds was strongly correlated with declines of Chinook, coho, and sockeye populations, although these same populations had population trends with moderate to strong evidence of positive trends with increasing forest disturbance and mountain pine beetle defoliation. As a result, most populations showed no threat when summing across different freshwater habitat indicators (Fig. 5a; Appendix C: Figs. C5–C9). The one exception was chum salmon in Lillooet, for which there was strong evidence of habitat threat that was driven by the negative impact of non-forestry roads and mountain pine beetle.

The vulnerability of populations to increases in pressure values differed among species and FAZs, reflecting the different sensitivities that were estimated in the model. There were 75 species/FAZ/indicator cases that showed high vulnerability, with a change in the proportion of populations that would be classified as threatened (p_{threat}) of more than 0.5 when pressure values were increased to the 97.5th quantile among watersheds (see Online Supplement for maps). Of these, 23 cases also had a $p_{\text{threat}} \geq 0.8$ under increased pressure values (Table 4). The majority of these 23 cases involved sockeye salmon (n = 11 cases; Table 4), followed by coho salmon (n = 8), and Chinook and pink salmon (n = 2 each). In terms of habitat pressure indicators, increases in the density of non-forestry roads was the most common indicator appearing in the 23 most vulnerable cases (n = 8 cases), with riparian disturbance and forest disturbance also showing up repeatedly (n = 5 each).

For most cases, vulnerability was heightened because of a strong negative relationship with the habitat indicator for that FAZ. For example, coho salmon in the South Thompson (STh) showed an increase

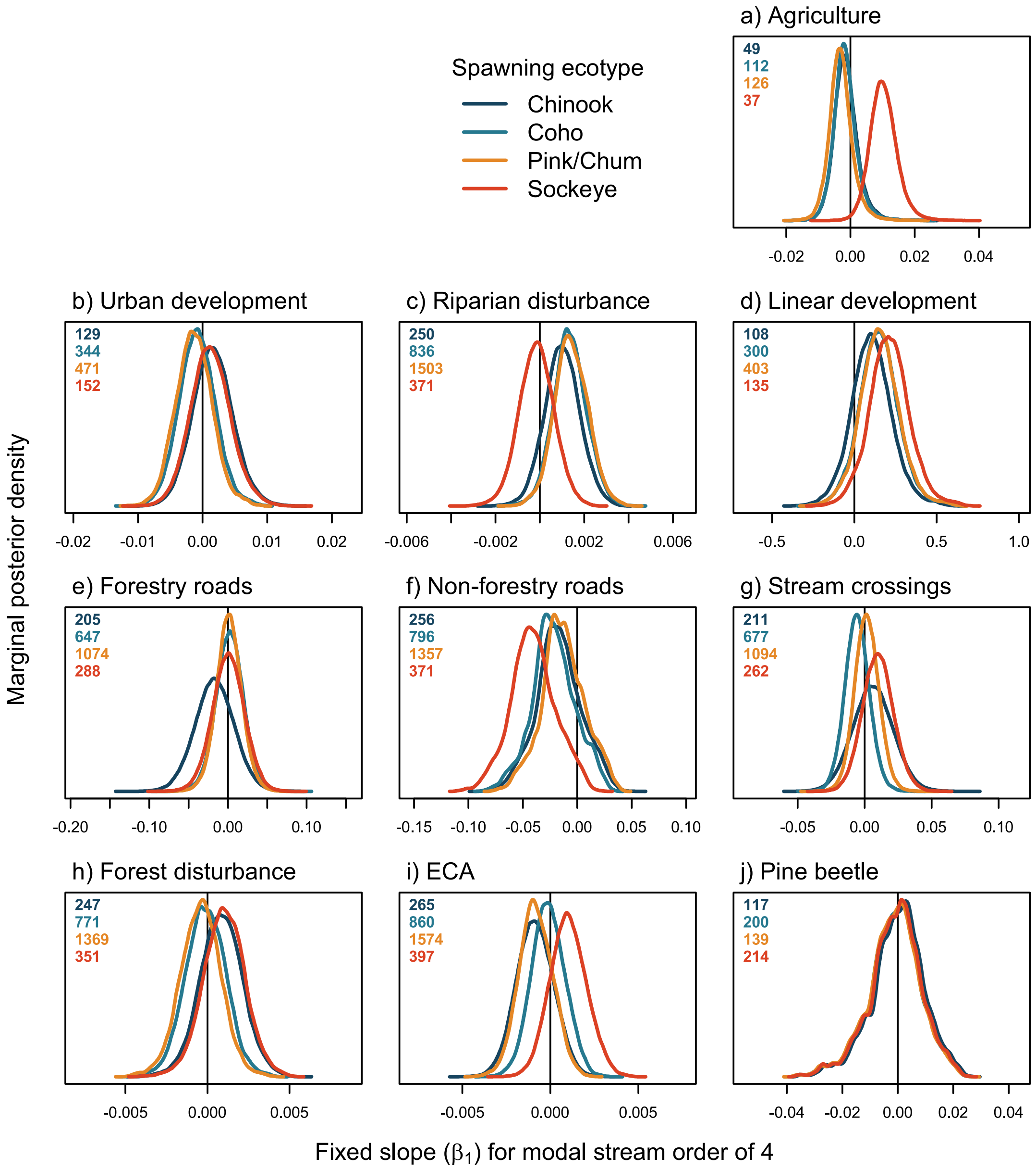

Fig. 3. The marginal posterior densities for the fixed effects of ten habitat indicators (a–j) on population trends for four spawning ecotypes (coloured lines; β_1 in Eq. 3). The coloured numbers in the top-left of each panel are the number of populations of each ecotype that had non-zero pressure values for the given indicator.

in p_{threat} of 0.879 with an increase in ECA of 41.84 %. At current pressure values, a relatively small proportion of coho populations in STh were threatened ($p_{\text{threat}} = 0.11$; Table 4), but this proportion rose sharply to $p_{\text{threat}} = 0.988$ with increasing pressure values (Fig. 5c) because the relationship between population trends and %ECA was strong and negative for these populations (Fig. 5a).

Vulnerability did not increase much in some FAZs even though there was a strong negative relationship estimated in our model because the current pressure values or proportion threatened was already high. For example, although sockeye salmon were found to be highly sensitive to the density of non-forestry roads across FAZs (Fig. 4a), given the already threatened status of many sockeye populations, the impact of increasing the density of non-forestry roads was minimal. Such was the case in the Upper Fraser River (UFR), where all populations are currently declining at rates that would have them classified as threatened (Fig. 6b). Here, the proportion threatened was predicted to decline slightly with increasing pressure (Fig. 6c) only because of the uncertainty in our model parameters (Fig. 6a). However, in Haida Gwaii the sockeye salmon population trends are currently more optimistic, and thus more vulnerable to impacts from increasing pressure values (Fig. 6d-f).

For populations that currently have positive population trends, vulnerability did not increase linearly with incremental increases in pressure values but remained at low levels until population trends declined to the point that the threshold for being classified as threatened was reached. These cases represent situations where increases in pressure values can eventually erode positive populations trends and increase the conservation risk to salmon. For example, the effect of %ECA on pink population trends in the Middle Fraser (MFR) was negative (Fig. 7a), but because most populations currently have positive trends (Fig. 7b), the p_{threat} changed little until the %ECA increased more than ~15 % (Fig. 7c).

4. Discussion

Negative trends in spawner abundance dominated across species in our analyses, with the strongest declines for sockeye and Chinook

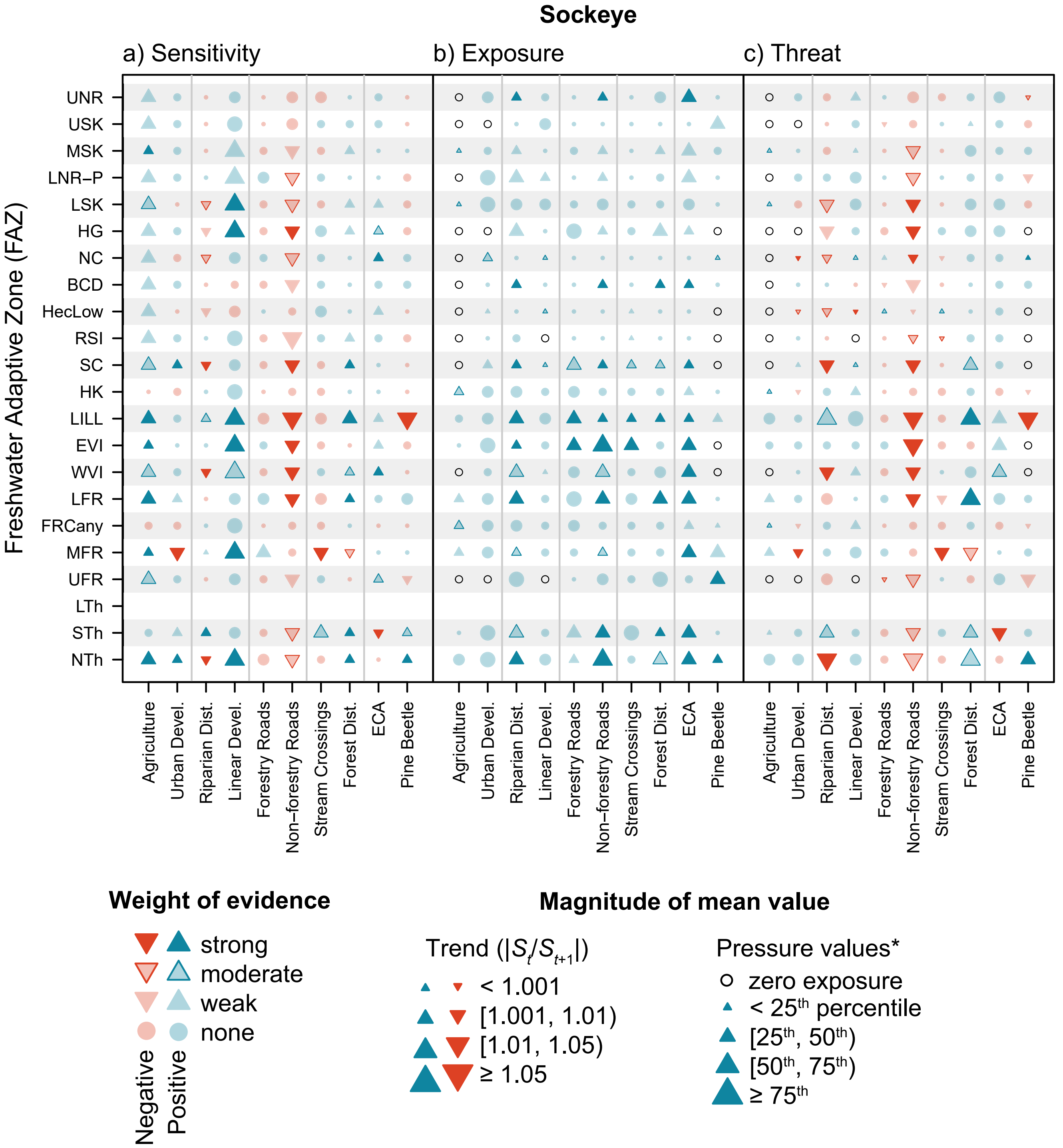

Fig. 4. The (a) sensitivity, (b) current exposure to pressures, and (c) resulting threat to sockeye salmon population trends within 22 FAZs (y-axis) from 10 different habitat pressures (x-axis; Table 2). See Table 3 for specific definitions of sensitivity, exposure, and threat. The point size, color, and shape distinguish the magnitude and direction of effect, and the shading and outline indicate the weight of evidence (i.e., strong, moderate, weak, or no evidence; see legend). For sensitivity and threat, the magnitude is measured in units of annual change in spawners (absolute value). For exposure, the magnitude of pressure values is shown as a percentile of the non-zero pressure values among all watersheds. If all watersheds within the FAZ had zero pressure, then an open black circle is shown. Corresponding figures for other salmon species can be found in Appendix C.

populations in interior FAZs. This result aligns with the general consensus that salmon populations are declining throughout much of their BC range (Dorner et al., 2008). However, we found no evidence of general relationships between population trends and ten different habitat pressure indicators at a province-wide scale, highlighting the challenge of attributing these declines to any one factor. Our original hypothesis was that increasing pressure values would be associated with more negative trends in spawner abundance, but in some cases these relationships were reversed (although weak). Given the broad spatial scale of our study, these results should be used as a cautionary flag to trigger more in-depth investigations into the effects of habitat pressures, rather than definitive evidence of relationships. Further investigations need to consider a more mechanistic approach that includes various pathways of effects when testing for relationships between landscape

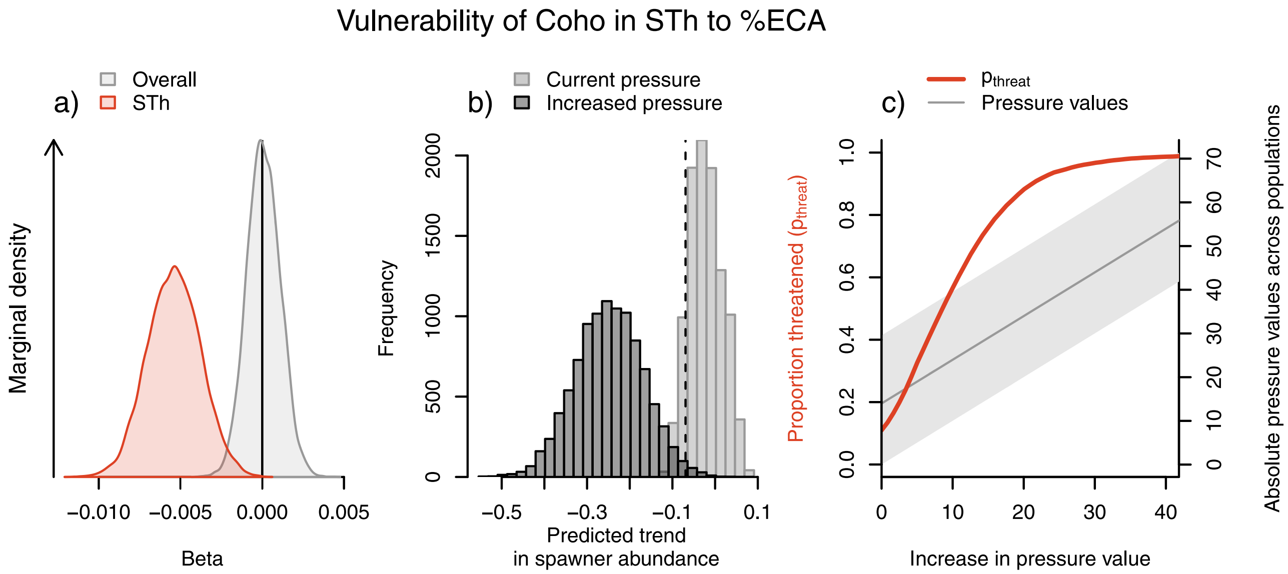

Fig. 5. (a) The predicted effect of ECA (Table 1) on population trends of coho salmon overall ($\beta_{1,s_i,j} + \phi_{1,j}o_i$) and in the STh FAZ ($\beta_{1,s_i,j} + \theta_{FAZ_i,j} + \phi_{1,j}o_i$). (b) Histograms of the predicted trends for 10,000 random draws of population and parameter values at current pressure values (light grey) and increased pressure values (dark grey). The vertical dashed line is the threshold below which a population would be classified as threatened. (c) The change in the proportion of coho populations within the STh FAZ that would be classified as threatened (red) with increasing pressure values. The grey line and polygon show the mean and 95 % central range for absolute pressure values among watersheds (i.e., current pressure values for populations within the FAZ plus the increase shown on the x-axis). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

These 23 species/FAZ/indicator combinations were the most vulnerable, having a change in p_{threat} of >0.50 and a value of p_{threat} of ≥0.8 with increased pressure values. Bolded cases are shown in Figs. 4–6.

Species	FAZ	Indicator	No. populations		Current pressure		Increased pressure		Change[4] in p_{threat}
			Total	Currently exposed[1]	Pressure value[2]	p_{threat}[3]	Pressure value[2]	p_{threat}[3]	
Chinook	LTh	%Forest Dist.	3	3	2.27 (1.11, 3.20)	0.129	54.06 (52.90, 54.99)	0.838	0.708
Chinook	STh	%ECA	12	12	10.86 (0.38, 19.41)	0.48	52.64 (42.22, 61.25)	0.999	0.518
Coho	**STh**	**%ECA**	**36**	**36**	**13.97 (0.02, 29.55)**	**0.110**	**55.82 (41.86, 71.39)**	**0.988**	**0.879**
Coho	MFR	%Forest Dist.	9	8	9.93 (0.00, 28.10)	0.005	61.81 (51.79, 79.89)	0.871	0.866
Coho	MFR	Stream Crossings	9	8	0.50 (0.00, 1.31)	0.005	2.02 (1.52, 2.83)	0.849	0.845
Coho	HG	Non-forestry Roads	118	93	0.44 (0.00, 2.12)	0.000	3.48 (3.03, 5.15)	0.841	0.841
Coho	NTh	%Riparian Dist.	29	29	25.10 (1.23, 99.47)	0.092	97.41 (84.85, 100)	0.863	0.77
Coho	LTh	%Forest Dist.	5	4	14.63 (0.00, 44.48)	0.232	66.76 (51.79, 96.27)	0.933	0.702
Coho	LILL	%Pine Beetle	15	14	1.55 (0.00, 4.71)	0.489	48.44 (46.91, 51.61)	1.000	0.511
Coho	LILL	Non-forestry Roads	15	15	0.94 (0.34, 2.50)	0.489	3.97 (3.37, 5.53)	0.999	0.51
Pink	MFR	%Forest Dist.	6	5	4.20 (0.00, 12.10)	0.159	56.06 (51.79, 63.89)	0.929	0.77
Pink	LTh	%Forest Dist.	4	4	5.63 (1.11, 15.70)	0.054	57.49 (52.90, 67.50)	0.811	0.757
Sockeye	**HG**	**Non-forestry Roads**	**14**	**12**	**0.88 (0.00, 2.05)**	**0.122**	**3.90 (3.03, 5.08)**	**0.995**	**0.873**
Sockeye	NC	%Riparian Dist.	27	12	1.86 (0.00, 21.69)	0.000	85.27 (83.62, 100)	0.819	0.819
Sockeye	LNR-P	Non-forestry Roads	7	6	0.61 (0.00, 1.33)	0.044	3.65 (3.03, 4.36)	0.862	0.818
Sockeye	RSI	Non-forestry Roads	13	8	0.13 (0.00, 0.55)	0.015	3.17 (3.03, 3.58)	0.826	0.811
Sockeye	HecLow	%Riparian Dist.	71	33	1.71 (0.00, 23.37)	0.003	84.98 (83.62, 100)	0.809	0.807
Sockeye	WVI	%Riparian Dist.	60	56	14.62 (0.00, 66.33)	0.153	92.95 (83.62, 100)	0.954	0.802
Sockeye	WVI	Non-forestry Roads	60	56	1.28 (0.00, 2.92)	0.153	4.30 (3.03, 5.95)	0.920	0.767
Sockeye	LSK	%Riparian Dist.	20	16	14.43 (0.00, 33.75)	0.065	94.90 (83.62, 100)	0.825	0.759
Sockeye	EVI	Non-forestry Roads	9	9	2.60 (0.39, 5.80)	0.408	5.62 (3.42, 8.83)	0.964	0.556
Sockeye	LILL	Non-forestry Roads	8	8	0.80 (0.34, 1.26)	0.450	3.83 (3.37, 4.29)	1.000	0.55
Sockeye	LILL	%Pine Beetle	8	7	1.45 (0.00, 4.71)	0.450	48.36 (46.91, 51.61)	1.000	0.55

1. The number of populations for the given species and FAZ that currently have non-zero pressure values in their spawning watershed. 2. The mean (min, max) pressure values among watersheds for the given species and FAZ. 3. The proportion of 10,000 simulated projections of the annual change in spawner abundance accounting for variability in current exposure and uncertainty in model parameters; see main text for details. 4. The change in the proportion of population trends that would be classified as threatened with the maximum increase in pressure values.

disturbance and population trends.

We did observe variable (and sometimes strong) responses of populations at finer spatial scales (i.e., FAZs). Structuring our analysis by FAZs, which are areas that share similar geology, climate, and stream morphology (Holtby and Ciruna, 2007), may have helped control the inherent watershed and biological variability that may mediate relationships between habitat pressure indicators and biological trends. Although the strong relationships that did show up could be spurious (there were a total of 88 FAZ/spawning ecotype combinations with slopes estimated for each of 10 indicators), the variable responses at this finer scale suggest species, FAZs, and disturbances that may warrant further study, and underscore that local conditions likely mediate the population-habitat relationships.

Detecting relationships between population trends and freshwater

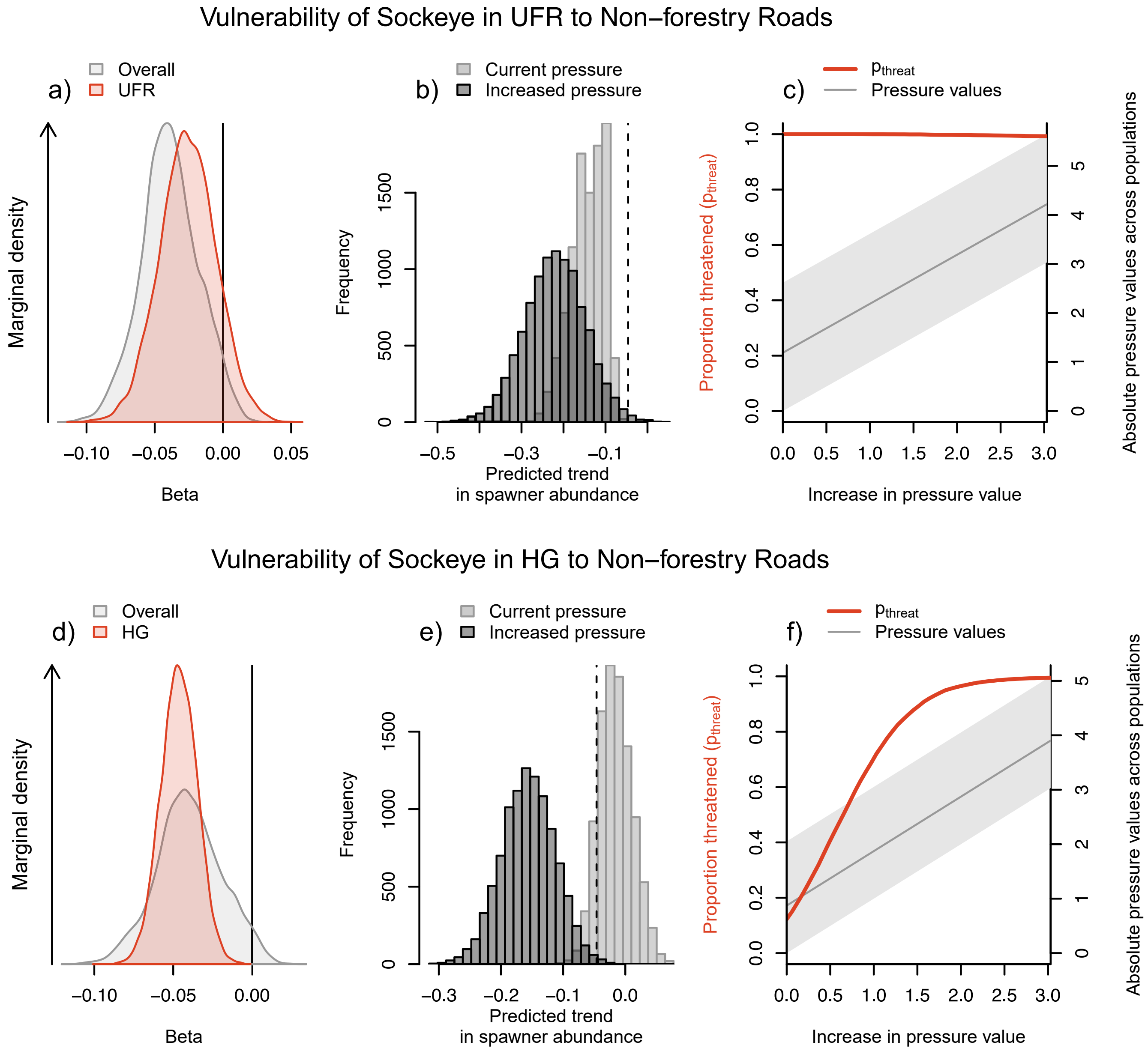

Fig. 6. The predicted effect of non-forestry roads on population trends (a, d), histograms showing the distribution of population trends at current and increased pressure values (b, e), and projected change in the proportion of populations that are threatened over increasing in pressure values (c,f) for sockeye populations in two different FAZs with different current trends: Upper Fraser River (a–c) and Haida Gwaii (d–f).

habitat pressure indicators at broad spatial scales is challenging for several reasons. Pacific salmon have complex life cycles that span multiple habitats over several years, with the potential for cumulative effects and non-linearities (e.g., thresholds) mediating the impact of habitat condition on population dynamics (Munsch et al., 2020). We assumed a linear relationship between population trends and habitat pressure indicators within spawning watersheds across many populations, which may not adequately capture the complexity of the system. In addition, there are many factors that we did not consider in our analysis that may overwhelm, confound, or mediate the effect of the freshwater habitat pressures (Bateman et al., 2016). In a similar study of freshwater habitat impacts of Fraser sockeye salmon, Nelitz et al., (2012) found the strongest predictor of salmon survival (i.e., recruitment residuals) to be distance of spawning habitats from the ocean, suggesting there are additional pressures along migration routes (or combinations of pressures) that were not captured by the ten habitat pressure indicators that we considered. We tried to structure our analysis to account for some of these effects (e.g., by estimating separate intercepts for different rearing ecotypes and MAZs), but there were trade-offs between increasing model complexity and available data to inform both freshwater habitat indicators and salmon population dynamics. Because of this complexity, our failure to detect a strong statistical relationship in the data does not mean that there is no impact of these or other habitat pressures on salmon populations.

The different responses among FAZs allowed us to differentiate groups of salmon that might be most vulnerable to increases in pressure values. However, we found that vulnerability was not just determined by how sensitive populations were to habitat pressure indicators. Current pressure values and current population trends determined the extent to which increasing pressure values impacted the proportion of populations that were threatened within a FAZ. This result highlights the importance of considering the current state of the landscape and of populations when assessing where habitat protection might have the most impact. The benefit to salmon may be greatest when protecting

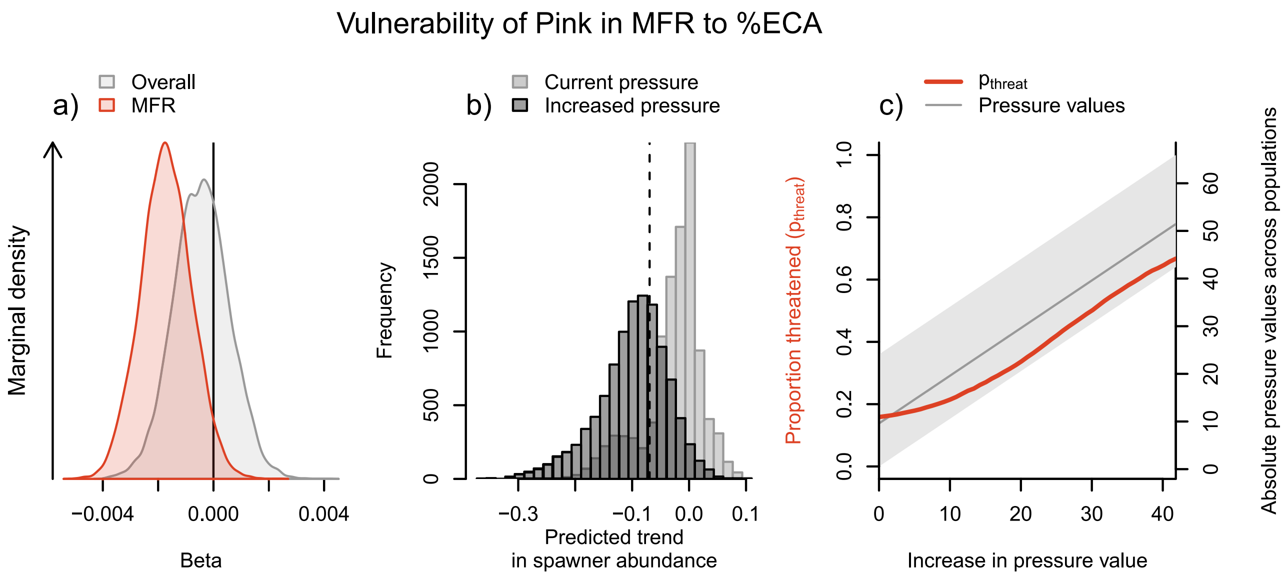

Fig. 7. The predicted effect of stream crossings on population trends (a), histograms showing the distribution of population trends at current and increased pressure values (b), and projected change in the proportion of populations that are threatened over increasing in pressure values for coho salmon populations in the Middle Fraser (MFR) FAZ (c).

intact habitats where there is greater potential for harm than to protect already degraded habitats, and populations that are not currently declining may have some buffering capacity to absorb increases in pressure values before they are at risk of being threatened. We did not consider how habitat restoration (i.e., reducing pressure values) might improve population trends, which would be a natural extension of this work.

In a few cases, we found that increasing pressure values led to a reduction in the proportion of populations that were threatened, even when the mean relationship between an indicator and trends for a species and FAZ was negative. This was because many of the estimates of sensitivity were highly uncertain. In particular, in cases where most populations are currently threatened, this uncertainty meant that some populations were predicted to have increasing trends that resulted in a decline in p_{threat}. This result highlights the importance of considering parameter uncertainty – and not just mean values – when making projections and assessing vulnerability.

Our results are consistent with previous research that identified idiosyncratic responses of salmon populations to freshwater habitat disturbance (Andrew and Wulder, 2011). Other studies report strong effects of certain variables on population aggregates with high quality data. For example, Bradford and Irvine (2000) found strong negative relationships between the annual change in recruitment for Thompson River coho salmon populations and the proportion of land under agricultural and urban use, the density of roads, and an aggregate score of overall freshwater habitat concern. Wilson et al. (2022) reported strong negative effects of logging on steelhead, cutthroat trout, and coho salmon in the Keogh River on Vancouver Island. Importantly, that study quantified logging as the 15-year cumulative area of logging activity (km^2) in the watershed and thus were able to consider annual differences in both survival and habitat change. Although these studies shed light on drivers for specific populations, they may not be generalizable to broader spatial scales.

The lack of temporal resolution in our test of the population-habitat relationship may be one key factor that limited our power to detect relationships. We did not have access to historical time series of land use changes at the broad spatial scale we needed, and so our habitat pressure values were simply a snapshot in time. We had to assume that, for example, if agricultural development negatively impacted salmon, then we would see a relationship across populations between the proportion of watersheds developed for agricultural purposes as of 2018 and the trend in spawner abundance from 1950 to present. In reality, land development may have happened over a relatively short period of time many decades ago, and thus the biological response (i.e., trend in spawner abundance) was not measured on the appropriate timescale. Further, “shifting mosaics” of optimal habitat in space and time also depend on regional climate and successional processes (Brennan et al., 2019) – factors we did not consider. Better matching the timescales of habitat impact to the biological response of salmon populations would require both improved collection, archiving, and access to data on historical patterns of land use change as well as information on how these changes impact salmon through time. The latter requires long-term monitoring of salmon responses to land use change across species and regions, which is currently limited.

Our understanding may also be improved with inclusion of rearing habitat, by considering the impacts of land use alteration on populations through influences on fry to smolt survival. By focusing on what data was available over time and space, we were only able to analyze the population impacts of land use change on freshwater spawning habitats. As many juvenile salmonids rear in river reaches or lakes that would be in a different watershed than that included in our analysis, there may be alternative mechanisms of impact we did not account for. Moreover, species- and population-specific differences may become stronger when considering rearing habitats, as there is high life history diversity in freshwater use across all five species of Pacific salmon.

Because this was an observational study, we were limited by the natural distribution of both salmon and habitat pressures (Fig. 1). We found that the threats, status, and vulnerability tended to more negative for populations in southern British Columbia where human population density and landscape disturbance are higher. For example, many pressures were concentrated in the Fraser River region, where there are numerous other impacts that may interact (Nelitz et al., 2012). Habitat pressures like mountain pine beetle were also very limited in their distribution, with exposure concentrated in the interior Fraser and Thompson systems (Fig. 4b). In addition, climate change is having more pronounced impacts on southern salmon populations (Grant et al., 2019), which may lead to both real and apparent increased sensitivity of those populations to habitat pressures.

Finally, better accounting for the population dynamics of salmon when estimating a response variable may improve power to detect an effect of freshwater habitat pressures. We estimated population status as the linear trend in spawner abundance but applying spawner recruit models to estimate (time-varying) productivity of populations, accounting for density-dependent effects and changes in catch, may provide a more accurate measure of the biological response. Indeed, there is increasing recognition of the importance of changes in smolt-to-adult survival in driving year-to-year variability in salmon abundance (e.g., Welch et al., 2021). Several studies have attempted to account for such effects using spawner-recruit analyses (Bradford and Irvine, 2000; Nelitz et al., 2012; Wilson et al., 2022), but on smaller scales than considered here. Improving the availability of catch data (e.g., through a central, publicly accessible database like NuSEDS) would make such analysis possible on broader scales.

In conclusion, we did not find strong evidence for broadly generalizable relationships between Pacific salmon population trends and freshwater habitat indicators. This result highlights the diversity and complexity of salmon population responses to habitat change but does not invalidate the utility of habitat pressure indicators for broad-scale prioritization of areas requiring further monitoring or restoration. A multi-scale approach to habitat assessment that includes finer-scale information on current environmental conditions (i.e., habitat state indicators) may clarify the potential for population impacts. Despite uncertainty in the population-habitat relationships, our vulnerability assessment clearly indicated some populations were more vulnerable than others. Current levels of habitat degradation and current population trends were also important determinants of vulnerability and should be considered when prioritizing areas for habitat protection. As data on habitat pressures, habitat conditions, and population responses accumulate for more watersheds, we will gain a clearer picture of the appropriate spatial scale at which to test population-habitat relationships and target recovery planning.

CRediT authorship contribution statement

Stephanie J. Peacock: Conceptualization, Methodology, Software, Formal analysis, Data curation, Writing – original draft, Visualization. **Douglas C. Braun:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Emma E. Hodgson:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Brendan M. Connors:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Katy Bryan:** Data curation, Writing – review & editing. **Katrina Connors:** Conceptualization, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stephanie Peacock reports a relationship with Pacific Salmon Foundation that includes: consulting or advisory and employment.

Data availability

Pressure values for habitat pressure indicators were provided by the Pacific Salmon Foundation and can be downloaded from the Salmon Data Library: https://data.salmonwatersheds.ca/data-library/. Salmon spawner abundance data are available from the New Salmon Escapement Database through Open Data Canada: https://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aafe8c5ee6. Code for the data compilation and analysis can be found on GitHub at https://github.com/sjpeacock/DFO_popHab, with the version corresponding to this submission archived at https://doi.org/10.5281/zenodo.7335697.

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Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.109935.

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