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Climate Change and Marine Food Webs: Navigating Structural Uncertainty Using Qualitative Network Analysis With Insights for Salmon Survival

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ABSTRACT

Effectively modeling the impact of climate change on any population requires careful consideration of diverse pressures. Potential changes in interactions with other species must be accounted for. As communities reassemble and shifts in abundance and distribution cascade throughout ecosystems, cumulative impacts on species of conservation concern need to be explicitly examined. A structured qualitative analysis of alternative responses to climate change across the food web can play a valuable role in the design and interpretation of quantitative models. A particular advantage of qualitative network analysis is the ease with which a wide range of scenarios representing structural and quantitative uncertainties can be explored. We tested 36 plausible representations of connections among salmon and key functional groups within the marine food web using qualitative network models. The scenarios differed in how species pairs were connected (positive, negative, or no interaction) and which species responded directly to climate change. Our analysis showed that certain configurations produced consistently negative outcomes for salmon, regardless of the specific values for most of the links. Salmon outcomes shifted from 30% to 84% negative when consumption rates by multiple competitor and predator groups increased following a press perturbation from climate. This scenario aligns with some recent observations during a marine heatwave. Feedbacks between salmon and mammalian predators were particularly important, as were indirect effects connecting spring- and fall-run salmon. We also identified which links most strongly influenced salmon outcomes in other scenarios. Our results emphasize the importance of structural uncertainty in food webs and demonstrate a tool for exploring it, paving the way for more targeted and effective research planning.

1 | Introduction

A changing climate accelerates the compounding of uncertainties in species interactions and other ecological processes, leading to increasingly divergent projections for population dynamics. This challenge is particularly daunting in large, open ecosystems such as marine environments, where shifting climatic conditions are likely to drive changes in ecological communities (Brodie et al. 2022; Smith et al. 2022). As species adjust their geographic ranges and local abundances in distinct ways

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(Morée et al. 2023), the structure of food webs evolves, introducing further complexity.

While climate vulnerability and risk assessments have emphasized the uncertainties associated with changing food webs (Crozier et al. 2019; Li et al. 2023; Urban et al. 2016), accurately predicting their impact on focal species requires a more mechanistic understanding of species interactions than is often available. One of the most common methods for projecting climate impacts—species distribution models—typically overlooks species interactions altogether (Melo-Merino et al. 2020). Neglecting feedbacks and indirect effects via food webs can result in overconfidence in model projections. Despite data limitations, the explicit exploration of uncertainties arising from food web interactions is essential for identifying and mitigating climate-related risks.

Unfortunately, most ecological projections of future climate scenarios fail to explicitly explore the uncertainty associated with species interactions (Urban et al. 2016). Because marine food webs can involve hundreds of species, most models of marine ecosystems are highly complex (e.g., Ecosim (Couture et al. 2024; Stock et al. 2023) and Atlantis (Morzaria-Luna et al. 2022)). These models are capable of propagating climate effects through a large number of potential trophic pathways, but it can be difficult to isolate individual effects and time-consuming to explore wide-ranging sensitivity analyses. Ensemble modeling across various quantitative models helps explain different conclusions and provides more robust scientific advice (Heneghan et al. 2021). However, relying solely on quantitative models in these endeavors requires substantial effort and time while still potentially obscuring significant unknowns.

In contrast, previous work has shown that qualitative network analysis (QNA) can help guide and interpret quantitative models and play a valuable role in model ensembles (Ferriss et al. 2022; Metcalf 2010; Reum et al. 2021), in addition to providing insights in data-poor systems (Reum et al. 2020; Rosellon-Druker et al. 2021; Szymkowiak and Rhodes-Reese 2020). QNA is qualitative in estimating the magnitude of species interactions but quantitative in constraining those interactions between −1 and 0 (negative impacts) or 0 and 1 (positive impacts) as well as in quantifying potential direct and indirect linkages that determine net impacts on a focal species. By evaluating the ratio of positive to negative outcomes for a given node in the network over a very broad range of parameter values (0–1), QNA offers a heuristic approach that efficiently refines the most salient questions regarding food web structure that might have emerged from expert opinions, conflicting results from quantitative models, or parameter values that may never be estimable. We used this approach to study an ecologically, economically, and culturally important species, Chinook salmon *Oncorhynchus tshawytscha* . Although salmon are relatively well studied in some respects, crucial gaps remain in understanding how species interactions influence their survival, especially in the ocean (Wells et al. 2020).

For Pacific salmon, temperature plays a profound but poorly understood role in marine survival. Although most temperate populations are expected to decline in a warming climate (Abdul-Aziz et al. 2011; Crozier et al. 2021; Kao et al. 2015; Piou et al. 2015; Shelton et al. 2021), relationships with climate variables change over time (Litzow et al. 2020; Malick 2020; Ohlberger et al. 2021), pointing to the importance of considering the role of biotic interactions for predicting responses to climate change. Salmon experience a relatively narrow temperature range in the ocean compared to freshwater—well below critical thresholds (Burke et al. 2016). Therefore, direct mortality from acute thermal stress is unlikely. Rather, reduced survival in warmer water is more likely mediated by food web interactions, including energetic costs and fatal consequences of reduced performance in suboptimal conditions. Measuring all possible species interactions in complex systems is unfeasible. Therefore, despite extensive research, the strengths of many of these interactions—particularly competition and predation—remain unquantified (Wells et al. 2020). This paper addresses these uncertainties by exploring food web linkages and trophic interactions using a qualitative analytical framework.

We apply qualitative network analysis (QNA) for a more holistic perspective on ecosystem structure relative to single-species models, but without the extensive data demands and computational restrictions of end-to-end ecosystem models (Geary et al. 2020; Kaplan and Marshall 2016). QNA operationalizes a conceptual model to examine the dynamic behavior of a community while depending only on the sign (positive or negative) of a species interaction (Dambacher et al. 2009; Levins 1974; Puccia and Levins 1985). In QNA, interaction strengths between species are represented as coefficients in a community matrix (Levins 1968). Matrix stability is assessed by analyzing the matrix's eigenvalues, indicating whether small perturbations will die out (stability) or grow (instability). Thus, matrix stability ensures robust network configurations, making it useful for exploring and validating ecological scenarios and interaction strengths. This simulation-based approach, where matrix stability is the primary criterion for "possible," can efficiently explore a wide parameter space of link weights (Melbourne-Thomas et al. 2012). In our case, at least, the decisive parameter space was much narrower than it had seemed in the absence of any network criteria. Therefore, this approach can rule out non-plausible regions of the parameter space and identify the most consequential potential link weights affecting an outcome, clarifying the power needed in empirical studies.

In this paper, we have four objectives: (1) Develop a conceptual model of the salmon-centric marine food web, incorporating various alternative representations for different possible structures. (2) Clarify our existing hypotheses that link climate warming to salmon marine survival, providing a clear framework for understanding these connections. (3) Apply QNA to investigate the stability and expected outcomes of various models, particularly focusing on the proportion of negative responses in salmon populations to simulated climate perturbations. (4) Perform sensitivity analyses to pinpoint the most critical species interactions driving the outcomes for salmon. We conclude with recommendations to prioritize research that will resolve the relative magnitudes (small vs. large) of a limited number of interactions. With targeted research, we expect that the greatest risks for salmon mediated by food web dynamics can be identified.

2 | Methods

2.1 | Study System

The Northern California Current (NCC) is a highly productive coastal ecosystem in the northeastern Pacific Ocean (Hickey and Banas 2008). We focus on the region from northern Oregon, United States, to southern British Columbia, Canada, which is particularly important for Pacific salmon and steelhead (*Oncorhynchus* spp.) from the Pacific Northwest. Our conceptual models reflect what is known about the early marine stage of spring-run and fall-run Chinook salmon that spawn across a wide range of habitats from coastal Washington to the mountains of Idaho. Chinook salmon enter the ocean in their first ("subyearling") or second ("yearling") year and spend 1 to 3+ years at sea before returning to natal streams to spawn. Spring-run smolts migrate quickly through the NCC to Alaskan waters using an offshore route, while fall-run smolts stay nearer to shore and travel more slowly along the coast (Anderson et al. 2019; Fisher et al. 2014). Many of these populations are listed as threatened under the US Endangered Species Act (NMFS 2022).

2.2 | Conceptual Model

QNA starts with a signed digraph representing how a community's different functional groups (nodes) are connected. The key aspects of this approach involve selecting which nodes to represent and determining how they are connected, indicating positive, negative, or neutral interactions (links). Variations in both the nodes and links result in alternative models that can be compared using matrix stability criteria and validated with field observations.

2.2.1 | Base Network Description

We built our initial trophic digraph after reviewing the literature on climate impacts on salmon (Crozier and Siegel 2023) and consulting with experts involved with NOAA ocean surveys that study salmon, their prey, and predators (especially the Juvenile Salmon and Ocean Ecosystem Survey, the Northern California Current Ecosystem and Newport Line Survey, the Joint U.S.-Canada Integrated Ecosystem and Pacific Hake Acoustic Trawl Survey, and the Groundfish Bottom Trawl Survey), as well as bird and mammal specialists (mostly NOAA staff, but also academic, state and tribal biologists, see acknowledgements). Fortuitously, two contemporaneous projects allowed validation of our network: an updated diet database for the NCC (Bizzarro et al. 2023) and an end-to-end ecosystem model food web for the Northern California Current that quantified energy transfers to and from salmon groups before and after recent marine heatwaves (Gomes et al. 2024).

We identified 3–4 functional groups within several broad trophic categories that play unique roles in terms of their connections. Categories represent (a) non-biotic drivers that influence the ecosystem, (b) Chinook salmon life history strategies, (c) prey, (d) competitors, and (e) predators. Our initial conceptual model digraph in Figure 1 shows these groups as nodes in our "Base" network. Arrows represent a positive impact, circles represent a negative impact, and no symbol at the end of a line indicates a neutral impact. Most of the signs are based on the assumption that predators benefit from consuming prey, while prey are depressed by predation. Neutral effects occur if the benefits or costs are negligible or cancel each other out (representing tradeoffs within a group) and are not modeled explicitly—i.e., the pair is not connected in the matrix so no value is associated with that link. For example, we assume that forage fish abundance is independent of salmon abundance despite interactions between these two nodes.

The salmon life history strategies represent combinations of (1) "stream-type" versus "ocean-type" (Quinn 2018), which differ in whether juveniles spend a full year rearing in freshwater before migrating to the ocean, and (2) spring-run versus fall-run ecotypes, which differ in the timing of adult return to freshwater and some aspects of their ocean behavior (Sharma et al. 2012). The typical size of these fish differs when they enter the ocean, which affects which prey they consume the most. The prey functional groups represent differences between a zooplanktonic versus piscivorous diet (Daly et al. 2009) and fish prey that are appropriately sized in the early versus late summer (Litz et al. 2019). Salmon, like many other fishes, are largely opportunistic and will typically eat whatever other fish are the right size and in the same location. So, some of the functional groups can be more size-based than taxonomically defined. Other species might better represent these groups for different salmon populations. Nonetheless, we modeled the network with certain representative species from the NCC in mind.

The climate drivers here are theoretical, but they are assumed to be correlated with warming (node a1) and some other independent climate forcing (node a3). Salmon follow three life history pathways distinguished by age and the season they arrive in the ocean—yearling (e1) and early subyearling (e2) groups smolt in spring, and late subyearling (e3) smolt in summer. We selected these groups because their diet depends on their size (which depends on age) and what food is available. The marine community they encounter varies seasonally due to systematic changes in winds and currents and the location and timing of reproduction in other species. These complex changes are represented here through differential links between early and late smolt migrants, as well as prey and predator nodes. For example, late subyearlings are more vulnerable to hake predation than early subyearlings because hake migrate northward over spring and summer from their spawning grounds in California. Late smolts also benefit more from age 0 spring- and summer-spawning forage fish than early smolts . In this model, we contrast a broader fall-run ecotype, which exhibits all three of these juvenile pathways in the PNW, with a strict dependence on the spring-yearling life history exhibited by interior Columbia and Fraser River spring-run populations (Waples et al. 2004). We note that other spring-run populations display different tactics. Therefore, the names here are specific to this study system, but the diversity of behaviors can be mapped to other systems.

We modeled the body condition of salmon (e1, e2, e3) as a direct response to food availability (b1, b2, b3). Subsequently, the

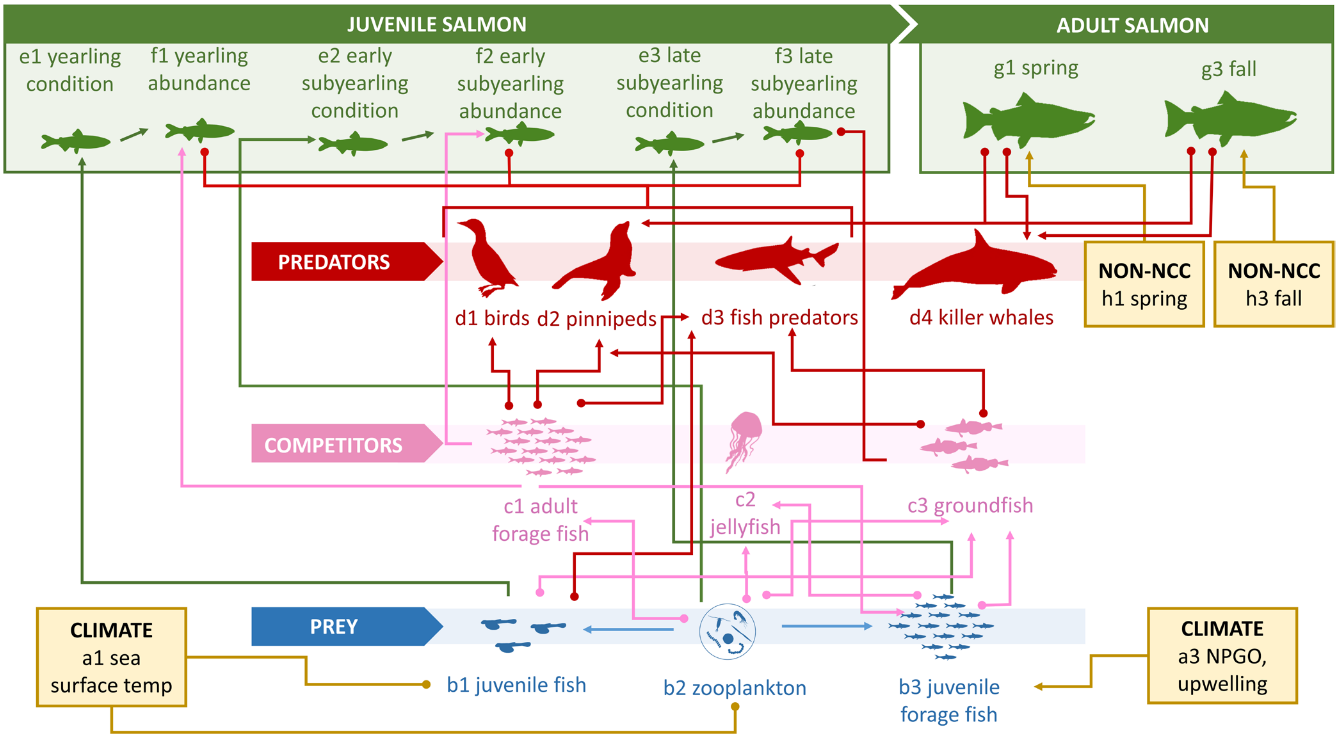

FIGURE 1 | Network diagram showing the simplified pathways by which climate indices (a1 and a3) could affect salmon. Links connect prey (blue), competitors (pink), predators (red), and salmon themselves (green) in two age classes (juvenile and adult) and two races (spring- and fall-run). The diagram distinguishes predators that preferentially consume juvenile vs. adult salmon and has different pathways representing early (in spring) and late (in summer) smolt entry into the California Current Large Marine Ecosystem. Arrows represent a positive impact, circles represent a negative impact, and no symbol at the end of a line indicates a neutral impact. See Table S1 for an explanation of the nodes and Table S2 for an explanation of links.

effects of predation (d1, d2, d3) influence their abundance (f1, f2, f3). While condition and abundance are not necessarily separated in time, constructing the network this way allowed us to differentiate regulation by competitors and predators more clearly.

We distinguish between three types of competitors, such that each has uniquely signed links. Gelatinous species (c2) are assumed to be trophic dead-ends (Doyle et al. 2007) and hence share salmon prey but are not consumed by predators. Forage fish (c1) positively impact salmon in our base model because they may serve as alternative prey for salmon predators, reducing predation pressure on salmon (Phillips et al. 2021). We removed this benefit to salmon in one of the model variants to explore this uncertain relationship. Hake (Pacific whiting, *Merluccius productus*) are very abundant in the NCC and are represented in the c3 node. Their diet overlaps with juvenile salmon, but they can also be occasional predators, particularly in summer (Wells et al. 2024).

We distinguished between predators that eat juvenile but not adult salmon (bird, d1, and fish, d3), predators that eat both juvenile and adult salmon (pinnipeds, d2), and predators that specialize in adult salmon (Southern Resident killer whales, d4). Most predators (d1, d2, and d3) rely on forage fish (c1) more than salmon, so this important relationship is captured in the model. See Tables S1.1 and S1.2 for a more thorough description of each node and link with example indices.

2.2.2 | Hypothesized Pathways for Temperature Effects

We assembled hypotheses from the literature explaining the main impacts of climate on Pacific salmon (for a review, see Crozier and Siegel 2023). We identified six hypotheses to characterize the relative sensitivity of different nodes to temperature (Figure 2). H1 strictly follows bottom-up forcing, with node a1 acting negatively on spring prey nodes b1 and b2, based on Daly et al. (2013). The remaining hypotheses include this well-established link while adding other direct effects. H2 reflects a higher bioenergetic cost for salmon in warmer years that reduces condition (e1, e2, and e3, Daly and Brodeur 2015). H3 models an increase in competitor nodes. H4 models a positive climate impact on three of the four predator nodes to control for the number of links added, while H5 adds positive climate impacts to all predator nodes. In H6, all nodes affected by H1-H5 experienced direct effects of climate.

We conceptualize positive effects on competitors and predators as an increase in consumption, meaning any increase in their impact on other species. Increased consumption could result from increased bioenergetic costs leading to more prey per predator, a shift in spatial distributions that causes more spatial or temporal overlap with salmon, an increase in relative preference for salmon, perhaps due to a decline in another prey item, or an increase in the abundance of the competitor or predator.

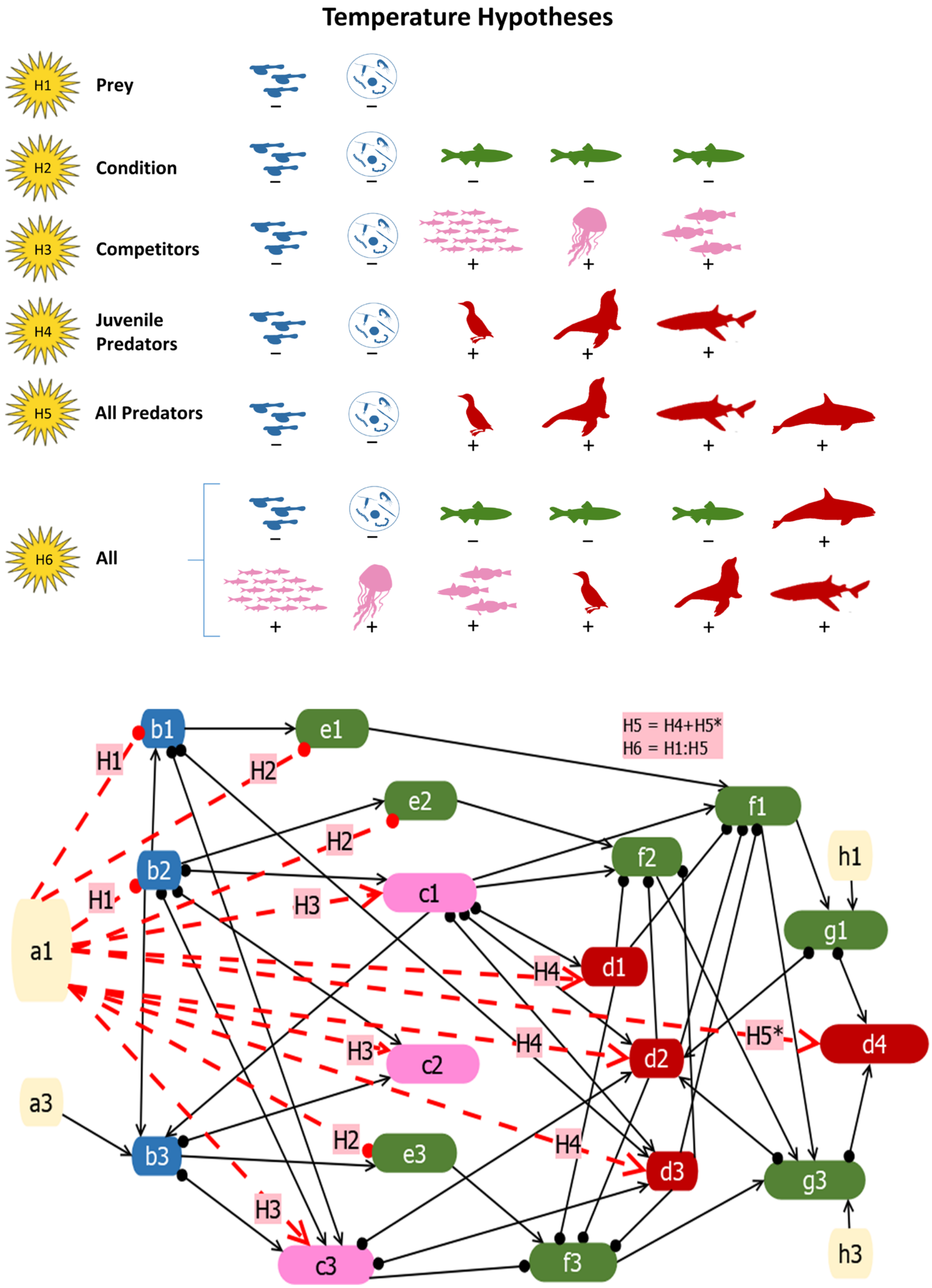

FIGURE 2 | The temperature hypotheses (H1–H6) added direct links from climate to specific nodes. These hypotheses highlight the diversity of processes that are affected by global change. The sign (+ or –) below each icon in the top panel shows whether climate (a1) had a positive or negative impact on that node. The hypotheses are labeled for the main functional group that was affected in that hypothesis. The network diagram in the bottom panel shows the same links in Figure 1 in black solid lines plus all links that were added in H6 (all red dashed lines). Subsets of red lines show which links were added in the other hypotheses (see top panel). The specific links added in H1-H6 are listed in Table S3.

2.2.3 | Alternative Food Webs

One of the advantages of QNA is that alterations to the conceptual model are easy and quick to execute, facilitating the exploration of many assumptions that are usually fixed in more quantitative models. We therefore altered the basic network structure to determine the robustness of our main conclusions to details in the conceptual model. We did this by examining each major node in the conceptual model and adding or subtracting links to that node. We selected which link to add or remove by revisiting the unanimity of support among experts and the depth of the literature that had initially supported the link. Also, in some cases, the direction of a link could differ depending on which representative species of a functional group or which age class within that species is most dominant, which could be uncertain in the literature or vary over time. Alternative food webs reflected both uncertainty and potential future changes (non-stationarity) in food web structure. Our intent was to be illustrative of network sensitivity rather than exhaustive of all possible variations.

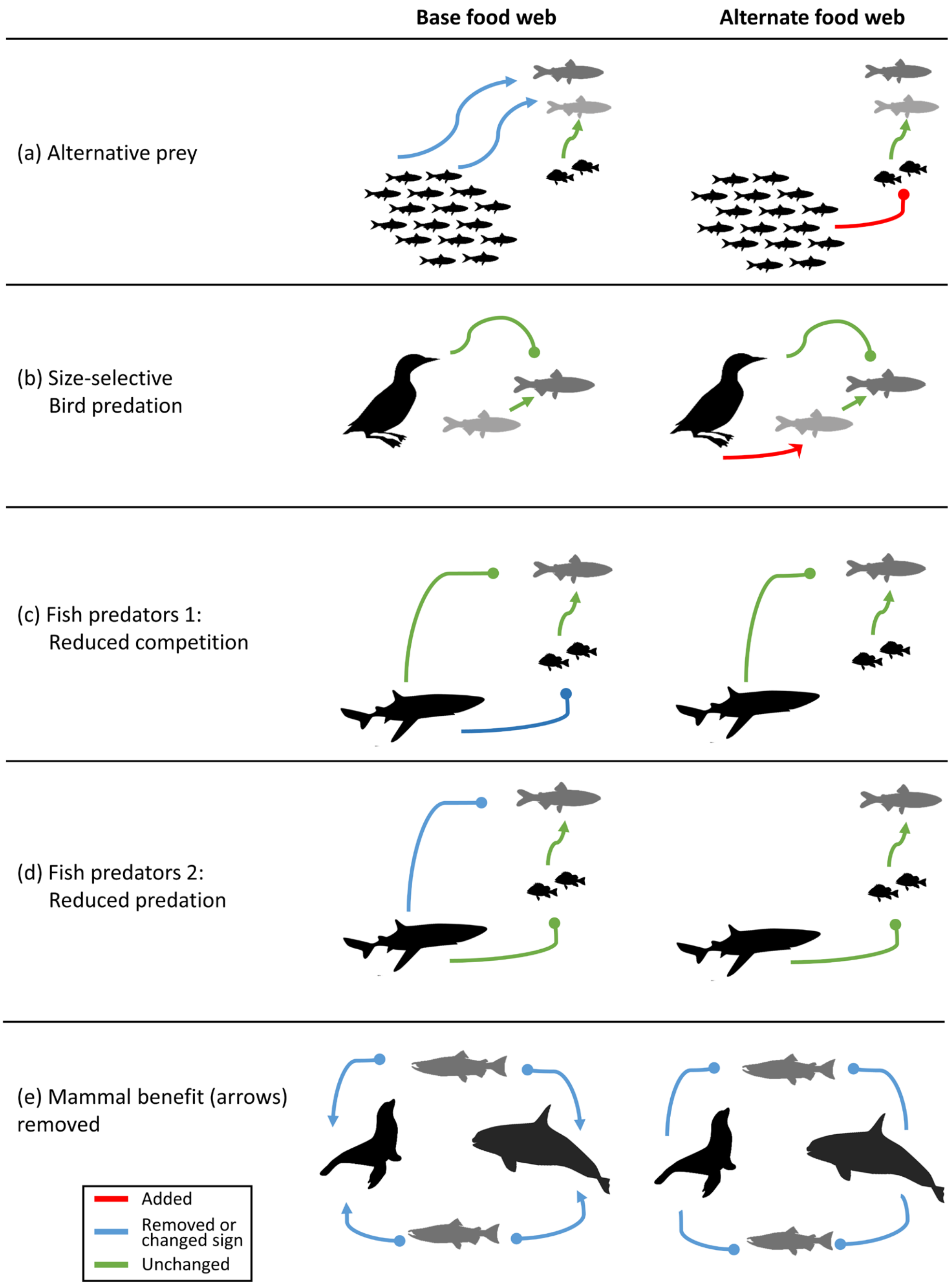

FIGURE 3 | Alternative networks added, removed, or changed the sign of particular links. Changes reflected (a) different relationships with forage fish, (b) higher bird mortality in smaller versus larger smolts, (c) reduced salmon competition by ground fish, (d) reduced predation from ground fish, and (e) removal of feedbacks between salmon and mammal population sizes. Colors indicate which links were added (red), deleted or sign-changed (blue), or unchanged (green). Juvenile salmon condition is light grey, while salmon abundance is dark grey. See Data S2 for additional descriptions of these food webs.

We developed five alternative food webs to manipulate the roles of particular nodes. Specifically, we modified the impact of (1) forage fish (c1) by removing their positive impact as alternative prey on salmon survival (Figure 3a) (Koehn et al. 2017). We modified (2) bird predation (d1) by adding size selectivity in the form of preferential consumption of smaller smolts (Vasbinder et al. 2024) in addition to decreased abundance (Figure 3b). (3) We reduced competition from fish predators (d3) by removing their link to yearling prey (b1, Figure 3c) to explore the role of reduced complexity overall, given that this node had a large number of impacts on other nodes. (4) We reduced predation by fish (d3) by removing their link to yearling smolts (f1, Figure 3d) because predation rates by piscivorous fish are extremely hard to measure and are likely to be highly variable. Given these rates will likely remain uncertain, we wanted to explore salmon sensitivity to these parameter values in as many ways as possible. Finally, we altered the 5) mammal nodes (d2 and d4) by reducing the benefit they accrue from eating juvenile and adult salmon (Figure 3e). We did this to explore tradeoffs between salmon ecotypes and because mammal populations are subject to other constraints besides salmon, which could limit their population growth. These food webs are explained further in Data S1. The combination of six food web structures by six temperature hypotheses produced 36 different scenarios.

2.3 | Qualitative Network Analysis

In QNA, each node in the signed digraph represents a "population." Changes in the density of one population impact other populations through a matrix of interaction coefficients, also called link weights. These coefficients represent the direct effect of one node on another, i.e., the partial derivatives of each differential equation describing their respective population dynamics, evaluated at the equilibrium (Melbourne-Thomas et al. 2012). The stability of the equilibrium is evaluated from the eigenvalues of the community matrix (Levins 1968; Puccia and Levins 1985). In simulations, coefficients for the entire matrix are drawn from uniform distributions from −1 to 0 for negative interactions or 0 to 1 for positive interactions, depending on the sign defined by the digraph (Figure 1) (Dambacher et al. 2009). All nodes also had self-limitation links (from −1 to 0 on each node), which act like a density-dependence constraint. This dampening parameter was required for efficient simulation computing times and is also biologically reasonable.

All sets of coefficients that produce stable matrices are retained for future analysis ("accepted models"). Note that although analysis relies on stable matrices for mathematical tractability, this assumption does not require that the ecosystem itself be stable or that the response be linear (Bender et al. 1984). Stability avoids transitory oscillations and captures a more persistent, directional response. The response to the press perturbation therefore reflects the expected direction of response in one community member, given the specification of other relationships. Over decades, the community could establish a new equilibrium with new qualitative relationships, so we consider this analysis to apply to the near-term responses to climate change. New matrices are drawn until a pre-defined number of stable matrices are attained. The digraph could be more likely when more random sets of coefficients produce stable matrices. Therefore, our first test in model comparison was the acceptance rate of each digraph. We used the package QPress (Melbourne-Thomas et al. 2012) accessed from the GitHub repository "SWotherspoon/QPress" (https://github.com/SWotherspoon/QPress). We completed all analyses in R (v4.3.1; R Core Team 2023).

We next analyzed the impacts of a press perturbation on the climate node a1, such as the gradual warming of ocean waters due to climate change. A press perturbation is a persistent pressure imposed on a community by forcing a positive (or negative) change on a particular node to assess how the density of other nodes changes (Bender et al. 1984; Glasby and Underwood 1996). Outcomes are positive if there is an increase in the population growth rate after the perturbation or negative if the growth rate decreases.

We generated 100,000 community matrices (i.e., simulations for the press perturbation) per network. We summarized the net outcome of a press perturbation as the number of positive outcomes minus the number of negative outcomes divided by the total number of simulations (thus scaling our results between −1 and 1). Therefore, a negative mean outcome had more negative than positive outcomes, and vice versa. We used the same thresholds as Sobocinski et al. (2018) to define mean outcomes as "consistently negative" between −1 and −0.6, "weakly negative" between −0.6 and −0.2, "neutral" between −0.2 and 0.2, "weakly positive" between 0.2 and 0.6, and "consistently positive" when greater than 0.6.

The response variables of primary interest were adult spring-run and fall-run salmon and how their mean outcomes varied across our alternative hypotheses of temperature impacts and food web structures. We also reported the responses of all other nodes in the network (Data S2), which could be compared with field observations in the future to assess network likelihood further.

2.4 | Sensitivity Analysis

We assessed the sensitivity of our results to individual links in the network. From these results, we identified data that would be most useful in validating our hypothesized mechanisms. We used boosted regression trees (BRT, Elith et al. 2008) to compare the relative importance of each link for predicting a positive or negative outcome for the two adult salmon nodes after a climate perturbation. BRT builds on the classification and regression tree (decision tree) group of models, in which each link is tested at each branch in the tree to make the best split between positive and negative outcomes for salmon. We constructed many decision trees by resampling the data and iteratively limiting the subsequent sample to the outcomes not correctly assigned by the previous tree. The final model is a sum of the weighted predictions from all individual trees.

We fit the BRT to link weights from 10,000 simulations for each network explored. We used the gbmStep function in the package "GBM" (Greenwell et al. 2022) to optimize the number of trees developed to minimize the predicted deviance using cross-validation while including no less than 1000 trees, based on Elith et al. (2008). Most of the resulting BRT models included 2000–5000 trees, a tree complexity of 15, a learning rate of 0.01, and a bag fraction of 0.5, determined after initial explorations using the base model. We ran the analysis separately for spring- and fall-run. We examined the relative influence of all variables, an output of the gbmStep function. Relative influence reflects the number of times a variable was selected by the decision model, weighted by the improvement to model fit after each split (Friedman and Meulman 2003). We highlight the variables whose cumulative influence accounted for 20% of model performance. The full influence table is publicly available with the rest of the model code (Crozier 2025).

3 | Results

3.1 | Network Stability

Across the 36 networks we fit through simulation, most of them required a similar number of attempts to find stable matrices. There was one exception: the food web in which mammal benefits were reduced was particularly high in the model acceptance rate (93%) (Table S4). The remaining food webs had 66%–70% acceptance rates. Networks with higher acceptance rates are not necessarily a better representation of the real world. They

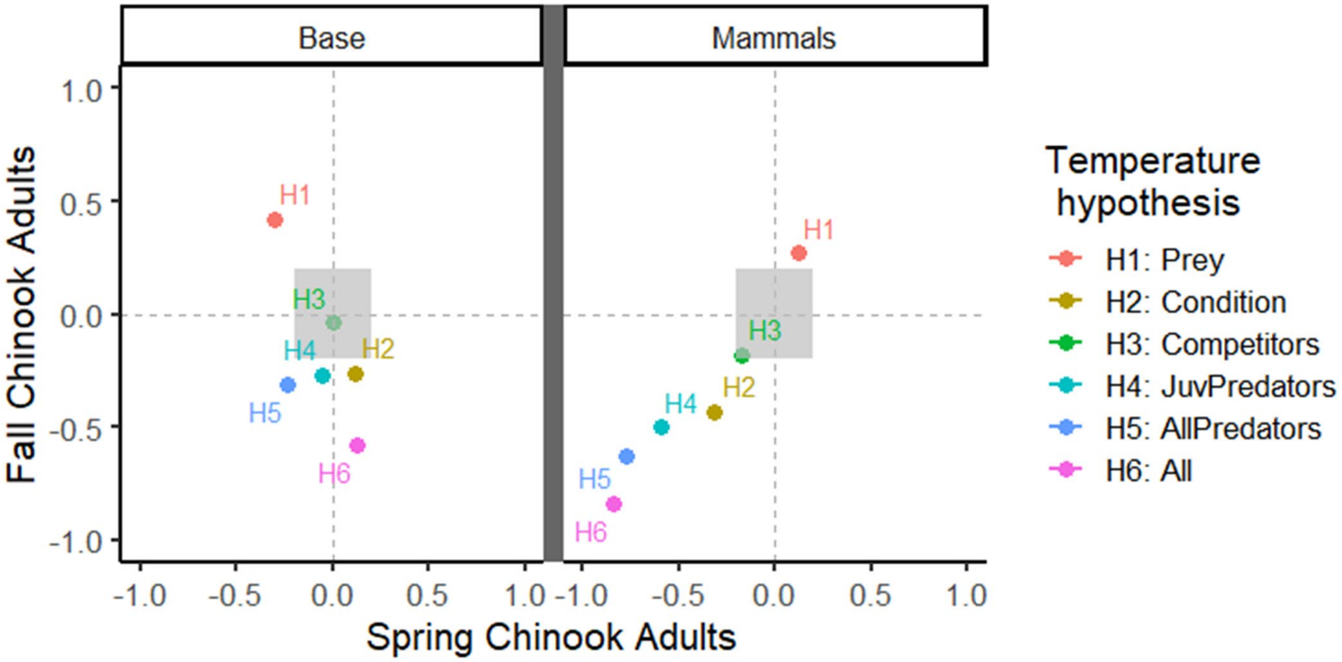

FIGURE 4 | Comparison of mean outcomes for spring- and fall-run adults across the temperature hypotheses found in Figure 2. The grey box outlines the jointly "neutral" response area between −0.2 and 0.2 on both axes. The axes indicate the net outcome for either spring-run (x-axis) or fall-run (y-axis) calculated as positive outcomes minus negative outcomes divided by the number of simulations. The left panel shows results from the 'Base' food web, whereas the right panel shows results when the positive impact of salmon consumption is removed from mammalian predators (see Figure 3e).

might, however, be more stable as a community because there is a greater variety of possible individual link weights that lead to stability.

3.2 | Sign Determinacy After Climate Perturbation

Sign determinacy for adult salmon was within the weakly positive to weakly negative range across most scenarios we explored. However, certain combinations of particular food web and temperature hypotheses dramatically shifted the mean outcome into the consistently negative range, while others produced unusually positive outcomes. Here we investigate scenarios in more detail that produced a more neutral range of outcomes (H1, base model) and the most extreme outcomes (H5 and H6, mammal food web).

Base network—When we imposed a press perturbation of a positive sign on the a1 node, we assessed the mean response, from −1 to 1, in spring and fall adult salmon. We found that most of the temperature hypotheses for the base food web produced mean outcomes for spring-run that ranged from neutral to weakly negative (0.13 to −0.33) (x-axis in Figure 4, left panel, Figure S2.1 and Table S4). The more negative outcomes for spring-run occurred when prey and all predators were directly affected by temperature (H1 and H5). Fall-run displayed a wider range of outcomes than spring-run (y-axis in Figure 4, left panel), from negative for H6 (−0.58) to weakly positive for H1 (0.42). Note that H1 was the worst outcome for spring-run and the best outcome for fall-run. For responses in all other functional groups, see Table S5.

Mammal network—Changing the digraph in Figure 1 to remove the positive impact of salmon consumption on mammalian predators (Figure 3e) shifted most spring- and fall-run outcomes into the weakly or consistently negative categories (Figure 4, right panel). The two ecotypes showed similar responses to the temperature scenarios—most points in the right column lie roughly along the 1:1 line. The mammal network modification also increased the spread of outcomes across temperature hypotheses. In the mammal food web, the All Predator (H5) and All Group (H6) temperature hypotheses were strongly negative for both spring- and fall-run (H5 spring: −0.76, H5 fall: −0.61, H6 spring: −0.84, H6 fall: −0.85).

Size-selective bird predation—This food web tended to produce more favorable outcomes for fall-run when compared with the other food webs, although they were still mostly in the neutral zone (Figure 5, right panels). H1 was weakly positive, and H6 was weakly negative for fall-run. For spring-run, outcomes were also neutral or weakly negative but slightly worse than those of the other food webs (except the mammal food web, Figure 5, upper left panel). The remaining food webs produced mostly neutral to weakly negative outcomes for both runs and were roughly similar to the base food web (Figure 5). H1 tended to be more positive for fall-run and negative for spring-run and is labeled as an outlier in Figure 5.

Temperature hypotheses—Treating all of the food webs as inherent uncertainty in the current community structure, we have grouped them in box and whisker plots and plotted them for each temperature hypothesis in the lower row of Figure 5. The most consistently negative responses (less than −0.6) for

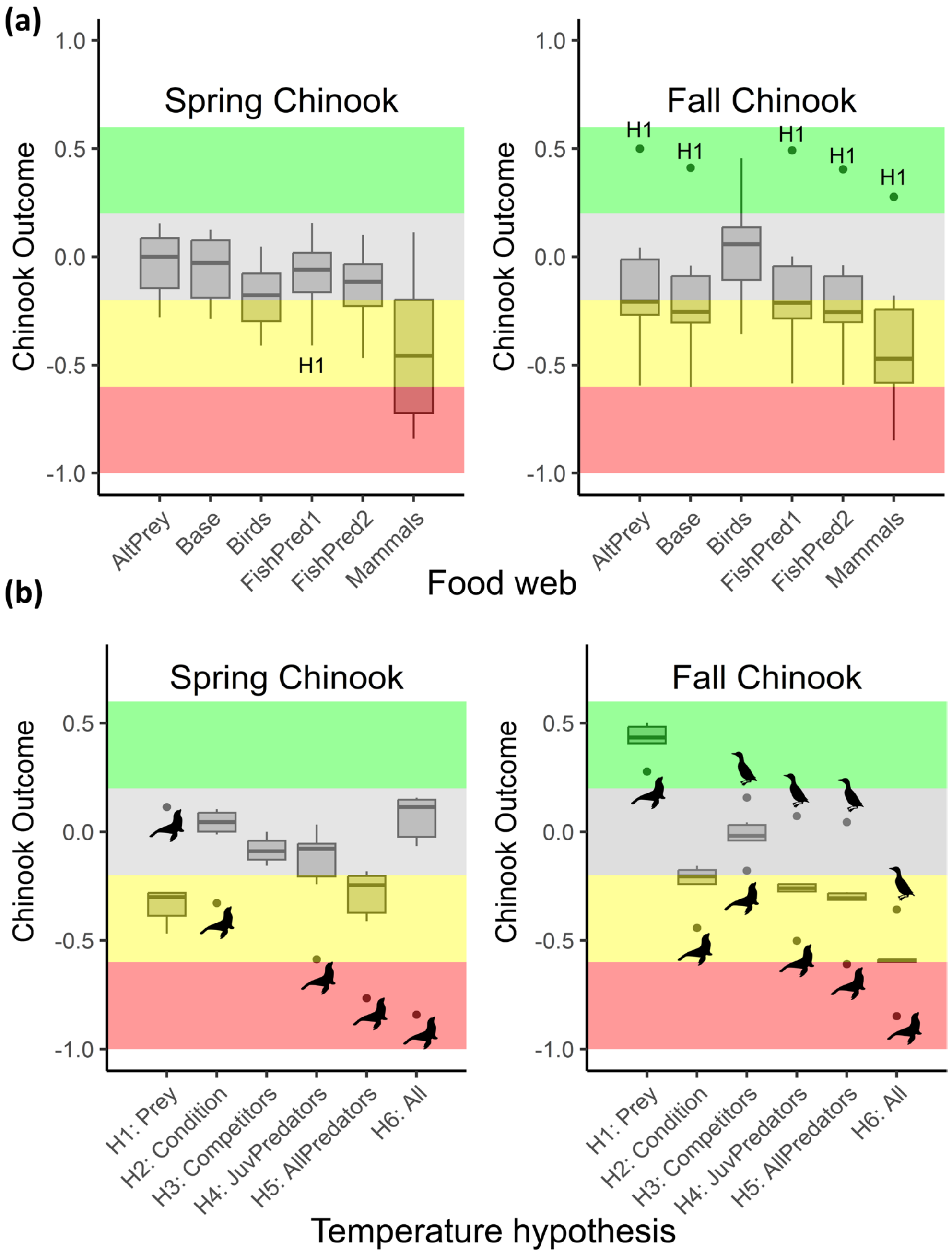

FIGURE 5 | Boxplots show the spread of outcomes for either spring-run (left) or fall-run adult salmon (right) across 36 scenarios. Outcomes are partitioned across alternative food webs (top) and for a given temperature hypothesis (bottom) after a positive press on climate. The boxes show the interquartile range, and whiskers show at most 1.5 times that range. Individual boxplot outliers are identified with sea lion icons (mammal food web), birds (size-selective food web), or H1 (bottom up temperature hypothesis). Green rectangles indicate weakly positive outcomes, grey is neutral, yellow is weakly negative, and red is consistently negative.

spring-run and fall-run occurred in the mammal food web when competitors and predators were impacted directly by climate (H5 and H6). Weakly positive outcomes for fall-run occurred in all food webs in the bottom-up (H1) temperature scenario. The remaining scenarios were largely neutral or weakly negative for both runs.

In an additional analysis of the network's sensitivity to node-specific climate impacts, we quantified the responses for spring- and fall-run when adding a climate impact to each node one at a time. We show responses to both positive and negative links from a1.Clim1 node to each additional node for both the base and mammal networks in Table S6. In the base network, adding direct climate impacts on the adult stage or in the conditions outside the NCC caused a consistently negative response in spring-run. When climate had a negative impact on other links, the spring-run response was either weakly negative or neutral. In the mammal network, those same links, plus other impacts directly on salmon nodes and some predators, caused weakly negative outcomes for spring-run. We note that an additional negative impact from conditions outside of the NCC is a significant concern and warrants further investigation. Recent papers have described increased competition with pink salmon in the north Pacific as an explanation for reduced survival in sockeye and Chinook salmon (Connors et al. 2024; Kendall et al. 2020; Ruggerone et al. 2023), which would be consistent with this modeled result.

3.3 | Sensitivity Analysis

The simulations were designed to explore the full range of possible parameter values across all pairwise interaction strengths. The sign-determinacy analysis demonstrated that there are roughly similar numbers of parameter combinations that can produce positive and negative outcomes for adult salmon, although negative outcomes were more frequent overall. The purpose of the BRT analysis was to identify which links were most important in determining whether the outcome for salmon was positive or negative. We focused our analysis on similarities and differences between the most influential links in the scenarios that differed the most in mean outcomes—H1 was especially differentiated between spring- and fall-run, while H5 and H6 differed markedly between the base and mammal networks. We therefore present results for spring- and fall-run in the base and mammal networks in three temperature scenarios (H1, H5 and H6).

The BRT analysis revealed that variation in which links were most influential differed more across temperature hypotheses than run type. In the H1 scenario, the most influential links were the self-limiting constraints on salmon (e1, e2, f1, or f3) for both salmon runs and for both the base and mammal networks (these links are colored green, and H1 is shown in the first column in Figure 6 and Figure S3.1). The next most frequently important link was piscivorous fish predation in three of the four network/ecotype combinations (all but the base model, fall-run). For fall-run in the base model, the intensity of climate forcing on the prey base was more influential than fish predation (Figure S3.1). These results are consistent with the logic of bottom-up forcing, where the dampening factors regulate how responsive salmon are to changes in the prey base. Pressures from competitors and most predators were much less decisive. Fish predators played an interesting and somewhat counterintuitive role—increased predation improved salmon outcomes in the model. It is notable that the alternative food web in which that link was removed altogether had similar or slightly more negative outcomes for both runs (Figure 5), suggesting it plays an indirect and perhaps dampening role across the network.

In the H5 scenario, the strength of climate forcing on prey, birds, and mammals was highly influential in all run and model combinations (black bars, middle column, Figure 6 and Figure S3.1). Salmon transition rates between juvenile and adult abundance (f1 to g1 and f3 to g3, green bars) were the next most important parameters in the base model for both spring and fallruns. For fall-run, self-regulation in juvenile abundance (f3 to f3) was highly influential in both base and mammal networks. For spring- but not fall-run, self-regulation among predators and the benefit to killer whales (base) or predation on adults from killer whales (mammal network) also appeared in the top 20% of explanatory variables (red bars). These patterns reflect the tension, particularly for spring-run between climate increasing predator consumption rates (i.e., the combination of climate forcing and self-dampening in predators) and salmon being able to resist the increased pressure (i.e., salmon transition rates and self-dampening).

In H6, similar factors were important as in the other two hypotheses, but a new role appears for competitors, particularly in the mammal network. Climate forcing on gelatinous species and mammal consumption of hake were in the top five variables in the mammal network. Hake was also in the top 20% of importance in H5 in the mammal network, and climate forcing on gelatinous species appeared in the H6 base network for fall-run. The benefit to pinnipeds of consumption of adult salmon also appeared in the H6 base model for fall-run. These patterns demonstrate that indirect pathways, via competitors, could swing the balance against salmon survival. The high proportion of negative outcomes in the mammal H6 scenario indicates that if these links are positive in sign, they all have to be very small in magnitude (near 0) to produce a positive outcome for salmon.

In summary, increasing the ways in which climate acts directly on the network increases the number of functional groups that can exert strong pressure on salmon, possibly determining their fate. Therefore, if we can assume that climate directly impacts primary and secondary productivity, but not higher trophic levels, then research directly on salmon and their prey might be sufficient to quantify the impacts of climate change (Figure 7, H1). However, if competitors or predators experience connections to climate that are independent from bottom-up forcing, then we need to measure those responses and include them in any projection models for salmon (Figure 7, H5 and H6). Of particular importance was the responsiveness of mammal population abundance to salmon density. The links from salmon to pinnipeds and killer whales had profound impacts on salmon outcomes directly (Figure 7 rows 2 and 3 from the base network) and for the roles of other indirect links (Figure 7, row 4 from the mammal network). Indirect links connected competitors and predators to salmon, which is perhaps not very surprising. More surprisingly, they also connected spring- and fall-run ecotypes: note the importance of fall-run juvenile (e2, e3, f3) and adult (g3) links for spring-run outcomes in Figure 7. Thus indirect links connect the entire food web, including salmon populations that may only interact via their predators.

4 | Discussion

This study explored 36 plausible representations of the most influential interactions among climate, marine community groups, and salmon life stages, along with additional analyses of one-at-a-time climate impact scenarios (Table S6). Our findings identified key links influencing salmon outcomes, highlighting the importance of predator–prey dynamics, competitive interactions, and climate-induced changes in species' consumption rates. These insights suggest that qualitative network modeling can be a valuable tool for assessing ecological risks in both data-poor and data-rich systems.

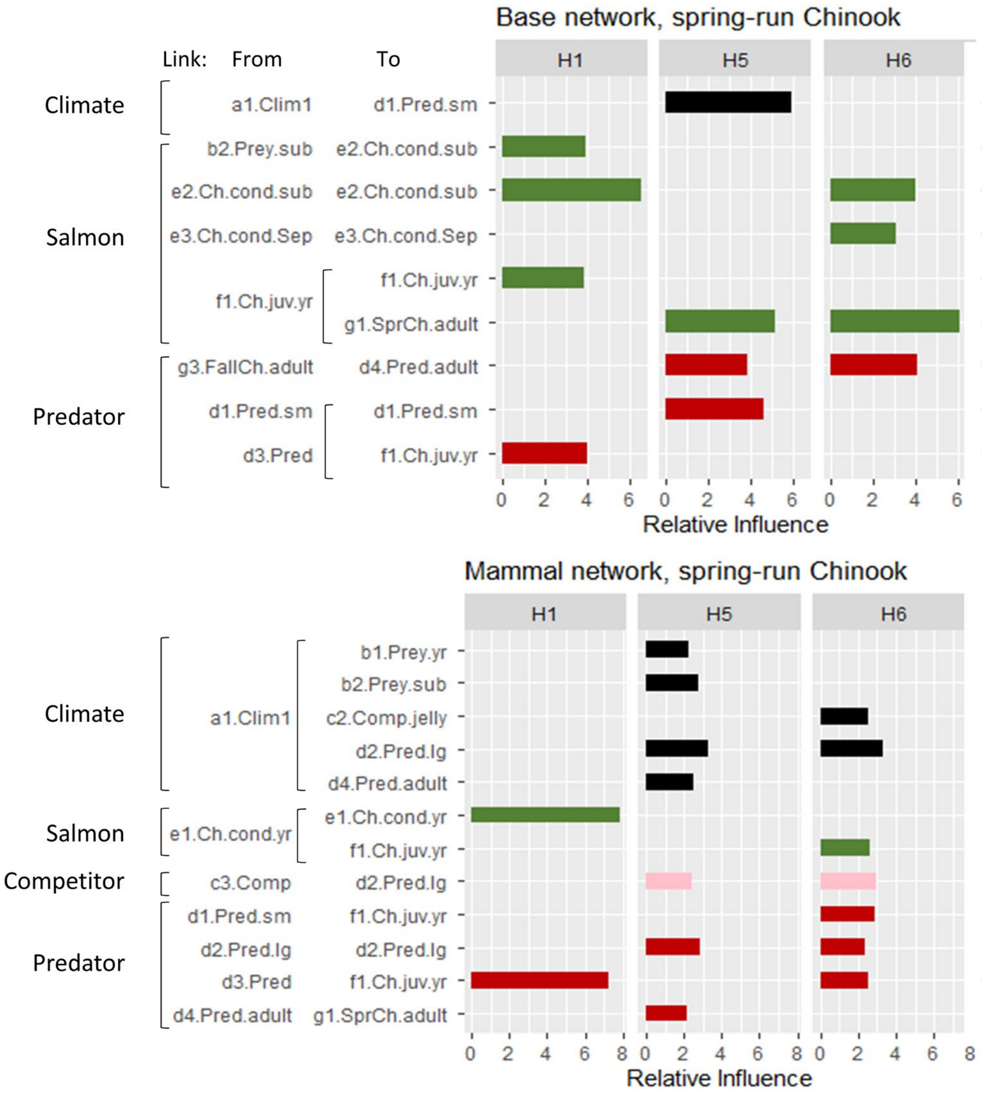

FIGURE 6 | The most influential links for spring-run adult salmon outcomes from the boosted regression tree analysis. Each panel shows the relative influence of variables that constituted the top 20% of explanatory power for a particular scenario (i.e., food web and temperature hypothesis combination). The analysis assessed the importance of a specific weight assigned to each link for predicting adult salmon outcomes (i.e., a positive vs. negative response to climate forcing). Base food web (Figure 1) results are shown in the top panel, mammal food web (Figure 3e) results are shown in the bottom panel. The first column shows the H1 scenario (bottom-up), the second column shows the H5 scenario (temperature-amplified predation), and the third column shows the H6 scenario (all groups directly affected by climate, see Figure 2). We grouped all links that included a climate driver in black, predator in red, competitor in pink, and salmon self-limitation, prey response, or life stage transition in green. The y-axis names indicate the starting (From) and ending (To) nodes involved in the link, where ‘a’ indicates a climate node, ‘b’ indicates salmon prey, ‘c’ indicates a competitor, ‘d’ indicates a predator, ‘e’ is salmon condition, ‘f’ is juvenile salmon abundance, and ‘g’ indicates adult salmon nodes (see Figure 1). Figure 7 shows an iconographic representation of the links in the top three panels and bottom right panel of this graph. For fall-run salmon results, see Figure S3.1.

4.1 | The Importance of Diverse Pressures From Climate Forcing

We compared network structures that varied in both species relationships (alternative food webs) and climate sensitivity (alternative temperature hypotheses). Scenarios that included direct links from climate to predators and competitors (H5 and H6) and lacked strong dampening feedbacks to mammalian predators showed nearly universally negative effects on salmon, regardless of the strengths of other interactions (Figure 5). Other scenarios had more equivocal results, suggesting compensation across the network. Clarifying the extent to which multiple functional groups may increase their consumption rates is necessary for predicting climate-related threats.

Several mechanisms could lead to increased consumption rates. Firstly, temperature (Clarke and Fraser 2004) and dissolved oxygen (Pörtner and Farrell 2008) impact metabolic rates. As metabolic rates increase, organisms can increase their consumption rates to meet their energetic needs (Deslauriers et al. 2017). Secondly, range expansion or range shifts could increase the spatial overlap between salmon and more voracious competitors or predators (Daly et al. 2024, Morley et al. 2018).

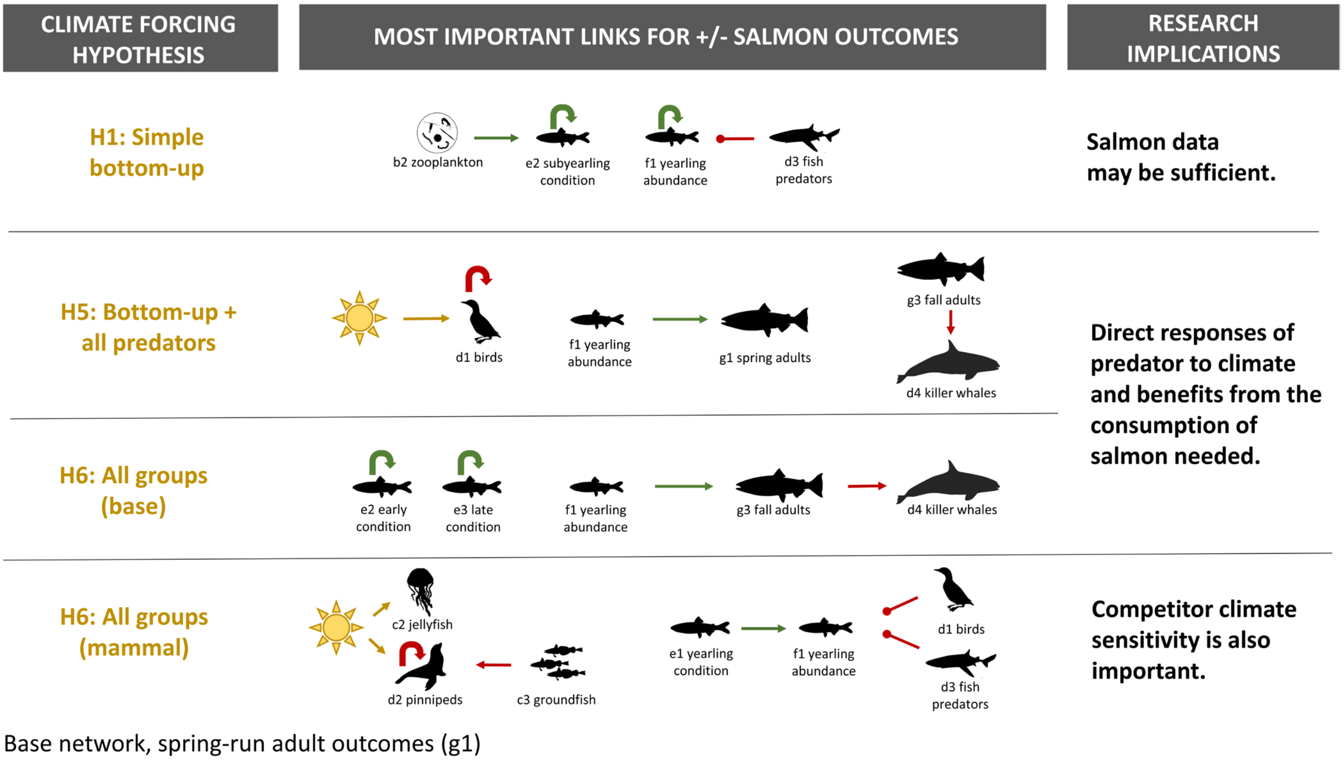

FIGURE 7 | Research implications of boosted regression tree results for spring-run salmon. This schematic shows the links that were most informative in the BRT analysis in separating positive from negative outcomes for spring-run Chinook salmon (data shown in Figure 6). Arrows indicate all of the links that cumulatively explained 20% of the variance for three of the temperature hypotheses (H1, H5 and H6) in the base food web, and H6 in the mammal food web in order to connect the results from the analysis to research implications. Despite the interconnectedness of the entire food web in all scenarios, specific quantification of competitor and predator dynamics was not necessary in the H1 scenario, but was when other species have their own direct responses to climate change (H5 and H6). Straight lines with arrows (positive effects) or circles (negative effects) identify a link between functional groups, while curved lines indicate self-limiting parameters on a node.

Salmon populations are tied to their freshwater spawning streams, so they cannot shift their latitude of ocean entry, although patterns of marine residency may change (Abdul-Aziz et al. 2011; Shelton et al. 2021). Thirdly, changes in prey availability can lead to a switch toward other species. For example, when rockfish are less available, common murres in California shift their diet toward anchovy, which circumstantially increases their consumption of co-located salmon (Wells et al. 2017). Fourthly, changes in salmon growth rates, including temperature-induced smaller body sizes, could increase their vulnerability to predators (Tucker et al. 2016; Vasbinder et al. 2024). Contraction of typical prey sizes leads to an increase in the number of prey consumed in breeding murres (Schrimpf et al. 2012). Thus, consumption of salmon may increase in a warmer environment through in situ physiological processes and spatial redistribution.

Other network analyses have also emphasized the risks of multiple stressors on fish species, particularly stressors with synergistic impacts (Babcock et al. 2016; Wedding et al. 2022). Synergistic effects can easily produce nonlinear consequences and tipping points in complex systems, which are especially problematic for threatened and endangered species (Fagan and Holmes 2006). However, we are unaware of any papers that directly assess the risk of climate-induced intensification of multiple trophic pressures on the ocean stage in salmon. Diverse responses across functional groups could help explain shifting relationships between longstanding climate indices and salmon survival (Litzow et al. 2019). Most models of salmon responses to climate avoid the exploration of explicit mechanistic relationships by invoking large-scale climate indices (e.g., the Pacific decadal oscillation, North Pacific gyre oscillation) to explain total return rates, without modeling age- or location-specific processes. Although authors often invoke competitor and predator pathways to justify the importance of climate indices, these pathways are not quantified (e.g., Peterson et al. 2014; Wells et al. 2020).

Recent work has clarified that competitive interactions among salmon species and between wild and hatchery salmon could be important drivers of salmon decline (Connors et al. 2020; Kendall et al. 2020; Ruggerone and Irvine 2018; Ruggerone et al. 2023). Competitive interactions are accentuated in unfavorable climatic conditions, likely due to reduced productivity (Connors et al. 2020). The documented patterns have generally occurred outside the NCC, which is consistent with our finding that climate forcing on the non-NCC node could be more detrimental than many of the NCC-only components we have focused on (Table S6). Similar models with Alaskan species in mind could be explored in the next step.

The role of predators in the open ocean remains largely unknown, except for specific bird/salmon interactions mediated by krill or anchovy abundance (Phillips et al. 2021; Vasbinder et al. 2024) and pinniped/salmon interactions at migration pinch points (Moore and Berejikian 2022; Wargo Rub et al. 2019). Our model suggests a pathway to quantifying the risk for salmon of compounding pressures with climate change. BRT analysis identified particular links in the network that predicted negative salmon responses. Further examination revealed that these links tended to be close to 0 or have an absolute magnitude near 1 in the alternate salmon outcomes, suggesting detectability in the wild.

The 2014–2016 marine heatwave (Gentemann et al. 2017) provides a natural experiment on community responses to rising temperatures. Survival of several seabird and mammal species in the NCC dramatically decreased, largely due to declines in their prey (McCabe et al. 2016; Trainer et al. 2020). However, responses across top predators are mixed. A systematic analysis of eight cetaceans predicted responses during the heatwave based on habitat models (Becker et al. 2019). Their models correctly anticipated changes in abundance and distribution in 8/9 species (5 species increased and 3 species decreased). Projections of future range shifts in 15 top predators in the California Current predicted that 9 species (3 birds, 3 tunas, 1 pinniped, 1 shark, and 1 turtle) would likely increase their core range northward; California sea lions showed no change, while 5 species (3 sharks, 1 whale, and 1 turtle) would contract their core habitat area (Hazen et al. 2012). However, rising temperatures are also likely to intensify impacts from harmful algal blooms (Ralston and Moore 2020), warm-water-associated diseases (Burge et al. 2014), and spread of viruses to marine mammals (Postel et al. 2022; Ramey et al. 2017). Future work could quantify the risk these threats pose and their impact on the consumption of salmon.

Numerous competitors and potential fish predators expanded their biomass in the NCC during recent heat waves, including certain gelatinous species, California market squid, Pacific pompano, jack mackerel, and Pacific hake (Brodeur et al. 2019; Morgan et al. 2019). Some salmon prey also increased in abundance (krill, juvenile rockfish, and crab larvae) (Morgan et al. 2019). Gomes et al. (2024) used an end-to-end ecosystem model to characterize changes in modeled consumption rates based on the biomass changes. They found strong increases in the newly observed gelatinous tunicate pyrosome and jack mackerel, with decreases in consumption by birds and pinnipeds. Chinook salmon, other forage, and ground fish declined during the heat wave in observed abundances (Ford 2022) and modeled biomass (Gomes et al. 2024).

Negative impacts on salmon during warmer periods therefore appear to be better explained by increased competition than climatically reduced productivity directly. Note that not all taxa are equally sampled, and an extreme event such as a heat wave (a pulse perturbation) does not necessarily represent the cumulative effects of global warming (a press perturbation). Nonetheless, given those observations, the competitor scenario (H3) and the most comprehensive climate impacts scenario across competitors and predators (H6) seem to be more consistent with the data than H5. More work is needed for a coherent assessment of the cumulative impacts on consumption across these functional groups.

4.2 | The Importance of Predator Dynamics in the Model

We pinpointed critical connections influencing salmon responses. The main determinant was the degree to which a rise in salmon as prey led to an increase in mammalian predators through heightened local abundance or increased per capita salmon consumption. Initially, we assumed these predators benefited from consuming salmon. Southern Resident killer whales specialize in Chinook salmon (Hanson et al. 2021); furthermore, salmon abundance is correlated with their body condition (fat reserves) and mortality (Stewart et al. 2021). Similarly, sea lion abundance peaks locally during salmon runs (NMFS 2016b) while seals track salmon and steelhead during their outmigration (Moore et al. 2021), indicating a benefit from consuming this prey.

Nonetheless, several factors may constrain mammalian population responses to fluctuations in salmon abundance. Pinniped populations may be at carrying capacity due to other constraints (Carretta et al. 2021), and Southern Resident killer whales face many threats that could constrain their populations regardless of salmon abundance, including inbreeding (Ford et al. 2018) and anthropogenic disturbance (NMFS 2016a; Southern Resident Orca Task Force 2019). These constraints were represented in the model as self-limitation in predators, and they were important links (Figure 6). NCC salmon are relatively rare compared to forage fish and constitute a small percentage of prey for pinnipeds (Lewis 2023; Scordino et al. 2022). Other fish prey, such as invasive American shad (*Alossa sapidissima*) (Lewis 2023), hatchery-produced salmon, or different salmon ecotypes could sustain predators. Rather than focusing on responses to increases in salmon, the crucial factor in the model may have been whether predation declines when salmon decline, allowing salmon populations to recover. Without negative feedbacks, mammal populations (especially killer whales, see Figure S2.1b) stayed stable or increased despite salmon declines, leading to more consistently negative outcomes for salmon. Thus alternative prey, whether from salmon or other species, is of paramount concern.

Based on these results, future research should explore: (1) independent responses of competitors and predators to climate change, (2) the relationship between mammal consumption of spring- vs. fall-run salmon, and (3) mammal responses to declines in salmon populations (Figure 7). If strong relationships cannot be ruled out, they should be included in any intermediate-complexity models. Empirical studies could test each mechanism listed in the previous section for increased consumption rates. To estimate the dampening factors affecting salmon, we propose significantly more effort be directed at tracking juvenile salmon with active tags to quantitatively partition causes of mortality, especially as related to growth rates. New research could also focus on the redistribution of pinnipeds in response to sea level-driven loss of haul-out sites, as well as the energetic fate of gelatinous species. A challenging question is how to measure consumption of one salmon ecotype in response to increases and decreases of many alternative prey, especially given the unknown relative abundances of these prey in a highly heterogeneous landscape. Future studies could be designed to measure all available prey in specific areas within individual sea lion foraging ranges, and video prey that is ignored, chased, and captured. Salmon ecotypes, on the other hand, are reasonably estimated, so the proposed tradeoff between run types and species is amenable to analysis. Simultaneous consumption rates by different predator groups would also need to be measured. Although mammals were the focus here as the primary consumers of adult salmon, certain fish, such as salmon sharks, could be in this category, and more important than previously realized (Manishin et al. 2021; Seitz et al. 2019). MICE models exploring alternative predator–prey behavior rules, combined with projected range shifts, could test these hypotheses and be validated against historical observations.

4.3 | Limitations of the Study and Future Work

This modeling approach assumes that pairwise interactions are always in the direction modeled, although it allows for time-varying interaction strengths (Dambacher et al. 2009). It also does not track population abundances or nonlinear responses, so it should not be considered a prediction. Rather, it is a way to identify potential pathways of indirect and compounding effects that should be further examined with empirical validation and quantitative models.

Our results should be interpreted with appreciation for aspects of the ecosystem that are not fully represented. There are many nuances to the ecology underlying each hypothesis that we could not fully capture. Dynamics within our functional groups are also complex. For example, hatchery salmon, which compose over 90% of Columbia and Puget Sound salmon (Hess et al. 2025; WDFW et al. 2023), could negatively impact wild salmon (Connors et al. 2024; Harvey et al. 2016; Kendall et al. 2020; McMillan et al. 2023; Ruggerone and Irvine 2018). Potential impacts include spreading disease (Connors et al. 2012; Robinson et al. 2020), imposing apparent competition (Connors et al. 2020; Kendall et al. 2020), and increasing predation rates when large pulses of hatchery fish movements over narrow temporal windows help concentrate predators (Moore et al. 2021; Nelson et al. 2019; Rub et al. 2019; Tidwell et al. 2023). These and other ideas could be explored further.

Our approach allowed all links to have the same range of possible magnitudes (+/− 0.001–1), which may allow low-density groups to have an unrealistically strong impact while underrepresenting very high-density species. While semi-quantitative versions of this approach are possible (Forget et al. 2020), our approach better accounts for new species entering the system, which was a major driver of change during the recent heatwave (Gomes et al. 2024), as well as unexpected long-term changes in community dynamics. Our approach is, therefore, more robust to the full uncertainty in climate impacts than a semi-quantitative approach.

A similar contrast could be made with a MICE model. MICE models attempt to restrict the network to the minimum complexity necessary to describe observed population dynamics (Plagányi et al. 2014). However, if the model lacks potential for indirect effects from a dramatic increase in a competitor or new species, it might miss the cumulative impacts that we identified. Reducing intermediate complexity models down to just 2–3 species would fail to capture important compensatory and compounding processes. Testing the hypotheses in a fully quantitative ecosystem model (e.g., ecopath/ecosim) or a relatively complex MICE model is recommended.

These approaches should complement spatial distribution models that focus on range shifts (e.g., Cheung et al. 2015). Spatial models could help identify species that may enter or depart a region, motivating attention on their potential impacts on focal species. However, these models are strongly constrained in covariates they consider and the importance of direct and indirect species interactions. Therefore, none of these approaches are stand-alone. They each provide thought experiments on ecosystem processes and present alternative futures that are most robust when considered together.

5 | Conclusion

Our findings provide critical insights to enhance salmon conservation efforts. First, indirect predator–prey interactions significantly influence salmon outcomes, potentially undermining the effectiveness of narrowly targeted management actions. Second, accurately quantifying predator responses—particularly from marine mammals—to fluctuations in salmon abundance is essential given their substantial influence on salmon population resilience. Third, conservation strategies should explicitly account for the diversity of salmon life histories, as these influence vulnerability to climate change.

Qualitative network models (QNMs) provide a crucial initial step, guiding targeted data collection and streamlining research priorities before embarking on resource-intensive quantitative ecosystem modeling. Integrating insights from QNMs into quantitative frameworks such as Management Strategy Evaluation (MSE) and Models of Intermediate Complexity for Ecosystem assessments (MICE) will enhance our capacity to predict and mitigate climate-driven ecological risks.

Author Contributions

Lisa G. Crozier: conceptualization, formal analysis, investigation, methodology, project administration, resources, software, validation, visualization, writing – original draft, writing – review and editing. **Dylan G. E. Gomes:** methodology, writing – review and editing. **David D. Huff:** conceptualization, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Model code and outputs that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.28586312.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.