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Using social-ecological models to explore stream connectivity outcomes for stakeholders and Yellowstone cutthroat trout

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Abstract

Despite growing interest in conservation and re-establishment of ecological connectivity, few studies have explored its context-specific social–ecological outcomes. We aimed to explore social and ecological outcomes to changing stream connectivity for both stakeholders and native fish species impacted by habitat fragmentation and nonnative species. We (1) investigated stakeholder perceptions of the drivers and outcomes of stream connectivity, and (2) evaluated the effects of stakeholder-identified connectivity and nonnative species scenarios on Yellowstone cutthroat trout (YCT) populations. Our study was conducted in the Teton River, Idaho, USA. We integrated two modeling approaches, mental modeling and individual-based ecological modeling, to explore social–ecological outcomes for stakeholders and YCT populations. Aggregation of mental models revealed an emergent pattern of increasing complexity as more types of stakeholders were considered, as well as gaps and linkages among different stakeholder knowledge areas. These results highlight the importance of knowledge sharing among stakeholders when making decisions about connectivity. Additionally, the results from the individual-based models suggested that the potential for a large, migratory life history form of YCT, in addition to self-preference mating where they overlap with rainbow trout, had the strongest effects on outcomes for YCT. Exploring social and ecological drivers and outcomes to changing connectivity is useful for anticipating and adapting to unintended outcomes, as well as making decisions for desirable outcomes. The results from this study can contribute to the management dialogue surrounding stream connectivity in the Teton River, as well as to our understanding of connectivity conservation and its outcomes more broadly.

KEYWORDS
connectivity, individual-based model, mental model, social–ecological systems, stakeholders, Yellowstone cutthroat trout

INTRODUCTION

Connectivity is a key component of aquatic and terrestrial ecosystems (Erős & Campbell Grant, 2015; Hodgson et al., 2011; Moore, 2015; Taylor et al., 1993). The ability of animals to move and disperse among connected habitats is imperative to sustaining metapopulations (Fagan, 2002; sensu Hanski, 1999; Taylor et al., 1993). Connectivity loss and subsequent habitat fragmentation are linked to local extinctions, as well as declines in biodiversity and ecosystem function (Brauer & Beheregaray, 2020; Hanski, 1999; Thompson et al., 2017). Conserving and reestablishing ecological connectivity is an increasingly prominent goal among land managers and conservation groups as a strategy for restoring wildlife migratory corridors and reconnecting populations, as well as addressing the challenges of climate change, land-use planning and land conservation, water management, biodiversity protection, and wildfire mitigation (Bixler et al., 2016; Crooks & Sanjayan, 2006). Proponents of connectivity conservation also emphasize the social value of interconnected landscapes and the ecosystem services they provide, ranging from recreation to water quality regulation and pollination (Mitchell et al., 2013). The emphasis on reconnecting landscapes has led to the development of multimillion-dollar large-landscape conservation projects, such as the Yellowstone to Yukon Conservation Initiative and the US Department of Interior's Landscape Conservation Cooperative, which aim to establish ecological connectivity between both public and private lands across multiple US States and Canadian provinces (McRae et al., 2012; Torrubia et al., 2014). However, despite the focus of these programs, there remains uncertainty about how animal populations will respond to the re-establishment of habitat connectivity across scales and contexts (Magilligan et al., 2016). In addition, because measuring the social outcomes of reconnecting landscapes is difficult, it is unclear if the anticipated social outcomes from connectivity re-establishment can be achieved. For this reason, exploring the diversity of social and ecological outcomes to changing connectivity could strengthen the decision-making abilities of natural resource managers by providing a more complete frame of reference for the potential impacts of changing connectivity, and may help anticipate and mitigate unintended consequences or management trade-offs.

Rivers are an example of ecosystems widely fragmented by human activity where conservationists seek to restore connectivity for ecological function. Increasingly, such efforts are set in the context of thinking about these "riverscapes" (Fausch et al., 2002) as social–ecological systems (SES) (Dunham et al., 2018; Torgersen et al., 2021). It is estimated that two-thirds of rivers worldwide are affected by anthropogenic fragmentation (Grill et al., 2015, 2019). Due to the dendritic network structure of rivers, fully aquatic riverine species may respond to disturbance and changes to connectivity in unique ways compared with species inhabiting other habitat types, because natural dispersal can only occur in three or fewer directions (Fagan, 2002; Schlosser, 1995). Understanding and anticipating these unique responses is important for making management decisions about connectivity, especially in altered rivers.

Integrating social factors into the planning and implementation of connectivity restoration projects is essential for determining where and at what scale(s) efforts will be feasible and effective. This is because social factors, such as water rights and value orientations, present additional challenges to connectivity re-establishment, especially where conservation efforts span across multiple jurisdictional boundaries (Bixler et al., 2016) and involve shared resources like water and electricity (Hodgson et al., 2011; Null et al., 2014). Managers and researchers increasingly recognize the need to integrate social and ecological factors into conservation management and research. As a result, many increasingly view rivers as SES with dynamic and complex interactions between both social and ecological actors, meaning they recognize that changes to connectivity will affect not only ecological variables such as ecosystem function and population dynamics, but also social variables such as cultural and economic values (Carpenter et al., 2015; Charnley et al., 2018; Dunham et al., 2018; Hand et al., 2018; Parsons et al., 2016). Further, the effects on ecological and social variables can lead to complex feedback and outcomes within the SES (Dunham et al., 2018). Integration of social and ecological science across watersheds is important for the framing and analysis of resource problems and the identification of their solutions (Hand et al., 2018; Quintas-Soriano et al., 2021). Engaging stakeholders in science and management can help identify trends or issues unrealized by traditional natural science alone, and can assist with the prioritization of restoration projects (Bamzai-Dodson et al., 2021; Mckay et al., 2020; Murphy Jr et al., 2021). Further, using integrated methods to understand how stakeholders perceive and interact with an SES, and to identify the array of social and ecological variables within an SES, can aid in decision-making and detect both social and ecological research problems.

Fishes are particularly susceptible to the effects of habitat fragmentation as well as the negative impacts of interactions with nonnative fish species. Reduced habitat area, quality, and connectivity increase extinction risk by preventing recolonization of unoccupied habitat, and reducing genetic exchange, life history variability, and effective population sizes (Dunham et al., 1997; Neville et al., 2006). Populations with life history diversity, including migratory forms, may exhibit more stable dynamics in the face of environmental changes (Moore et al., 2014; Rieman & Dunham, 2000). In addition, migratory individuals often grow larger, are more fecund, and live longer than resident (i.e., nonmigratory) individuals (Crespi & Teo, 2002; Gross, 1987; Holecek & Scarnecchia, 2013; Tallman et al., 1996). Due to those traits, migratory individuals can disproportionately contribute to population recruitment by producing more offspring over their lifetimes (Moore et al., 2014). Therefore, life history variability, particularly the ability to develop large, migratory life history forms, can be important for sustaining metapopulations, and can mediate interactions with nonnative species including hybridization (DeRito et al., 2010) and competition (Al-Chokhachy et al., 2016, 2021). Given these outcomes, the conservation of migration and dispersal pathways is key to fish population persistence (Barrett & Armstrong, 2022; Carim et al., 2016; Fausch et al., 2002; Rieman & Dunham, 2000). However, the impacts of fragmentation on fish metapopulations become complicated in some drainages where local populations of native fish are disconnected from one another, but are also separated from nonnative fish species which can transmit diseases to, out-compete, predate on, or hybridize with them. The same barriers that fragment native fish populations may also prevent invasions of nonnative species. For example, in Colorado, Greenback cutthroat trout (*Oncorhynchus clarkii stomias*) have been displaced mostly by brook trout (*Salvelinus fontinalis*), and have become confined to a few high-elevation headwater streams, the invasion of which is mediated by natural and man-made barriers (McGrath & Lewis Jr, 2007; Peterson et al., 2004). The trade-off for native fish management between isolation and invasion demonstrates the risks and benefits of restoring connectivity for fish metapopulations (Fausch et al., 2009). It remains unclear if the benefits of restoring connectivity between isolated native fish populations (e.g., restoring gene flow and a migratory life history form) could offset the effects of invasive and nonnative species. Examining these trade-offs is important for fish conservation, as it can assist managers in weighing desirable outcomes and identifying context-specific solutions (Fausch et al., 2009; Korsu et al., 2010; Peterson et al., 2008).

Despite extensive research demonstrating the negative impacts of habitat fragmentation on fish metapopulations, little is known about the long-term outcomes of restoring connectivity among populations, particularly where reestablishing connectivity may facilitate the spread of nonnative species. Similarly, little is known about the social outcomes of restoring stream connectivity, as there may be complex stakeholder interests and goals across a single watershed beyond just fish populations, all of which could be affected by changes to connectivity. Assessing these multifaceted outcomes is difficult, as measurement of social and ecological variables can be complex and time-consuming. Furthermore, there is often a mismatch between the timeframes for research and the immediacy often demanded for management action. Examining these two problems in tandem, using both social and ecological methods, can provide a richer SES context that would not be possible through natural science methods alone, and can therefore offer valuable insight into the social–ecological outcomes of changing stream connectivity. In this study, we aimed to explore social and ecological outcomes for both stakeholders and a valued native fish species impacted by habitat fragmentation and nonnative species.

To explore social and ecological outcomes, we asked two questions. Our first research question was: How do stakeholders perceive the social–ecological drivers and outcomes of changing stream connectivity, and how does combining knowledge from multiple stakeholder types affect the overall complexity of those drivers and outcomes? To answer this question, we used an interview-based, mental-modeling approach. Mental models are unique and personal internalized representations of external reality that people use in their daily interactions with the world around them. They are based on individual perceptions, experiences, and understandings, and can drive decisions and behaviors (Jones et al., 2011). In SES research, researchers draw on mental models to build an understanding of stakeholder perceptions and decision-making processes, as well as assess the social and ecological outcomes of different management actions (Hamilton et al., 2019; Jones et al., 2011, 2014). This method allowed us to achieve the following objectives: (1) describe stakeholder perceptions of stream connectivity, including its drivers and outcomes; (2) compare those perceptions among stakeholder groups; (3) compile stakeholder perceptions into a single mental model of the entire system; and (4) identify desirable outcomes and management priorities to develop scenarios for an individual-based modeling phase, which would allow us to explore ecological outcomes for fish populations.

Our second research question was: How would different stream connectivity and nonnative species scenarios affect Yellowstone cutthroat trout (YCT) populations? To address this question, we used a spatially explicit, individual-based modeling approach. Spatially explicit, individual-based models (IBMs) of metapopulations are one simulation tool that can allow for testing different management scenarios, including varying scales and spatial arrangements of connectivity for riverine fishes. A specially explicit individual-based model produces broad-scale patterns that emerge from the interactions of individual agents and can therefore serve as a tool for understanding drivers of metapopulation-level processes. Previous studies have demonstrated ecological and management applications of IBMs (Day et al., 2018; Frank & Baret, 2013; Landguth et al., 2017; Mims et al., 2019; Nathan et al., 2019); however, placing model outcomes in an SES context by testing scenarios informed by a wide range of stakeholders may provide more relevant insight into management applications of IBMs. This method allowed us to achieve the following objectives: (1) evaluate the relative effect of stakeholder-identified connectivity scenarios on YCT abundance and hybridization with rainbow trout; (2) determine if the potential for a large, migratory life history form of YCT within the model can mitigate negative interactions with nonnative fish species, including hybridization with rainbow trout, competition with brook trout, and predation by brown trout; and (3) link YCT outcomes to broader SES outcomes derived from the mental models. We chose to focus our study on YCT outcomes because of local efforts to conserve their populations as a valued recreational and ecological resource, and because stakeholders indicated during early engagement that research questions regarding YCT and stream connectivity were of most interest to them. Because the outcomes of connectivity conservation efforts for YCT will influence both social and ecological systems beyond the trout themselves, we chose to incorporate a mental-modeling approach into our study design to elucidate the broad range of social–ecological effects of connecting streams in the Teton River watershed. In particular, we did this because these broader social and ecological outcomes could not be modeled in our individual-based modeling exercise but understanding them is essential to ensuring stream connectivity conservation is effective and minimizes undesired unintended consequences. By building an understanding of the environmental system before entering the decision space (Clifford et al., 2022), our study aims to understand the stakeholders themselves and the SES as a whole, which can contribute to their ability to make decisions.

METHODS

Study area

The Teton River drainage is located in Eastern Idaho on the western slope of the Teton Range. It is a major tributary to the Henry's Fork, which drains into the Snake River. The Teton River drainage lies within the Greater Yellowstone Ecosystem (GYE) and is considered a stronghold for YCT (*Oncorhynchus clarkii bouvieri*), which currently occupy about 27% of their historical range within the GYE (Al-Chokhachy et al., 2017). The headwaters of the Teton River and the upper reaches of many of its tributaries lie on public lands, including National Forest, Bureau of Land Management, and National Park Service jurisdictions. The valley floor consists primarily of private land, much of which is used for crop production. The Teton River, its tributaries, and their associated aquifer are diverted for irrigation purposes. Because of this, many streams contain physical fish passage barriers, including head gates and dams. Although it is likely that sections of some Teton River tributaries naturally go dry in the late summer, irrigation diversion has decreased the period of continuous flow from headwaters to the mainstem (Peterson, 2011). As such, seasonal dewatering and altered flow and temperature regimes also act as fish passage barriers. As a result, the YCT metapopulation has become fragmented as fish cannot migrate between tributaries and the mainstem and interact with each other, and some smaller populations are isolated altogether. YCT are designated as a species of special concern in the state of Idaho and are of particular interest in the Teton River drainage due to the impacts of habitat fragmentation and nonnative species (Al-Chokhachy et al., 2017, 2018).

In addition to migratory barriers, YCT persistence in the Teton River is affected by several nonnative fish species—namely, brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*)—that can have negative interactions with YCT where they co-occur. More specifically, brook trout can compete with and, in some cases, completely replace YCT (Benjamin & Baxter, 2010; Seiler & Keeley, 2009), and brown trout are known to predate on juvenile salmonids (McHugh & Budy, 2006; Yard et al., 2011). Additionally, rainbow trout can hybridize with cutthroat trout species where the two species co-occur, which threatens the genetic integrity of native cutthroat trout populations (Rhymer & Simberloff, 1996; Weigel et al., 2003). The invasion of nonnative species in the Teton River drainage is heterogeneous and dependent on the connectivity of individual streams to the rest of the network. For example, fish passage barriers, including seasonal dewatering and other seasonal or partial barriers, may prevent the invasion of certain species (Benjamin & Baxter, 2010). In general, however, nonnative species may invade any stream to which they have access (Benjamin et al., 2011; Benjamin & Baxter, 2010).

Conservation groups and fisheries managers prioritize native trout in the Teton River drainage, but their goals may be complicated by other stakeholder interests, including those of farmers, real estate developers, recreationists, and business owners. For example, managers may find it challenging to balance managing stream flow to sustain fish populations while ensuring water availability for other stakeholder needs, such as boating and irrigation. This diversity of interests, and the possibilities of collaboration, have inspired efforts in the area to balance the needs of farms and fish through collaborative management; however, these efforts are only just emerging (Friends of the Teton River, 2017).

Framework

Figure 1 outlines the framework we used in this study. To answer research question 1, we used a qualitative, mental-modeling approach to map stakeholder perceptions of stream connectivity and the social–ecological system. We conducted semistructured interviews with stakeholders to elicit mental models and collect information about their management priorities and expectations for the future of the Teton River drainage, including local populations of YCT. Through data derived from these interviews, we then developed connectivity scenarios based on stakeholder interview responses to test in the individual-based modeling phase to answer research question 2. We used IBMs to explore ecological outcomes for YCT populations. Integrating these methods allowed us to explore the social–ecological outcomes of changing stream connectivity in the Teton River drainage. More details on each of these approaches are described below.

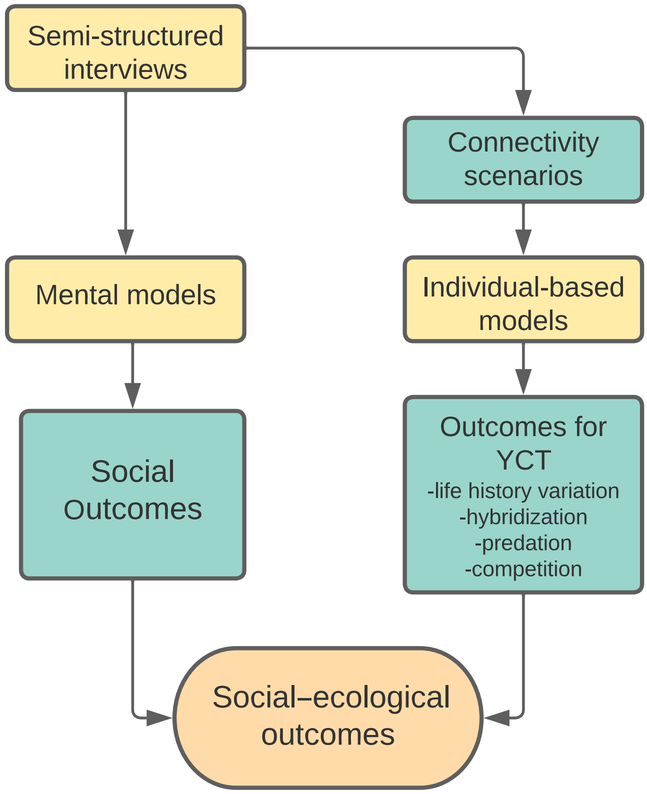

FIGURE 1 Framework: the study began with semistructured interviews with stakeholders. We derived mental models and connectivity scenarios from the interview data. We then parameterized IBMs with the connectivity scenarios to explore outcomes for Yellowstone cutthroat trout (YCT). Outcomes from each of these modeling approaches allowed us to explore social–ecological outcomes of changing stream connectivity. It is worth noting that because this is an interdisciplinary, mixed-methods study, our methods and interpretation borrow from multiple paradigmatic approaches. Mixed-methods research purposefully mixes methods in data collection, data analysis, and interpretation of results, with the aim of viewing phenomena from different viewpoints and through diverse research lenses (Shorten & Smith, 2017). Here, we mix qualitative social science approaches and quantitative ecological modeling.

Method for research question 1: Mental modeling

Using a semistructured interview guide, we conducted 21 one-on-one interviews with a broad range of stakeholders in the Teton Valley. Initial contacts were derived from a list of stakeholders participating in an existing stakeholder research advisory group, as well as web searches for contacts from particular agencies or industries. While identifying participants, we used a "sample for meaning" approach, whereby participants are chosen and stratified based on shared identities and personal experiences in relation to a particular context (Luborsky & Rubinstein, 1995). The stakeholders selected to participate in the study were those with influence, investment in, or decision-making abilities regarding water use, stream habitat, trout fisheries, and other interests related to the Teton River and the surrounding area. This included habitat managers, irrigators, and user groups (Appendix S1: Table S1), all of whom have shared interest in the resources that the Teton River drainage provides, but may have different values, objectives, and expertise.

To adequately represent this array of perspectives, we drew participants from multiple agencies, industries, and organizations, and then stratified them by their primary interests (or "meaning"; Appendix S1: Table S1). These five meaning groups (agriculture, conservation, development, fisheries, and recreation) represent some of the prominent interests in the Teton River drainage. In addition, we interviewed a member of the Shoshone-Bannock Tribes, but they were not included as a member of any of these meaning groups; this was at the recommendation of the individual we interviewed. It is worth noting that the participants we interviewed do not necessarily have a singular meaning that they attach to the Teton River, so there was overlap among the different meanings for most participants. For example, a local realtor may deal with residential development as part of their professional role, but as a resident of the region, they may also be interested in angling and recreation. The formation of this sample ensured that a variety of variables and outcomes were represented to assemble a more comprehensive mental model of the Teton River social–ecological system.

In addition to selecting participants through the process described above, we also used "snowball sampling," whereby participants were asked to identify other individuals who might be appropriate to interview. However, because snowball sampling is nonrandom and based on similar involvement within a social network, it can lead to a homogenous sample. This was mediated by asking participants to identify individuals of a particular type not yet captured—for example, an under-sampled agency, industry, or organization (Noy, 2008). We stopped sampling in each stakeholder meaning group once we reached saturation–meaning the point at which there is a diminishing return of new information from each new interview (Guest et al., 2006). We used ATLAS.ti 8 data analysis software (Atlas.ti Scientific Software Development GmbH, 2019) to code and analyze interviews following the approach outlined by Friese (2014). Following this approach, we evaluated saturation based on the number of new codes created during the coding process; that is, we stopped sampling each meaning group when only 0–1 new codes were generated per interview.

To construct participants' mental models, we used the software MentalModeler (Gray et al., 2013), which is modeling software that helps individuals and communities represent their knowledge in a standardized format that can be used for scenario development and analysis and has been used in many other studies of environmental issues and natural resource management (Clifford et al., 2022; Gray et al., 2015; Hamilton et al., 2019; Nyaki et al., 2014). The software was designed with the intention of allowing users to visualize SES and simulate scenarios as a decision-support tool (Gray et al., 2013). Here, it is a useful tool for examining stakeholder perceptions of stream connectivity and its outcomes and developing management scenarios from those perceptions. During the mental-modeling portion of the interview, participants were asked to identify variables affecting stream connectivity and stream flow, describe the relationships among those variables (i.e., positive or negative), as well as the anticipated outcomes when those variables are manipulated. A full description of the methods and software used to develop the mental models can be found in Appendix S2.

Due to the COVID-19 pandemic, all interviews took place using Zoom video conference software (Zoom Cloud Meetings, 2020), unless participants preferred a phone call. We used screen sharing in Zoom during the mental model exercise so that participants could see the mental model they were building, keep track of the data, and make changes where they wanted. If we conducted the interview on the phone, participants were asked to describe their perceptions of stream connectivity, its drivers, and its outcomes. We constructed the mental models afterward based on the concepts discussed during the interview, then emailed the finished model to participants for them to review and make changes as needed. All interviews were recorded and transcribed.

Once coding was completed and all individual mental models finalized, we aggregated individual mental models by stakeholder group meaning, which allowed us to visualize perceptions and knowledge among similar stakeholders. Individual mental models were also aggregated into a single collective model (hereafter referred to as the "aggregate" model), which enabled a complete visualization of stakeholder understandings of stream connectivity, causes and effects of stream connectivity (including effects on native and nonnative fish populations), and the social–ecological system as a whole. Combining the mental models of different subsystem foci (i.e., the different stakeholder meanings) into an aggregate model can reveal how some processes are incompletely described at the individual or group level, provide a more comprehensive understanding of the complexity of an SES, and reveal components, relationships, drivers, or outcomes which a single perspective might overlook (Gray et al., 2011). Furthermore, aggregating local knowledge from a diverse sample of stakeholders yields more accurate social–ecological mental models than a homogenous sample (Aminpour et al., 2021).

The aggregation of individual mental models required consolidation to better interpret the final aggregate model. In many cases, multiple participants included the same components and processes (with identical names) in their cognitive maps. However, participants also often used different names for the same component or idea (e.g., "aquifer" and "groundwater"), which we renamed to enable the compilation of common factors across cognitive maps (Hamilton et al., 2019). In several cases, participants used different language to describe similar or closely related components (e.g., "birds," "bears," "deer"). To avoid an overly complex model, in those cases, we combined those components into a broader idea that could encompass all of them (e.g., "terrestrial wildlife").

To test the potential responses of YCT to variable amounts of connectivity re-establishment, we developed a suite of stream connectivity scenarios from the interview data, which were then integrated into the parameter space for an individual-based model of the YCT metapopulation. This approach provided a unique opportunity to develop scenarios for IBMs based on responses from a variety of stakeholders, rather than a single agency or organization. To develop these scenarios, participants were asked to describe their management priorities and future vision for connectivity in the Teton River drainage.

Method for research question 2: Individual-based ecological modeling

To simulate YCT life history variation, as well as competition, predation, and hybridization dynamics with nonnative fishes under stakeholder-derived scenarios, we used the spatially explicit, individual-based, demographic-genetic ("demogenetic") modeling software CDMetaPOP (Landguth et al., 2017). CDMetaPOP has been used for a variety of taxa in a range of different ecological systems, including stream fish species (Landguth et al., 2017; Mims et al., 2019; Thatte et al., 2018). Detailed descriptions of processes simulated in CDMetaPOP can be found in Landguth et al. (2017) and the user manual: https://github.com/ComputationalEcologyLab/CDMetaPOP.

We developed four main scenarios to simulate across the landscape—named Status Quo, Opportunistic Restoration, Protect YCT, and Full Connectivity—to reflect the management priorities described in the interviews (Appendix S1: Table S2; Map of simulations in Appendix S1: Figure S1). Further descriptions of interview responses are in the Results section of this manuscript. Because of the variation in tributary characteristics and species distribution, two scenarios included three unique spatial arrangements to examine how combinations of different tributaries affected the distribution, abundance, life history variation, and hybridization dynamics of YCT across time. Notably, the "Opportunistic Restoration" scenario included combinations of 1, 2, and 3 isolated YCT populations being reconnected, whereas the "Protect YCT" scenario did not reconnect any populations of isolated YCT. To explore outcomes to changing connectivity for YCT separately, we sequentially added to model complexity by developing four parameter spaces: (1) all resident (i.e., only nonmigratory) YCT; (2) life history variation (i.e., potential for a large, migratory life history form of YCT); (3) hybridization; and (4) life history variation and hybridization (Appendix S1: Table S2). Additionally, we tested these parameter spaces with and without the simulated impacts of brown trout and brook trout, to understand the potential effects of competition and predation of nonnative trout on outcomes for YCT. We built 16 50×50 cost–distance matrices based on river meters among patches. Each of the eight connectivity scenarios included two matrices, to reflect barriers in both spring and summer. In the instance of seasonal dewatering or a partial barrier, a two-way barrier was set only for migration out of a patch (i.e., late summer/early fall in the simulation cycle). Input files for CDMetaPOP, including demographic parameters for resident and migratory YCT and RBT, can be found at (https://doi.org/10.5281/zenodo.8161826). A full description of the individual-based modeling methods can be found in Appendix S2.

We derived input parameters from the literature and surveys of the area. The probability of maturation for individual fish was modeled as a continuous function of size and calculated each year based on a logistic probability curve, derived from studies of YCT in an adjacent watershed, the South Fork Snake River, as well as the Teton River and other adjacent watersheds (Battle et al., 2010; Meyer et al., 2003). The growth of individuals was determined by a von Bertalanffy equation, with parameters derived from Battle et al. (2010). Fecundity was determined by a power function fit to YCT fecundity data acquired by Meyer et al. (2003) from across Eastern Idaho, including the Teton River and adjacent watersheds. Initial patch abundance of YCT (N) and the other species was derived from sampling data completed in 2020 via electrofishing surveys by Friends of the Teton River (FTR) and the Idaho Department of Fish and Game (IDFG). To simulate YCT competition with brook trout, the carrying capacity (K) for YCT in each patch was decreased by 25%. To simulate brown trout predation on YCT in mainstem patches, we incorporated additional mortality of 5% for migrating individuals and 10% for eggs; previous studies have suggested that brown trout predation on native cutthroat trout species can account for up to 20% of mortality (Budy & Gaeta, 2018). Rainbow trout (RBT) were incorporated into hybridization simulations with unique size class and genetic characteristics, and tracked using an H-index calculation (as in Nathan et al., 2019). For each patch where YCT and RBT co-occurred, we assumed an equal number of each species at initialization, prior to the demographic burn-in.

We conducted four Monte Carlo runs for all parameter sets, for 200 years with a 50-year demographic burn-in period. During the burn-in period, the "status quo" cost–distance matrix was used; after 50 years, the cost–distance matrix was changed to reflect each connectivity scenario. Hybridization dynamics began after the 50-year burn-in period. Life history variation was implemented at the patch level at initialization. Simulations were performed on a Linux high-performance computing cluster at the Idaho State University's Research Data Center. We used the metrics shown in Appendix S1: Table S3 to analyze simulation results. These metrics were calculated as means across the four Monte Carlo replicates, and 95% CIs around these means were calculated.

RESULTS

Research question 1: Aggregate, group, and individual mental models

Interview participants described many different variables, relationships, processes, and outcomes surrounding stream connectivity in the Teton River drainage. The aggregate mental model presented the range of hydrological, socioeconomic, ecological, and agricultural components described by all participants, as well as the complex relationships among them. The individual, group, and aggregate mental models, supplemented by coded interview data, allowed us to evaluate how a variety of stakeholders perceive the drivers and outcomes of changing stream connectivity. Our analysis revealed an emergent pattern of increasing complexity as more stakeholder perspectives were considered together in the aggregate model, indicating that outcomes to changing stream connectivity may be more complex than what any single stakeholder may be able to describe individually. We aggregated individual mental models by stakeholder meaning (group models), as well as into a collective mental model (aggregate model). Comparing the group mental models allowed us to see how different knowledge areas contrast and complement each other. Furthermore, aggregation of mental models showed that each stakeholder meaning group contributed some unique knowledge or perceptions to the aggregate model, and also revealed cases in which some outcomes were incompletely described at the individual and group level, but were completely understood when viewed at the collective level.

The aggregate (collective) model contained a total of 77 components and 304 relationships. The mean number of components and relationships in the individual models were 14.8 and 20.5, respectively (maximum: 22 and 39). The number of components and relationships also varied among the stakeholder meaning groups (Table 1). The ratio of relationships to components did not vary considerably among groups, but conservation and fisheries stakeholders presented slightly higher ratios. The ratio of relationships to components was noticeably higher in the aggregate model than in any of the group models. This is because there were many unique relationships that were only described by one stakeholder group (Table 2).

Overall, 35% (27) of the components observed in the aggregate model were described by only one stakeholder group, meaning that most components were identified by at least two stakeholder groups. These unique components are listed in Table 2. It is worth noting that although we did not assign the Shoshone-Bannock Tribal member to a particular meaning group, they named two unique components in their mental model: tribal treaties and traditional foods. In contrast, ~70% (214) of the relationships observed in the aggregate model were described by only one stakeholder group. This suggests that different types of stakeholders may recognize many of the same components, but they do not necessarily perceive the relationships between them in the same way, and that there may be relationships or outcomes that are unrealized by some types of stakeholders. However, the directionality of shared relationships between components did not differ among stakeholder groups.

There were many components and relationships that were shared between two, three, or four of the models, but only five components and one relationship were shared across all five group models (Appendix S1: Table S4). This demonstrates that there are many ways in which stakeholders conceptualize stream connectivity and related processes in the Teton River drainage.

Figure 2 depicts the aggregate mental model for all participants. Group mental models are shown in Appendix S1: Figure S2. Unsurprisingly, the aggregate model is visually more complex than the smaller group models. When visually comparing group models to each other and to the aggregate model, it is clear there were differences in how stakeholders perceive stream connectivity and related processes. More importantly, some stakeholder group models contained processes and

TABLE 1 Each meaning group sampled, and each group's number of participants, components (individual boxes in the mental model), and relationships (directional arrows drawn between components), as well as the ratio of components to relationships of each group model, and the metrics of the full aggregate model of stakeholders interviewed from the Teton River drainage.

Group	Participants	Components	Relationships	Ratio
Agriculture	3	24	43	1.8
Conservation	4	39	99	2.5
Development	3	24	43	1.8
Fisheries	7	50	120	2.4
Recreation	3	28	51	1.8
Aggregate	21	77	304	3.9

TABLE 2 The number of unique components (individual boxes in the mental model) and relationships (directional lines between components) described in each aggregated group mental model derived from interviews with stakeholders from the Teton River drainage.

Group	No. unique components	No. unique relationships	Examples of unique components
Agriculture	8	27	Conflict between water users; connectivity of farmland; irrigation mitigation; spring temperatures; unused surface flow; water right allocation; water rights
Conservation	2	56	Municipal water demand; wetlands
Development	1	18	Historical context
Fisheries	10	77	Early irrigation; fish barrier mitigation; fish entrainment; fish passage; flood irrigation; fluvial native fish; hatchery stocking; losing alluvial reaches; management costs; natural fish barriers
Recreation	4	32	Federal policy; hydropower; ski resort; Teton Dam legacy
Total	27	214	

outcomes that were missing from other group models, suggesting that some groups may have unique expertise and perspectives that other groups do not. In addition, the comprehensiveness (i.e., the number of components of each type: hydrological, socioeconomic, ecological, and agricultural) varied among group models, indicating that some groups may have a more holistic perspective than others. Furthermore, the connections between these group models were only fully realized when combined into the full aggregate model. Each group model, described below in more detail, contained some examples of this pattern.

Agriculture

For example, the mental model for the group of participants ascribed to the "agriculture" meaning included only one ecological variable (native fish populations), and it was described as an outcome only, with no effect on any other components. However, the agriculture group model also provided a clearer picture of the components and processes that impact irrigators (i.e., senior and junior water users), as well as the outcomes of those processes, than other models did. In particular, this model contained a relatively high number of unique components (Table 2), all of which pertain to agriculture, water use, or water rights; none of those components were mentioned in other group models. Many of the concepts seen in this model were missing from other group models. For example, participants explained that housing development decreases the connectivity of farmland and makes aquifer recharge more difficult, which impacts senior and junior water users and could indirectly lead to increased conflict between water users.

Development

The mental model for the group of participants ascribed to the "development" meaning contained the lowest number of unique components (1) and relationships (18). It also contained only one agricultural variable (irrigation diversions), which was only described as having a negative driver of other variables, including stream flow. Although participants stated that working with landowners and farmers was important for meeting conservation and management goals, no agricultural outcomes were shown in this model, further demonstrating unseen variables in stakeholders' perceptions of stream connectivity outcomes when only one group is considered.

Recreation

The mental model for the group of participants ascribed to the "recreation" meaning was the only model that did not include housing development. Instead, participants placed a larger focus on the growing local population and increased recreation activity in the Teton River drainage. Participants expressed support for increasing public access and leveraging interested recreationists to implement conservation projects. However, they also recognized the impact recreation use may have on stream habitat, that is, "loving it to death."

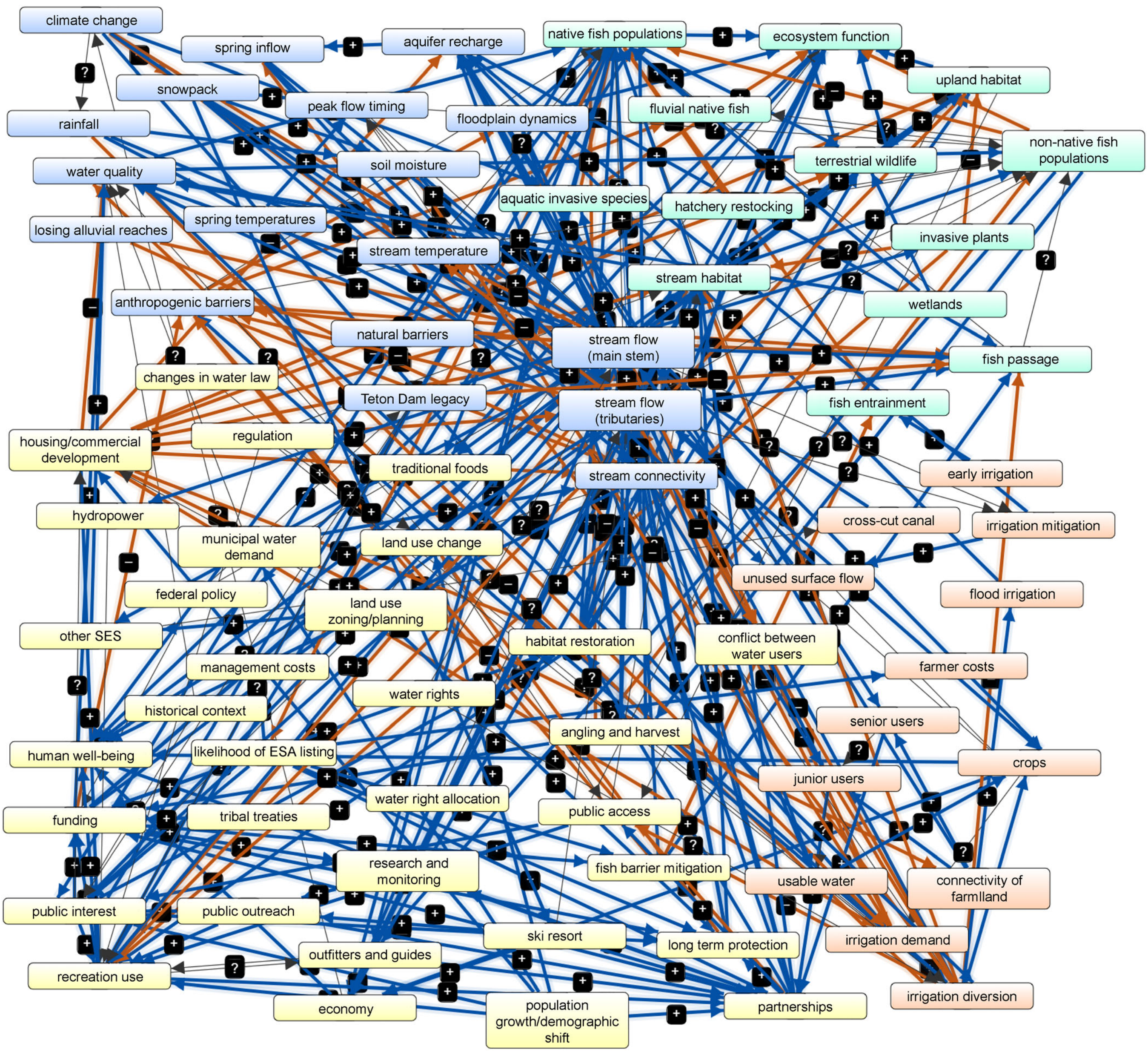

FIGURE 2 Aggregate mental model for all interview participants. Boxes indicate components; colors indicate the type of component: green = ecological, blue = hydrological, yellow = social, red = agricultural. Arrowed lines indicate directionality of relationships between components; color indicates type of relationship: blue = positive, red = negative, black = uncertain. Full resolution versions of the mental models can be found at the Zenodo repository: https://doi.org/10.5281/zenodo.8161826.

Fisheries

The mental model for the group of participants ascribed to the "fisheries" meaning it contained the highest number of unique components and relationships. This could be because participants had more specialized knowledge of fisheries-related concepts. Five out of 10 unique components were related to fish, including fluvial native fish and hatchery stocking. This model included more detailed agricultural components and relationships as compared to the recreation or development group models, but again they were perceived as mostly drivers of other variables and processes, rather than as outcomes. However, the model did include the connection between agriculture (crops) and the economy and human well-being.

Conservation

Of the five group models, the mental model for the group of participants ascribed to the "conservation" meaning was the most complex and interconnected, based on the high ratio of relationships to components. In addition, conservation-focused stakeholders tended to have larger and more interconnected individual models than the other types of stakeholders. This model included a high number of unique relationships (56), but only two unique variables, meaning that these stakeholders identified many of the same variables as others, but their model was characterized by more relationships between different types of variables than the other stakeholder groups we interviewed. For example, the direct relationships between ecological function, human well-being, and economy were all unique to this model. In addition, the relationships between population growth, housing development, municipal water demand, and irrigation demand, and the subsequent impacts on stream connectivity were all unique. Multiple types of outcomes were described, such as increased usable water (for farmers), and the social and ecological benefits of increased native fish populations, including economic benefits and increased terrestrial wildlife.

Outcomes

The individual, group, and aggregate mental models reflected a broad range of both social and ecological outcomes to restoring, maintaining, and losing river network connectivity, with implications for multiple types of stakeholders. Furthermore, many of these perceived outcomes were indirect–changes to stream flow or connectivity have direct outcomes, and in turn, those direct outcomes influence other factors in the SES. For example, increased stream flow and connectivity directly increased usable water for both farmers and tribal communities, as well as directly increased fish passage of both native and nonnative fish, increased water quality, and decreased conflict between water users. In addition, increased stream flow and connectivity directly increased water-related recreation and public interest. An indirect outcome of connectivity was that increased public interest increased housing development, which then decreased connectivity of farmland and aquifer recharge. Furthermore, increased recreation and public interest strengthened community partnerships, which then contributed to increased habitat restoration, aquifer recharge, and long-term protection of land. The aggregation of the mental models allowed us to explore these perceived outcomes and how they may occur, as well as how they interact with each other. For example, in the aggregated model, human population growth in the Teton Valley, as well as public interest in the resources the Teton Valley has to offer, led to increased housing development. Housing development can fragment farmland and make water management and aquifer recharge more difficult, which, in turn, can decrease stream flow and connectivity to the detriment of native fish populations, water quality, and water users. However, human population growth also led to an increase in public interest in conservation or restoration actions to benefit stream habitats, which can generate funding and resources for those efforts. Those efforts also had direct positive relationships with stream flow and connectivity. Human population growth also led to increased water-related recreation, which had both desirable and undesirable outcomes. Recreation can benefit the local economy, but also lead to overcrowding on the Teton River, which can negatively impact the experience for recreational river users. Higher levels of recreation may also have indirect, negative impacts on stream habitat and stream connectivity. Therefore, the aggregate mental model indicated that human population growth was an important driver of the SES and contributed to both desirable and undesirable outcomes for various stakeholders due to its indirect effects on stream connectivity. However, the aggregate model also indicated that connectivity of the Teton River and its tributaries may indirectly drive human population growth by facilitating quality recreation and angling experiences, which interview participants said were major draws for new residents and housing development.

Scenarios informed by interviews

Many participants were able to describe plausible stream connectivity scenarios in specific locations within the Teton River watershed. In particular, conservation and fisheries stakeholders outlined management priorities for stream connectivity, especially as it related to YCT populations. Four main approaches were described among participants: maintaining existing connectivity (status quo); restoring connectivity opportunistically, including between isolated cutthroat trout populations; restoring connectivity only in streams already invaded by nonnative fishes and protecting isolated cutthroat trout populations; and restoring full connectivity drainage-wide. However, interview participants expressed uncertainty about which approach is the most effective or the most realistic. In addition, participants also expressed that the social outcomes (e.g., outcomes related to irrigation, angling, or water recreation) of these different approaches were also unclear. For example, participants explained that restoring connectivity opportunistically with no particular criteria may encourage collaboration among willing landowners, funding bodies, and conservation organizations. However, opportunistic restoration may not adequately produce desirable ecological outcomes, and may result in unintended consequences, including the spread of nonnative species.

Mental models constructed by conservation and fisheries stakeholders reflected that the re-establishment of a large, migratory life history in YCT populations is one potential outcome of increased stream connectivity. Participants explained that increasing large, migratory YCT might benefit the YCT population through increased recruitment. Additionally, creating more available habitat and dispersal pathways might increase YCT resilience to stochastic events. However, the mental models also identified how improving connectivity might also allow nonnative fish to spread and negatively affect Yellowstone cutthroat trout populations through competition, predation, and hybridization. Participants raised the possibility that increasing the occurrence of a large-bodied, migratory life history might buffer YCT against the impacts of nonnative species; however, the mechanisms for this were not well understood, and the loss of isolated but genetically pure YCT remained a major concern. One fisheries stakeholder explained that large YCT could be valued and marketed from an angling and guiding perspective because they are unique to the American West as compared to the more widespread nonnative species. However, other fisheries stakeholders expressed that anglers generally enjoy catching a variety of species.

In the aggregate mental model, the components with the most connections to other components were stream flow, native fish populations, stream habitat, partnerships, stream connectivity, recreation use, and funding. This suggests these components are central to the system and likely exert influence over many different parts of the SES, meaning that changing them would probably lead to various desirable and undesirable outcomes. Additionally, uncertainties were not limited to fish management and conservation, but extended to irrigation and development as well. For example, the impacts of climate change on rainfall and water availability remain unclear, and the future trajectory of housing development remains uncertain due to public interest and changes to land zoning policies.

The four parameter spaces (Appendix S1: Table S2) allowed us to explore and compare possible outcomes, as interview participants expressed uncertainty as to how native and nonnative trout populations will actually respond to barrier removal and connectivity re-establishment. In addition, the last column of Appendix S1: Table S2 provides additional SES context for each scenario, to link modeled outcomes for YCT to broader social outcomes.

Research question 2 results: Individual-based ecological modeling

We integrated stakeholder-informed connectivity scenarios, YCT life history variation, hybridization between YCT and RBT, and brook and brown trout interactions into the existing CDMetaPOP framework to explore outcomes for YCT populations in the Teton River drainage. Outcomes for YCT under the different connectivity scenarios were strongly influenced by whether or not the potential for a large-bodied, migratory life history form of YCT was included in the model (i.e., simulations that included "life history variation"), as well as which assortative mating options was used in each simulation. We found that simulating such life history variation along with self-preference mating had strong positive effects on outcomes for YCT populations.

Hybridization

As expected, the relative abundance of YCT, RBT, and hybrids, were affected by which assortative mating option was simulated (Figure 3). The modeled outcomes varied more with assortative mating option than among connectivity scenarios. In particular, the scenarios Full Connectivity and Opportunistic Restoration 1 and 2 resulted in the complete loss of genetically pure YCT by year 75 under random mating (Figure 3A). By comparison, all other connectivity scenarios, including the Status Quo, resulted in a sustained YCT abundance of nearly 25% of the population, and a hybrid abundance near 75%. With random mating, pure RBT was completely lost by year 75. This pattern also occurred under self-preference mating (Figure 3C). Of course, no hybridization occurred when we simulated only intraspecific mating (Figure 3B). Under the latter condition, the Status Quo scenario resulted in a higher percentage of YCT over time, whereas the Full Connectivity scenario resulted in roughly equal abundance of YCT and RBT; however, this was partially because the models were initialized with these proportions. Under this model, the relative abundance of the two species did not change over time under any connectivity scenario.

Hybridization and life history variation

Adding YCT life history variation had a positive effect on the relative abundance of YCT compared with RBT and hybrids, but this depended on which assortative mating option was used. Under a random mating assumption, YCT life history variation did not have an effect on hybridization patterns (Figure 3D). Under intraspecific mating, no hybridization occurred, but YCT life history variation resulted in a steeper decline in RBT abundance over time and a steeper increase in YCT abundance over time compared with the simulations of intraspecific mating without life history

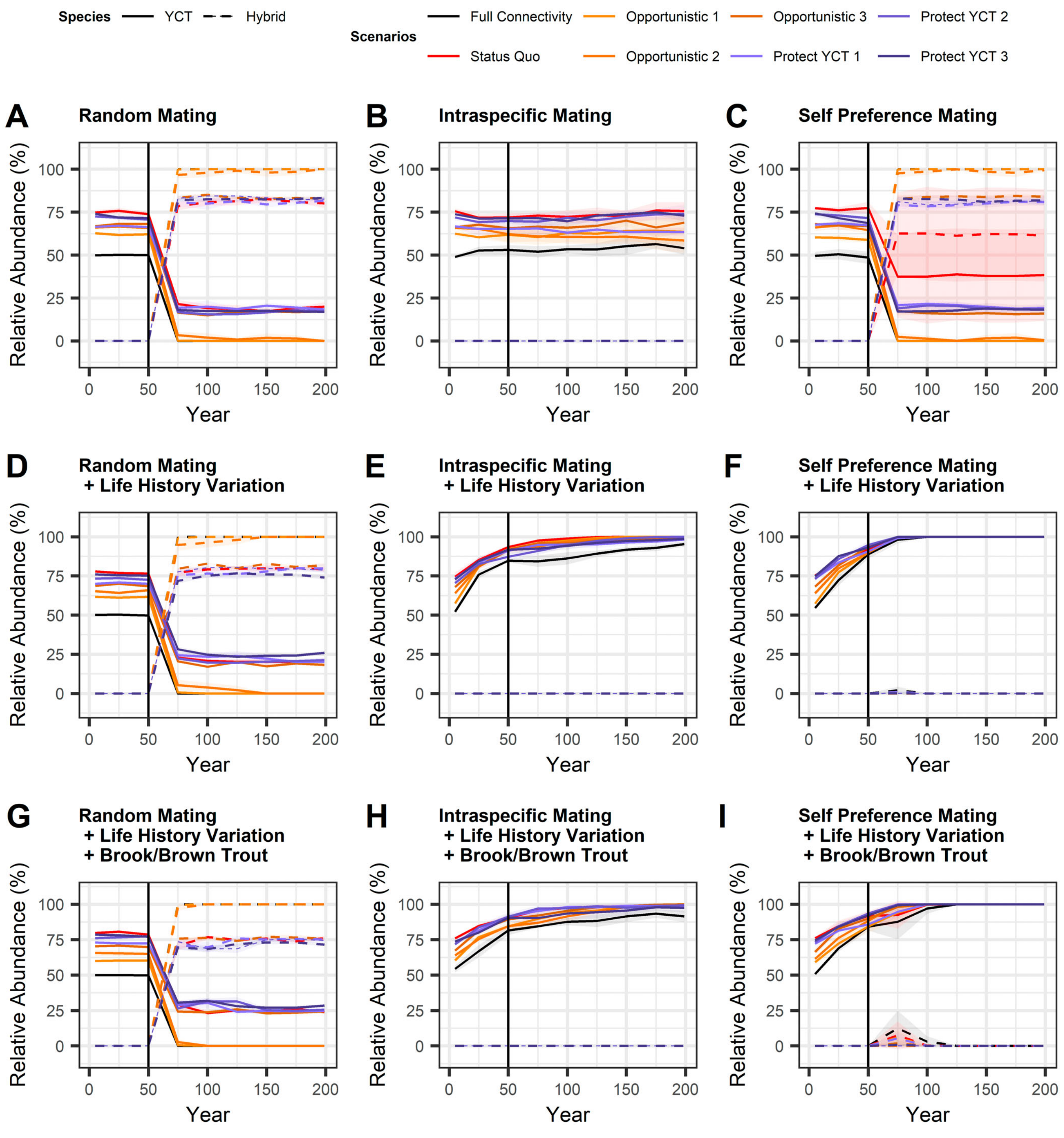

FIGURE 3 Relative abundance of species (Yellowstone cutthroat trout [YCT] or Hybrid) as percent of total fish population across all 50 patches, for each connectivity scenario (color), under the three assortative mating options, with or without life history variation and brown/brook trout simulated. Shading indicates 95% CIs. The vertical line at 50 years indicates the end of the 50-year demographic burn-in period. Panel labels (A–I) indicate which assortative mating option was modeled and whether life history variation and brown/brook trout were simulated.

variation (compare Figure 3B,E). The Full Connectivity scenario resulted in less than 100% YCT after 200 years, whereas all other connectivity scenarios resulted in nearly 100% YCT after 200 years and the complete loss of pure RBT. Under self-preference mating (Figure 3F), there was a slight increase in hybrid abundance in the first 50 years following the burn-in period. However, after year 175, hybrids returned to 0% for all connectivity scenarios. Thus, the potential for a large, migratory life history form of YCT mediated the effect on YCT from hybridization between YCT and RBT, but only when self-preference mating was simulated.

Simulating hybridization dynamics with YCT life history variation did not have a strong effect on the percent of migrants in the total fish population compared to models without hybridization. Similarly, simulating hybridization dynamics with YCT life history variation did not have a strong effect on the percent of large (>300 mm) migratory YCT in the total fish population compared to models without hybridization. Among hybridization simulations, however, we observed some variation in the percent of large, migratory YCT in the total fish population. Under random mating, there were no large migratory YCT by year 75 under the Full Connectivity, Opportunistic 1, and Opportunistic 2 scenarios; as noted above, these scenarios resulted in the complete loss of genetically pure YCT by year 75. All other scenarios under random mating resulted in a steep decrease in the relative abundance of large migratory YCT immediately following the 50-year burn-in period. Under self-preference and intraspecific mating options, the relative abundance of large migratory YCT remained between 0.10% and 0.25% for all connectivity scenarios throughout the 200-year simulation.

Hybridization, life history variation, and brook/brown trout

The addition of the impacts of brook trout and brown trout, with YCT life history variation, did not have a strong effect on relative abundance of YCT, RBT, or hybrids when random mating or self-preference mating between YCT and RBT was simulated, as compared with simulations run without brook and brown trout impacts (Compare Figure 3G,I and Figure 3D,F). When self-preference mating was simulated, there was a slight increase in hybrid abundance in the first 50 years following the burn-in period for the Full Connectivity, Status Quo, and Protect YCT 1 scenarios. However, after year 175, hybrids returned to 0% for all connectivity scenarios. The addition of impacts of brook and brown trout did not have a strong effect on relative abundance of YCT and RBT after 200 years under intraspecific mating, as compared to simulations run without brook and brown trout impacts (Compare Figure 3F,H). However, when brook and brown trout impacts were included, pure RBT remained present for longer following the 50-year burn-in period, particularly under the Full Connectivity and Opportunistic scenarios. The percent of migrants and the percent of large migratory YCT in the total fish population over time followed a similar pattern as simulations run without the impacts of brown and brook trout.

No hybridization

We also conducted simulations without RBT-YCT hybridization to compare YCT metapopulation dynamics with and without the potential for a large, migratory life history form, and with and without the impacts of brook and brown trout present. The total metapopulation size of YCT was consistently larger over time when a large, migratory life history form was not modeled. However, the pattern we observed in our simulations may largely be due to the lower fecundity of resident individuals allowing patch-level populations to maintain closer to the carrying capacity. CDMetaPOP does not model density-dependent dispersal, but it does model density-dependent mortality. When we modeled life history variation, YCT populations included a higher proportion of large, fecund individuals producing higher numbers of offspring, and more density-dependent mortality occurred as a result. This result may lack some realism, because in nature, individuals could disperse to a different patch rather than die as a consequence of carrying capacity. Therefore, in reality, the contribution of large, migratory YCT to population recruitment would probably be higher. Metapopulation size did not vary among connectivity scenarios when the potential for a large, migratory life history form was modeled. The addition of brook and brown trout impacts resulted in smaller YCT population sizes for all connectivity scenarios, with or without life history variation (Appendix S1: Figure S3). There was not considerable variation in population size (Appendix S1: Figure S3) or the percentage of the population being migrants over time among the different spatial arrangements.

DISCUSSION

Integrating mental models of stakeholder perceptions and individual-based ecological models allowed us to examine the complexities and uncertainties surrounding the social and ecological outcomes of changing stream connectivity in the Teton River drainage. Additionally, integrating stakeholder-informed scenarios into the development of IBMs allowed us to evaluate outcomes of connectivity re-establishment for YCT populations. The aggregation of individual and group mental models highlighted the range of perspectives on stream connectivity and its drivers and outcomes that are present in the Teton River SES and emphasized the importance of knowledge sharing to reduce negative impacts and unintended consequences of connectivity changes. As more perspectives were included in the aggregate mental model, the complexity of the model increased, and conceptual linkages could be made among different stakeholder interests. This illustrates that bringing together multiple perspectives may be necessary for understanding the relationships among social–ecological factors and desired outcomes across stakeholder interests when making connectivity management decisions. In addition, IBM results revealed patterns that suggest the ability for YCT to become large and migratory, modeled as an immediate response to barrier removal, may be an important factor for the persistence of genetically pure individuals across the metapopulation, even with the presence of nonnative fish species. In particular, modeling the potential for a large, migratory life history form, in addition to self-preference mating, had the largest effects on IBM outcomes for the future of YCT. Overall, the results from this study could guide further collaboration and knowledge sharing between stakeholders in the Teton River drainage, as well as inform the management of stream connectivity for YCT populations.

Mental models

The aggregate mental model contained, by far, the highest ratio of relationships to components. Higher ratios indicate a more complex, interconnected mental model (Eden, 2004). More complex mental models indicate a system with more indirect drivers and outcomes, and can be linked to more complete or detailed knowledge of a system (Gray et al., 2011). This suggests that combining the knowledge of many types of stakeholders provides a more accurate model of the Teton River drainage SES and the potential outcomes of changing stream connectivity. Additionally, the directionality of shared relationships between components did not differ among stakeholder groups. This indicates that there may not necessarily be disagreement among stakeholders about system functioning; rather, individual stakeholders have incomplete knowledge of the diversity of relationships which exist, and the outcomes which may occur. Aggregation of mental models can also reveal where some connections and relationships are incompletely described, because individual stakeholders may not necessarily recognize the complete pathway from one component to the next, or the resulting outcome (Hamilton & Salerno, 2020). Results from this study are consistent with the idea that individual-level cognition typically encompasses only a submodel of a complex system (Beratan, 2007). In our study, fisheries and conservation stakeholders included more ecological components and outcomes in their models while agriculture stakeholders focused more on agricultural components and outcomes. Individual stakeholders may have specialized knowledge, but this does not enable a complete understanding of unexpected or indirect outcomes of changing connectivity (Hamilton et al., 2019). For example, fisheries stakeholders had very detailed conceptualizations of fishery-related components and processes, which probably contributed to their higher relationship to component ratio, but their ideas about how connectivity could affect other stakeholders were less detailed. In particular, fisheries stakeholders described how shared components, such as stream connectivity and aquifer recharge, can impact stream habitat, fish passage, and fish populations, but they did not describe how shared components, such as stream flow or aquifer recharge, might impact water users. However, agriculture stakeholders described in greater detail how stream connectivity and aquifer recharge can impact water users, but did not describe ecological outcomes, such as native fish populations, in detail. Previous mental model analyses have shown that stakeholders often have "blind spots" in their conceptualization of SES, and that there may be gaps in system-scale understanding among different types of stakeholders (Halbrendt et al., 2014; Smythe & Thompson, 2015). Our analysis suggests that similar blind spots exist among stakeholders in the Teton River drainage, and identifying these gaps may be important for decision-making and future collaboration between stakeholders.

Although gaps in knowledge were evident among our study participants, aggregation and analysis of the group and aggregate mental models revealed the conceptual linkages between them. Indeed, some of the nonlinear and indirect pathways among components could only be seen at the collective scale. For example, although agricultural stakeholders only named one ecological component (native fish populations), their model showed the indirect impacts that farmland connectivity, crops, and aquifer recharge can have on native fish populations through changes in stream flow and connectivity; these impacts were not shown in other group models. When we connected the agriculture group model to other group models, further connections could be made between "native fish populations" and other social, ecological, and hydrological components such as angling, stream habitat, and floodplain dynamics. If we had only interviewed one type of stakeholder, or if stakeholders only considered their own mental models when making decisions, some relationships and their outcomes could be overlooked. We also observed complex relationships among social and ecological outcomes, such as the trade-offs between decreased connectivity of farmland and increased interest in conservation among new residents. Exploring social–ecological relationships prior to making management decisions, particularly those that may be nonlinear, complex, or difficult to identify, can reduce the likelihood of unintended outcomes as a result of management actions (Miyasaka et al., 2017). As shown in this study, mental modeling provides a useful tool for identifying gaps in stakeholder knowledge, connecting subsystems and perspectives, and exploring the complexity of conservation issues. Furthermore, integrating the knowledge of multiple stakeholder types can enhance the structural understanding of an SES by increasing knowledge of the various components and the relationships among them.

Identifying the gaps and linkages among different stakeholder group models underlines the importance of collaborative decision-making and knowledge sharing among stakeholders. In the Teton River drainage, collaborative management is ongoing, and stakeholder groups, ranging from conservation organizations to farmers to land managers, are actively working on a variety of conservation initiatives. While our results highlight the value of that work, they also suggest that each group model contributed some unique knowledge to the aggregate model, and so including groups such as those focused on agriculture or development could help avoid unintended consequences for factors such as irrigation or recreation. Furthermore, a mental-modeling approach can be valuable for future investigations and stakeholder engagement efforts in other systems, because it may help identify which perspectives are missing from other conservation collaboratives.

Individual-based models

Our analysis indicated that the most important factors for achieving positive outcomes for YCT (i.e., increased abundance) were the traits of the fish themselves and their behavior (i.e., large, migratory life history and self-preference mating), rather than different scales and approaches to barrier removal identified by stakeholders. However, there were some differences among connectivity scenarios that may provide some insight into the possible outcomes of the different management approaches associated with each scenario. For example, scenarios with relatively high connectivity (Full Connectivity, Opportunistic Restoration 1 and 2) resulted in the complete loss of genetically pure YCT under every random mating simulation, even when life history variation was modeled. Our result that life history variation is important for salmonid population persistence aligns with previous empirical studies (Hilborn et al., 2003; Neville et al., 2006). We found that modeling the potential for a large, migratory life history form in reconnected patches was an important factor for determining the relative abundance of YCT, hybrids, and RBT under certain conditions, and may be key to sustaining pure YCT populations in the long term. Other studies suggest that large-bodied, migratory life history forms in species of salmonid fishes can mitigate negative interactions with nonnative species (Al-Chokhachy et al., 2021; Dunham et al., 2008; Nelson et al., 2002). In our models, allowing simulated YCT to become larger, more fecund, and longer lived possibly gave them an advantage over RBT, but only when the partial, self-preference mating option was used. This is especially interesting because in these simulations, the occurrence of large, migratory YCT in the total fish population was fairly low (<1%), meaning that a small number of these individuals were leading to large differences in observed patterns. Our simulations align with empirical studies showing the presence of a migratory life history form, in addition to conditions that promote reproductive separation, can reduce the occurrence of hybridization (DeRito et al., 2010). Previous investigations from an adjacent watershed, the South Fork Snake River, have suggested that managing RBT populations through reproductive separation can have positive effects on YCT populations (DeVita, 2014; McCormick & High, 2020). Interestingly, the importance of self-preference mating or reproductive separation was not explicitly revealed in stakeholder mental models, but interview participants did mention that excluding RBT from important YCT spawning habitats might be an important management consideration in the future. In another trout hybridization simulations study, Nathan et al. (2019) found that mate preference (random vs. self-preference) alone did not have a strong effect on the abundance of Dolly Varden-bull trout hybrids in their study system. However, natural selection can also shift hybridization dynamics (Nathan et al., 2019), which could be implemented in further modeling efforts.

Little is known about the genetic and environmental drivers of the expression of migratory life history in YCT, or how these could interact as a result of restored connectivity. Other studies of salmonids indicate that the potential for migratory behavior can be retained in isolated populations. In the Elwha River, genetic diversity and migratory life history strategies of rainbow trout (steelhead) were preserved despite dam construction, and steelhead descendants rapidly recolonized post-dam removal (Fraik et al., 2021). It is unclear if YCT could respond to connectivity restoration in similar ways, and further research in this area will be important for effectively managing life history variation in YCT metapopulations. Further understanding of this plasticity, as well as closer analysis of the current distribution of large, migratory YCT in the Teton River drainage, could help managers evaluate where and how to reestablish connectivity to achieve desirable outcomes for YCT.

Mental model and IBM limitations, assumptions, and future directions

There were limitations of our study, both with mental modeling and individual-based modeling, and consideration of these may guide future research and model development. First, the interview data and resulting mental models are a function of what was asked, and participants likely possess more knowledge than what they were able to represent. For example, self-preference mating or reproductive separation of YCT and RBT were notably missing from the mental models, but this does not necessarily mean that stakeholders are unaware of these concepts and their role in the SES. Had we asked more detailed or specific questions about certain factors, such as reproductive separation, farming practices, or land-use zoning, participants' mental models may have been more complex due to highly detailed, specialized knowledge in those areas. Furthermore, the pool of stakeholders we interviewed was not a random sample, but did represent some of the prominent interests in the study area. The Jackson, WY-ID metro area has the largest wealth gap in the United States (Sommeiller & Price, 2018), and Teton County, ID has a quickly growing Hispanic population (US Census Bureau, 2019). Sampling for additional perspectives across socioeconomic and cultural groups could lead to further insight, unique knowledge, and complexity in the aggregate model. In addition, future studies could include a decision analysis component, where model results are presented in additional interviews with stakeholders to better use and understand our approach as a decision-support tool.

When parameterizing the IBMs, we made several assumptions surrounding life history variation that may have underestimated the contribution of large, migratory YCT to population recruitment over their lifetimes, and therefore underestimated the role of life history variation in mediating interactions with nonnative fish species. Large, migratory individuals existed before barriers were "removed" after the 50-year burn-in period, rather than as a result of barrier removal. Furthermore, the patch-scale parameters under the Status Quo scenario represent the current capacity for life history variation on the landscape; that is, any tributary patch connected to the mainstem had the capacity for large, migratory individuals. Because of this, we likely overestimated the distribution and abundance of large, migratory individuals under current conditions. However, we also used a conservative estimate for the maximum length (400 mm) of YCT, although less abundant, IDFG has sampled larger YCT in the Teton River drainage. In addition, we used a conservative maximum age of 7 years, although far less abundant, YCT over 8 years old were sampled by Meyer et al. (2003) in the South Fork Snake River. Furthermore, the lack of density-dependent dispersal within the CDMetaPOP framework led to an overestimate of patch-level density-dependent mortality where large, fecund YCT were reproducing.

Although we successfully incorporated YCT life history variation into the CDMetaPOP framework, there may be ways to improve this approach to be more realistic and provide more insight. Because life history variation was built into the parameter space, rather than as an emergent property of model behavior, we cannot draw conclusions about how much connectivity may be needed to sustain large, migratory YCT. Similarly, we assumed that habitat quality was the same across the entire landscape (e.g., growth rates and spawning frequency were the same for every patch). Migratory individuals are able to grow large, in part, because they can take advantage of a variety of resources and spatio-temporal heterogeneity in resource quality across a riverscape (Fausch et al., 2002; Gross, 1987; Northcote, 1997). In the Teton River, migratory YCT with access to the mainstem are able to grow large and move between tributaries and the mainstem. Our assumptions were largely due to limitations of the software itself, but there is also little known about what drives migratory behavior in YCT populations, and to what extent migratory genetics are retained in isolated populations of YCT in the Teton River. Developing a method for modeling the development of migratory behavior over time following barrier removal, as well as habitat quality parameters, may affect the onset and magnitude of its impact on measured outcomes. In addition, future field studies of YCT in the Teton River should focus on understanding the genetic and environmental drivers of migratory behavior. This would provide more insight into which connectivity scenarios might result in the most desirable outcomes for YCT, as well as how access to particular tributary or mainstem patches might be important for maintaining large YCT.

Another important assumption of the study was that mate choice is based on female preference for males within the same patch and that have a similar H index. This relationship assumes that mate pairs are more likely to comprise individuals of a similar genotype (e.g., H index), and that genotype is an accurate reflection of phenotype, the primary informant of mate preference in nature (Nathan et al., 2019). However, how YCT and RBT select mates based on a spectrum of genotypes and phenotypes in the Teton River drainage is unclear.

It is also unclear what other factors, such as spawn timing, may influence self-preference mating where there is spatial overlap. Furthermore, CDMetaPOP can only assume that assortative mating is the same for every patch, but it is likely that mate selection among YCT, RBT, and hybrids varies among tributaries depending on conditions. In addition, simulating migratory life history characteristics for RBT could result in different outcomes from what we observed. Some studies in other watersheds have found that YCT-RBT hybrids grow larger and migrate at an earlier age than YCT (Kovach et al., 2015; Strait et al., 2021); the possibility of RBT and RBT-YCT hybrids developing a migratory life history or other fitness advantages presents an additional challenge to managing hybridization between the two species. Future investigations should consider these dynamics in more detail and focus on understanding hybridization dynamics using genomic techniques (e.g., Hohenlohe et al., 2011) to more accurately simulate selection and introgression.

Implications for connectivity conservation and restoration

The IBMs allowed us to explore ecological uncertainties regarding YCT and nonnative trout that were discussed by interview participants. Furthermore, the results from the IBMs present some possibly unexpected ecological findings for the stakeholders we interviewed. In particular, the importance of reproductive separation between YCT and RBT was apparently not fully appreciated by interview participants. Although migratory YCT were included as a component in the mental models, their importance in determining outcomes for YCT populations and possibly other social–ecological outcomes is perhaps better understood by supplementing the results of the IBMs. Linking these results demonstrates the utility of integrating the two approaches. In the future, these results and recommendations could be presented to the stakeholders we interviewed to contribute to collaborative learning and inspire future investigations in the Teton River.

We did not observe large differences in outcomes among the different connectivity scenarios, but previous simulation studies have demonstrated the importance of landscape connectivity for recolonization and population persistence (Mims et al., 2019; Thatte et al., 2018). It is important to note that life history variation in YCT is one possible outcome of restoring connectivity. Allowing migratory YCT to grow large and become more fecund was a major driver of the patterns we observed in our simulations. Creating migratory corridors and managing high-quality mainstem habitats so that YCT can grow large may be important for mediating the impacts of nonnative species. Previous studies in the Teton River have suggested that access to productive habitat and migratory pathways can promote both life history variation and stable YCT populations, even where nonnative species persist (Al-Chokhachy et al., 2021). Reproductive separation (self-preference mating) between YCT and RBT may also be an outcome of restoring connectivity, although this can also be achieved through selective fish passage over barriers (Ardren & Bernall, 2017; High, 2010). However, fisheries stakeholders acknowledged that selective passage efforts would require infrastructure and resources, and that increasing harvest of RBT while improving conditions for migratory YCT are more likely and attainable goals.

One of the aims of this study was to place IBM outcomes in an SES context by linking the findings from both the IBMs and the mental models, to provide more nuanced insight into the management implications of IBM results. Developing stakeholder-informed scenarios with social–ecological conditions and implications aided in this analysis. Viewing the IBM results on their own would not have captured the complex relationships that large, migratory YCT and hybridization dynamics might have with other components of the SES. Additionally, the scenarios we developed may have implications for social–ecological factors such as irrigation and development, and the aggregate mental model allowed us to evaluate those outcomes. For example, under a Full Connectivity scenario, decreases in anthropogenic fish barriers may lead to decreases in irrigation diversion. Decreased irrigation diversion can lead to increased water quality and fish passage, but it may also negatively affect crops and therefore the economy. However, increases in stream connectivity due to habitat restoration or barrier removal can increase usable water availability and benefit junior water users in particular. Furthermore, one outcome observed in the IBMs was that, under certain conditions (namely, random mating and high or full connectivity), genetically pure YCT were lost by the end of the simulation. The aggregate mental model indicated that if the YCT population were to decrease, the likelihood of the species earning an Endangered Species Act (ESA) listing would increase, which would then increase management costs, funding, public interest, long-term (land) protection, and partnerships. Therefore, the ecological benefits associated with large, migratory YCT and reproductive separation from RBT can translate into social outcomes as well, including those factors associated with an ESA listing. Indeed, interview participants explained that one of the main motivations behind YCT conservation efforts was to avoid an ESA listing, which could alter water rights allocation to the detriment of irrigators. The "Protect YCT" scenario was inspired by this concern. By avoiding an ESA listing of YCT, management costs would decrease. However, funding, public interest, long-term protection, and partnerships among organizations could also be affected. Furthermore, previous studies (including those conducted within the Teton River drainage) have shown that the replacement of YCT by nonnative fish species may have ecosystem-scale implications, meaning that losing these native fish populations could have effects not limited to these fish themselves, but extending to the web of interacting species connecting streams and riparian zones (Benjamin et al., 2011; Benjamin & Baxter, 2012). Moreover, the aggregate mental model showed direct positive relationships between ecosystem function and social outcomes such as economy, human well-being, and traditional foods, whereas partnerships, funding, ecosystem function, and public interest are directly or indirectly increased by increased YCT populations. The aggregate mental model showed that increasing YCT populations would directly increase ecosystem function and public interest, as well as benefit recreational guides, angling, and human well-being, all of which had some relationship with partnerships, funding, or public interest. This pattern, in addition to the results from the IBMs, highlight the nonlinear and potentially far-reaching impacts that migratory YCT, as well as connectivity re-establishment in general, may have in the Teton River SES.

These results also highlight the need to consider complex social factors and outcomes, from a variety of stakeholder perspectives, in connectivity conservation more broadly. Despite growing interest in connectivity conservation and re-establishment, few studies have explored its context-specific social–ecological outcomes. SES outcomes are not often considered or quantified in the research or management of stream connectivity and fish population connectivity. Moreover, evaluating complex social–ecological relationships and outcomes may be helpful for making management decisions, because managers can better understand how the SES works, anticipate unintended consequences, and adapt to outcomes across scales and stakeholder interests. Our integrative approach allowed us to explore social–ecological outcomes of changing riverscape connectivity, identify gaps and overlap in knowledge among stakeholders, integrate stakeholder perspectives into quantitative models, and evaluate uncertainties surrounding a species of conservation concern and its response to changing river network connectivity. The results from this study can contribute to the management dialogue surrounding stream connectivity and fish populations in the Teton River, as well as to our understanding of connectivity conservation and its outcomes more broadly.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Jossie, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8161826.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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