BioScience, 2024, **74**, 624–639
https://doi.org/10.1093/biosci/biae081
Advance access publication date: 28 August 2024
Forum

Fish habitat models for a future of novel riverscapes

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Abstract

Multiple anthropogenic forces have pushed river ecosystems into undesirable states with no clear understanding of how they should be best managed. The advancement of riverine fish habitat models intended to provide management insights has slowed. Investigations into theoretical and empirical gaps to define habitat more comprehensively across different scales and ecological organizations are crucial in managing the freshwater biodiversity crisis. We introduce the concept of novel riverscapes to reconcile anthropogenic forcing, fish habitat, limitations of current fish habitat models, and opportunities for new models. We outline three priority data-driven opportunities that incorporate the novel riverscape concept: fish movement, river behavior, and drivers of novelty that all are integrated into a scale-based framework to guide the development of new models. Last, we present a case study showing how researchers, model developers, and practitioners can work collaboratively to implement the novel riverscape concept.

Keywords: river management, riverine processes, novel ecosystems, spatial scales, temporal scales

Anthropogenic activities (i.e., watershed management, urbanization, water use, water abstraction, and river regulation) and their associated instream modifications are ubiquitous in riverscapes globally (Macklin and Lewin 2019). A snapshot of large rivers, from a fish perspective, highlights examples where continued anthropogenic forcing produces permanent habitat alterations and reductions in biodiversity. For example, the construction of dams on the Yangtze and Yellow Rivers has caused the extinction of the Chinese paddlefish (*Psephurus gladius*) and has pushed multiple other species to near extinction (Scarnecchia 2023). Habitat loss and overfishing continue to diminish fish biodiversity in the Peruvian Amazon, which now threatens food security for 800,000 people (Heilpern et al. 2021). Extreme water abstraction prevents the Colorado River from reaching its mouth, eliminating critical estuary ecosystem functioning (Pitt et al. 2017). Multiple endemic sturgeon populations are classified either as vulnerable or as critically endangered in the Danube River Basin because of continued river fragmentation, poaching, changes in hydrogeomorphology, and pollution (Friedrich et al. 2019). It is common for rivers to experience multiple anthropogenic impacts simultaneously, which can induce lasting effects even when they subside (Moyle 2014).

Fish habitat models must be capable of diagnosing and quantifying anthropogenic impacts on fish and their habitat but very few models provide insight on the reversibility of such impacts at the scale the impacts were first introduced (Frissell et al. 1986, Wiens 2002). This shortcoming makes finding self-sustaining solutions for river and fish habitat restoration problematic. The forefront of fish habitat model development will require the capacity to untangle the interactions of multiple impacts, evaluate impacts at the appropriate spatial and temporal scales, and more holistically address impacts on fish biodiversity instead of focusing on individual species (Fausch et al. 2002, Torgersen et al. 2021). In the present Forum article, we provide a contemporary synthesis and direction for fish habitat models to maximize returns on river and fish habitat restoration and management. Specifically, we focus on mathematical or statistical models that explain, predict, or generalize phenomena and processes within lotic fish habitat ecology. We include four major themes: an introduction of novel riverscapes, an evaluation of current fish habitat models, three

Received: November 27, 2023. **Revised:** July 2, 2024. **Accepted:** July 16, 2024

data-driven opportunities to promote the model development process, and a scalable framework to facilitate application. We conclude the article with a case study to illustrate how these themes merge, which, in turn, provides an ideal future for fish habitat modeling.

Introduction of novel riverscapes with a focus on fish

Past definitions of riverscapes neglect to include the property of reversibility when considering impacts on riverine processes and fish habitat. Without reversibility, our fish habitat models will operate assuming that no impact is severe enough to permanently alter the ecosystems we intend to restore. To the contrary, unless anthropogenic impacts are reversible, a novel riverscape that is without historical precedent is inevitable (table 1; see Hobbs et al. 2009 for a complete view of novel ecosystems theory). A riverscape's pathway from a historical state to a hybrid and then to a novel state depends on the presence of anthropogenic forces acting on river processes and their reversibility (box 1; Hobbs et al. 2013). Minor impacts over the span of years are more reversible than say impacts that span centuries (Kondolf et al. 2006). Fish habitat quantity and quality degrades as riverscapes transition from historical to novel states. The hybrid state has ample restoration opportunities to reverse impacts but also has the risk of slipping into a novel state if impacts are left unchecked. Adapting fish habitat models to the novel riverscape concept could help us recognize which state our riverscapes exhibit and could help us prioritize habitat management and restoration efforts at a process level regarding reversibility.

The novel riverscape concept emphasizes that ecosystem restoration and habitat appraisal are opportunities that can be lost and that, under all practical considerations (i.e., limited time and money), are impossible to reacquire. Evidence of this reality is present in many aquatic ecosystems facing invasive species expansion, acidification, mercury pollution, and eutrophication, which require indefinite counter measures to maintain the ecosystem (Acreman et al. 2014). From a regulatory perspective, examples of novel riverscapes include the European Union classification of heavily modified water bodies, and, in the United States, Superfund sites. Novel riverscapes also raise the question on the effectiveness of one-size-fits-all management techniques present in rivers around the world (Hawley 2018). We contend that many fish habitat modeling shortcomings can be better addressed under the novel riverscapes concept.

There are varieties of novel ecosystem definitions (e.g., designed ecosystems) that have less to do with models (Higgs 2017), so we have not included them in our novel riverscape concept. But as a general rule, they all maintain we can certainly fail to reverse impacts in time, which results in permanent consequences (Hobbs et al. 2013, Morse et al. 2014). Our ability to manage fish habitat quality and quantity depends on the appropriate application and interrogation of fish habitat models. This means our current models and new models must address reversibility of impacts, must make use of the best available data to find solutions, and must be appropriately implemented at the scales impacts occur. Most importantly, if one's model does not consider the possibility of failure as an outcome, novel riverscapes may not only occur but may do so without detection (i.e., shifting baselines).

An evaluation of current fish habitat models

Fausch and colleagues (2002) highlighted the mismatch in connections among fish habitat, river management, natural processes, the anthropogenic impacts we seek to understand and manage, and the gaps that require new models and long-term data sets. Current fish habitat models support evidence-based decision-making as the freshwater biodiversity crisis continues (Tickner et al. 2020), but they exhibit numerous shortcomings that limit their full usefulness especially under the novel riverscape concept. The persistent debate about fish habitat model design among ecologists and engineers has unfortunately polarized each view instead of unifying their fields' respective talents to address these shortcomings (Railsback 2016, Beecher 2017, Stalnaker et al. 2017, Rinaldo and Rodriguez-Iturbe 2022). The novel riverscape concept helps us mutually identify critical strengths and weaknesses of existing models, so they are used appropriately and inform the design of new models to enhance our capabilities.

Throughout the evaluation, we hope to convey the importance of picking the right model or models for the job, and sometimes that means developing a new one and straying from tradition. Access to expert judgement to guide the decision-making on the right model to choose is sometimes hard to find. As a result, it is common to use the same tool over time for consistency's sake. Although this might be economically convenient, it inevitably involves a lot of risk to trust in only one model. This risk grows when new impacts are acting on the riverscape and the chosen model and its developers have little capacity to adapt to these changes. The combination of refining theory and model validation is crucial, but in practice, it is unfortunately less appreciated (Getz et al. 2018). No matter how sophisticated or simple a model is, it is not a purveyor of truth unless the model is verified. One must keep such rules in mind as we examine the technical capacities of different models in supplement S1 in the context of novel riverscapes. Our evaluation summarizes models commonly used to explore fish habitat relationships in rivers. We have separated the models into types that reflect areas of expertise concerning model development and their respective scales to help people navigate the wide variety of fish habitat models.

Fish habitat model origins

If we examine the legacy of fish habitat models (type 1; see supplement S1) and the concepts that support them, we find that little has changed (Railsback 2016, Beecher 2017, Nestler et al. 2019). The difficulty of modeling fish habitat from a practical perspective, where time and resources are severely limited, ushered in the practices of prioritizing individual species instead of broader biodiversity goals, and assessing impacts separately instead of jointly. For a historical example, the instream flow incremental methodology (IFIM) was an early decision support system concept designed to improve lotic water management on the basis of fish habitat model results (Stalnaker et al. 2017). Its practical implementation came with cautionary notes that users often ignored (Cooperative Instream Flow Service Group 1979, Stalnaker 1979b). This concept historically could not account for lentic systems or their connections, was not designed to generate minimum flow recommendations, could not predict fish production, and considered only the physical aspects of the stream and not chemical or water quality changes (Stalnaker 1979a). The source of numerous limitations in current fish habitat models and the resistance to adopt new concepts originate from this view and its definitions of fish habitat (Nestler et al. 2019).

Table 1. Glossary for fish habitat models and novel riverscape theory with examples.

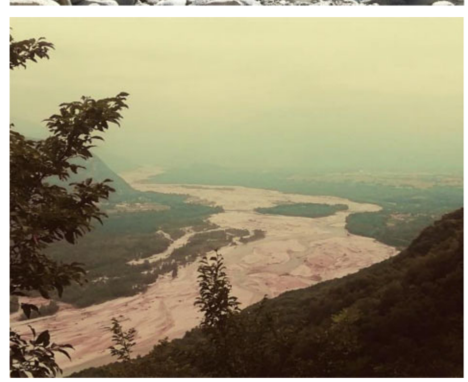
Term	Definition and example description	Example	Picture of example
Riverscape	Watershed and the adjacent terrestrial system that directly or indirectly influences the river ecosystem network and associated water bodies.	Ankobra river basin in Ghana with illegal alluvial gold mining operations. Temporary waste pools are created adjacent to the river to support mining operations.	
Habitat	A mosaic of (a)biotic spatial patches necessary for a species to fulfil life history requirements considering risk, resources, and conditions.	Elarm River in Iran showing a localized example of pool, riffle, run habitats adjacent to different riparian cover types. Each habitat type in this mosaic provides dynamically changing risks, resources, and conditions for each respective species.	
Suitability	The relative capacity of a habitat to sustain an organism over relevant spatiotemporal scales.	Yellowstone River headwaters in the United States showing a variety of natural barriers, substrates, hydraulic conditions, and cover that impose unique habitat selection opportunities for individual fish.	
Historical Riverscape	A riverscape where the trajectory of abiotic, biotic, and social characteristics shows the full range of natural variability unhampered by irreversible anthropogenic forces.	Tagliamento River in Italy. It is one of the last large free flowing rivers in Europe that exhibits braided channels that can also freely meander across a broad floodplain.	

Table 1. Continued

Term	Definition and example description	Example	Picture of example
Hybrid riverscape	A riverscape that has undergone reversible anthropogenic changes, altering the trajectory of abiotic, biotic, and social characteristics	River Badam in Kazakhstan with water diversion structures and reductions in floodplain habitat. Instream habitat is present but quality has been reduced.	
Novel riverscape	The combined trajectory of the abiotic, biotic, and social characteristics of the riverscape cannot be restored to the historical state, regardless of human management.	Bílina River in Czech Republic. This river was converted to pipes so a massive brown coal mine could be built without disturbance from the river and its floods. Plans to rebuild the river after the mine closes have been discussed but not yet decided.	

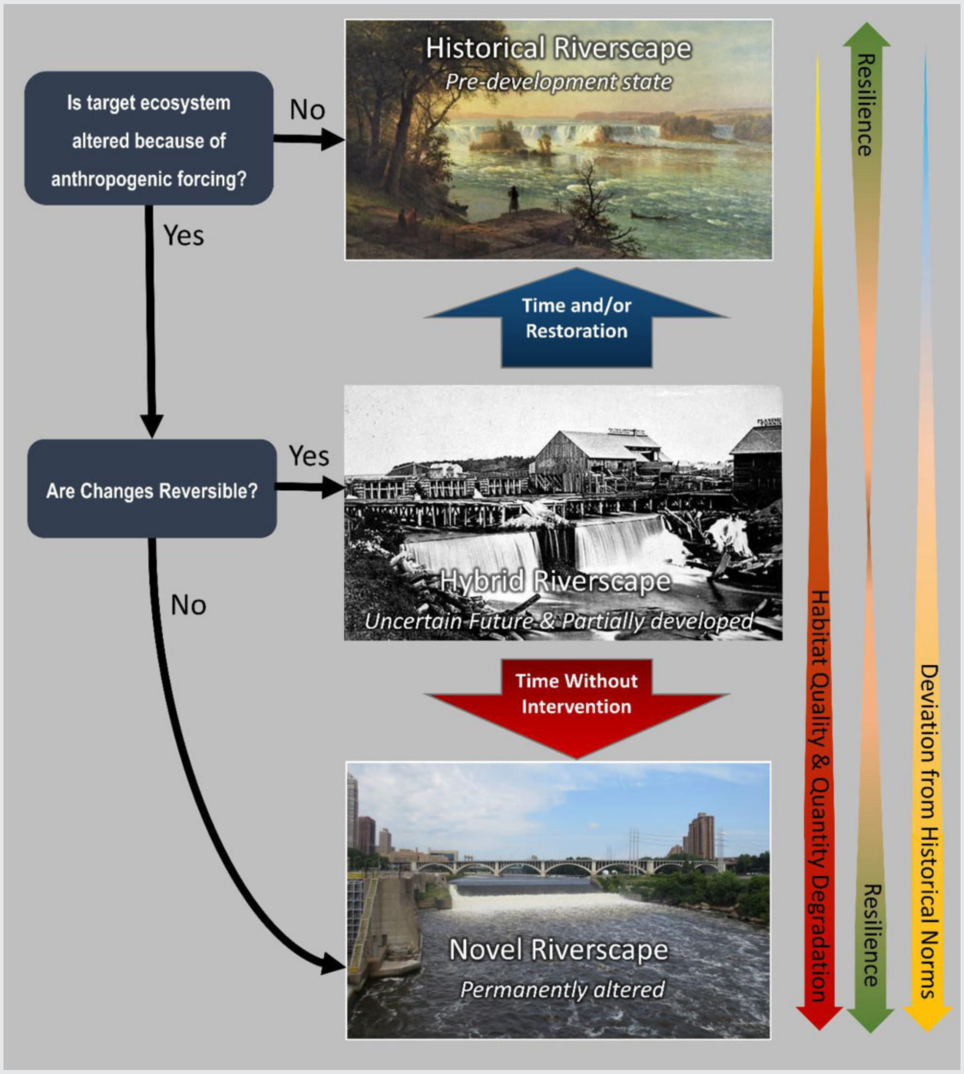
Physical fish habitat models

The intended supplemental model for IFIM was the physical habitat simulation system (PHABSIM; type 1). This approach informs how water depth, flow velocity, substrate, and cover operate on a gradient to determine fish–habitat relations within a river reach (Bovee 1982). PHABSIM is the precursor model to many other physical habitat suitability models (e.g., RHYHABSIM, MESOHABSIM, CASiMiR). Modern versions can incorporate bioenergetics, hydropower output scenarios, stress days, ice cover, and other parameters (Vezza et al. 2015, Rosenfeld et al. 2016, Naman et al. 2020, Wegscheider et al. 2020). More holistic and water resources-oriented models were developed with similar foundations (i.e., WEAP). They are all an index of habitat but only at the physical habitat level (Bovee et al. 1978, Bovee 1982, Hudson et al. 2003). As one of the original PHABSIM manuals so aptly puts it, "In essentially all situations, physical habitat is a necessary, but not sufficient, factor for the production of benefits. The analyst must never lose sight of the importance of factors other than physical habitat" (Milhous et al. 1989, p. I.4). Criticisms of physical habitat models have been focused on their lack of predictability given its output—weighted usable area (Railsback 2016), its systematic biases (Rosenfeld and Naman 2021), and violations of biological realism (Kemp and Katopodis 2017). They represent an early attempt at habitat modeling, and to its credit, it is one of the few models that prioritizes practitioners' needs because it can be implemented rapidly and is easily interpreted. Adapting these models to the novel riverscape concept is limited. One could begin by applying validated suitability criteria from one riverscape with a historical state and transferring it to a comparable riverscape with a hybrid or novel state for the same species. This would allow for an exploration of how the habitat quality and quantity for fish change in relation to the state of the riverscape.

Generic statistical models

Around the time of PHABSIM, there was a diversifying array of fish habitat models referred to as *standing crop models*, which were mostly generic statistical models (type 2; see supplement S1). In the present article, we make an important distinction: Some of these models relate fish quantity to habitat variables, whereas others model habitat on the basis of what the fish used (Fausch et al. 1988). This means that the first approach attempts to predict fish abundance given habitat conditions, whereas the second is a translation of habitat variables to predict what fish find suitable (Reiser and Hilgert 2018). In either case, low sample sizes, errors in measuring habitat variables, and the lack of a model selection procedure in the case of multiple competing models hampered these models in ways that could not be empirically validated (Fausch et al. 1988). The modern counterparts of generic statistical models, machine learning models and causal models (i.e., structural equation models), all have the functionality to compare competing models on the basis of prediction. Habitat measurements are still an issue, because the current classifications of geomorphological types dwarf the number of classes that are implemented by fish habitat modelers in the field, leading to unclear interpretations of habitat and its variability (Rinaldi et al. 2016, Belletti et al. 2017). The low sample size issue now affects machine learning and artificial intelligence models

Box 1. Novel riverscapes concept.



A simplified example of the novel riverscapes concept: Albert Bierstadt's painting of the St. Anthony Falls on the Mississippi River in 1880 is one of the clearest depictions of this historical riverscape. During the Industrial Revolution, St. Anthony Falls became engineered with temporary structures for industry but river hydrology was still relatively intact, leading to a hybrid riverscape (see Mazack 2016 for a more in depth historical overview). Owing to subsequent extinction of native mussels, unmanageable invasive plants and fish, reduced interactions with the floodplain, and construction of permanent water-management structures, the local riverscape has become a novel riverscape. Return to the hybrid or historical state is considered impossible in the foreseeable future. Therefore, it must be managed as a novel riverscape with full consideration of the permanent changes to its preindustrial habitat composition. The permanent change reinforces the need to clarify what suitability means in measuring and modeling fish habitat. The restoration actions that are considered may be a broad range of options that attempt to recreate aspects of its historical state (i.e., original look of the falls) but the riverscape will functionally operate on a novel trajectory (Ward et al. 2023).

because they require cost-prohibitive amounts of data relative to the size of the field site. The opportunity for novel riverscapes is to simulate data under a variety of riverscape states and sample sizes to assess model performance before encountering real data. The "squid" package (Allegue et al. 2022) and "caret" package (Kuhn 2008) in R are two packages that could enable robust sensitivity analyses of statistical models given commonly seen data limitations for fish habitat modelers.

Ecological statistical models

Ecological statistical models (type 3; see supplement S1) focus on population level inference and relations to habitat. What separates ecological statistical models from their generic counterparts is the practice to account for imperfect sampling and detection. A connecting issue that affects both type 2 statistical models and type 3 ecological statistical models is the major concern of confounding variables. Various techniques intended to evaluate model prediction (e.g., Akaike's information criterion) are being misused for causal questions (Arif and MacNeil 2022). For example, an observational study investigating the impact of habitat changes on fish production is a causal question where choices about the covariates in the model determine potential bias (Larsen et al. 2019). We strongly encourage statistical modelers to review the implications of confounding variables and how directed acyclic graphs can help ease some of these issues (Grace and Irvine 2019). Statistical movement models that relate fish movements to habitat have the added challenge that data is usually autocorrelated (autocorrelation may also be an issue for species distribution models), which can also bias results if the model is not adjusted the results (Silva et al. 2022). Uncovering the causal implications of impacts while untangling the errors associated with confounding can be addressed using the *dagitty* tool for graphical analysis of structural causal models (Textor et al. 2016). *Dagitty* provides a programming and graphical user interfaces to explore confounding and to recognize faulty ecological statistical models before data are incorporated. One could then explore how different impacts could increase or mask the effect size associated with different riverscape states.

Ecological individual-based models

Outside of ecological statistical models are ecological individual- or agent-based models. These are focused on modeling ecological mechanisms (e.g., feeding, competition, predator avoidance) and fish behavior to inform habitat selection, as opposed to selecting only a few abiotic factors (Piccolo et al. 2014). Agent-based models provide a robust means of understanding habitat selection and preference or the ecoevolutionary dynamics of fishes that have emerged as a result of energy allocation and timing of activities related to maintenance, growth, and reproduction in a seasonally changing environment (Hölker and Breckling 2005, Ayllón et al. 2016). One such model, InSTREAM, builds off of optimal foraging theory to inform habitat use under varying hydraulic conditions at the individual fish level (Railsback et al. 2021). On the other hand, ELAM (Eulerian–Lagrangian–agent method) relates agent behavior of individual fish to computational fluid dynamics simulations (Goodwin et al. 2006). Agent-based models serve as a potential basis for examining how ecological processes at the level of individual organisms link to population-level processes (Breckling et al. 2005, Grimm and Berger 2016). Incorporating many mechanisms, however, becomes data intensive to inform parameters, challenging to code, and is more feasible for single species at relatively small scales, as opposed to entire communities (Beecher 2017, Kerr et al. 2023, Mawer et al. 2023). Practitioners often criticize agent-based models as being too theoretical (Reiser and Hilgert 2018), but new approaches now allow for analytical approaches using approximate Bayesian computation (van der Vaart et al. 2015) to extract parametric relationships between agents. In other words, the rule-based world of agent-based models can be analyzed to produce parameters that directly link to the riverscape and habitat being studied. Studying agents under varying riverscape states and including aspects of reversibility could be readily compared and communicated to managers with this new approach.

Picking the right model

We have prioritized the most common models seen in riverine fish habitat modeling in our evaluation. Our introduction of new tools and approaches associated with each model could help adapt models to the novel riverscape concept. We also realize that our evaluation of current models highlights many trade-offs, which makes picking a model difficult, but it is still possible to make an informed choice, given the state of a riverscape (box 2). If none of the previous models seem to satisfy the needs of your riverscape, we now explore the future possibilities of fish habitat models. Our view of future models is intended to address some of the shared shortcomings in all the previously mentioned fish habitat models: Many models view river habitats as static when they are dynamic, with feedback loops, and are a function of the ecosystem's state (Anderson et al. 2006); they can only inform selected pieces of the riverscape regardless of how the riverscape may shift into more undesirable ecosystem states (Railsback 2023); greater incorporation of ecological and geomorphological components are needed, depending on the management focus (Orth 1987, Lancaster and Downes 2010), and modern theories on river and fish ecology suggest an even greater complexity of fish habitat relations than most models have previously considered (Humphries et al. 2019, Allen et al. 2020). These shortcomings show a substantial need to advance model development in ways that satisfy novel riverscapes. The stressors that act on rivers are becoming more diverse, forcing us to seek opportunities to build models with the latest technological advancements and data while still being user friendly and accessible (Torgersen et al. 2021).

Data-driven opportunities to advancing riverine fish habitat models

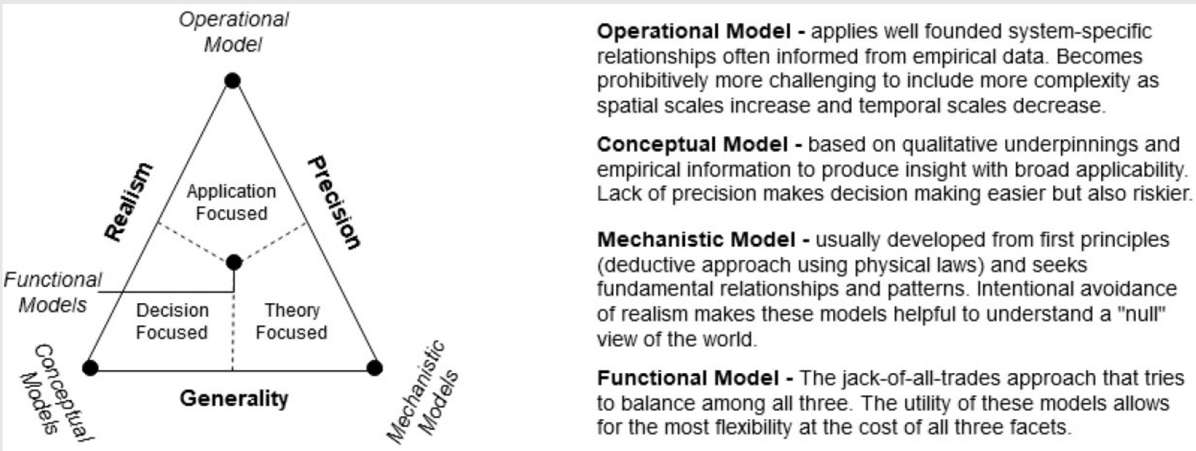
As riverscapes transition among states, there are only three opportunities for fish habitat models that both come directly from data pipelines (i.e., nearly continuous measurements at high frequency and sufficiently long timespans) and address fish habitat dynamics directly. We live in an era where data has become so plentiful and robust that merging these data pipelines into action is the new frontier of ecological data science (Besson et al. 2022) and a necessary next step to adapt fish habitat models to a novel riverscape future. The first opportunity concerns fish movement and the wealth of telemetry data shared in open databases (e.g., the European Tracking Network). The second opportunity concerns the geomorphologic, hydrologic, and hydraulic behavior of rivers, which is crucial to assess the state of a riverscape and the habitat it contains (Brierley and Fryirs 2022). In the present article, the data pipelines are global-scale hydrograph gauges and groundwater stations. The third opportunity, drivers of ecosystem novelty (i.e., stressors or disturbances), attempts to incorporate the many synergistic shapes, sizes, and effects of disturbances on fish habitat (Orr et al. 2022), many of which can be leveraged from remote-sensing data (Kuiper et al. 2023). Individually, they represent topics with immense depth but when combined, they act as the benchmark for the next generation of fish habitat models (figure 1).

Fish movement

Understanding not only fish movements in time and space but also *why* fish move is critical for developing effective models (Hughes 2000). Estimating the entire movement path of a wild fish's life is still out of reach, but our capabilities now allow us to piece much of it together with its corresponding habitat (Brownscombe et al. 2022). Often, we estimate a fish's movement at critical times within the fish's life history, such as spawning, but our paper's definition of fish movement concerns all movements from hatching until death without bias to particular life

Box 2. Best practices of picking a fish habitat model.

The application of fish habitat models in rivers covers a wide variety of models and restoration goals that often require expert guidance to be used effectively. Building off the classic Levins modeling paper (Levins 1966) and more recent modeling viewpoints (Railsback 2023), we illustrate a more modern triad of modeling trade-offs before diving into key questions of reflection that could help in choosing an appropriate model. This guidance could help any modeler better address issues associated with river impacts and the associated biological goals, legal–institutional settings, and site-specific opportunities and limitations.



We need the model to understand biological resource management goals in the context of water management goals. Thinking from the onset about what needs to be done in the river or stream is an ideal way to balance practicality and theoretical limitations prior to model application or extension. Realize that this may incorporate multiple perspectives. If flows are changing, investigate the management that permits that; if a species is going extinct locally, understand what management does to prevent that; if a stretch of river is being restored, learn what flexibility management has in the design process. One will quickly come to realize that this initial line of questioning shapes the scales involved.

The model considers the spatial and temporal scales of the study system in selecting fish habitat models. Scales in this case can be interpreted as either a small-scale stream or a kilometer scale, but both views can help nail down the quantitative boundaries a model uses. For instance, what is the smallest size of a habitat patch in the habitat model and how frequently does it change? Is it on the order of centimeters and seconds, which may be appropriate for a newly hatched fry, or on the order of kilometers and months, which may be appropriate for a migrating adult fish. Similarly, using the scales of policies and management to inform early on how a model can be translated into action makes results more relevant for practitioners.

We achieve the objective by matching the desired model data (i.e., the desired model traits) to water and fish management goals. Depending on the chosen scales, the desired data may come from a single discipline focus or come from a multidisciplinary approach. A model focused on a small side channel will use data and techniques for ecohydraulics, whereas a full watershed will use those for ecohydrology, each with their own approaches to measure habitat and related data.

The model depends on understanding the quality of information available to develop aquatic habitat requirements for target aquatic biota. The habitat requirements of some aquatic species are well known (e.g., stream salmonids) whereas the habitat requirements of other species are poorly known or understood (e.g., Atlantic sturgeon). Out of all the mechanisms that can influence the relationship between fish and their habitat, only some are useful to incorporate, and even fewer have been measured. Theoretical considerations and empirical evidence are useful in justifying what stays and what gets left out.

The model requires consideration of the trajectory of abiotic, biotic, and social characteristics of the target river. The diversity of habitats produced by rivers is a function of its state. Unknowingly building a model that uses parameters from a different system or the same system with different conditions may produce invalid results, especially if the river's condition is slipping into a new state.

stage (Bull et al. 2022) or life history strategies (i.e., anadromous, diadromous, potamodromous, nonmigratory; fish movement opportunity; figure 1). Advancements in fish telemetry have reduced tag sizes and increased tag battery life to study underrepresented fishes (Chen et al. 2014). Tag costs have also been reduced, allowing studies to track more individuals and log multiple types of measurement congruently (e.g., depth, predation, temperature; Deng et al. 2017, Weinz et al. 2020). Extending studies to include multiple species from a community level and their interactions is also feasible. More advanced telemetry stations are now capable of having live connections to multiparameter sondes (e.g., dissolved oxygen, pH, turbidity, salinity, chlorophyll a/b, phosphorus, nitrogen), providing a data pipeline on habitat quality (Jacoby and Piper 2023). Validating movement patterns with stable isotope methods such as natal origins (Brennan et al. 2015) or spatial patterns of diet (Bell-Tilcock et al. 2021) also offer interdisciplinary insight on fish habitat. Complementing all this information with ecohydraulics and the plethora of experimental studies gives a much clearer picture of fish movement in relation to habitat in the lab and in the wild as riverscapes change.

The barrier-free hypothesis (sturgeon need free-flowing rivers), which some tout as a general guideline for sturgeon population

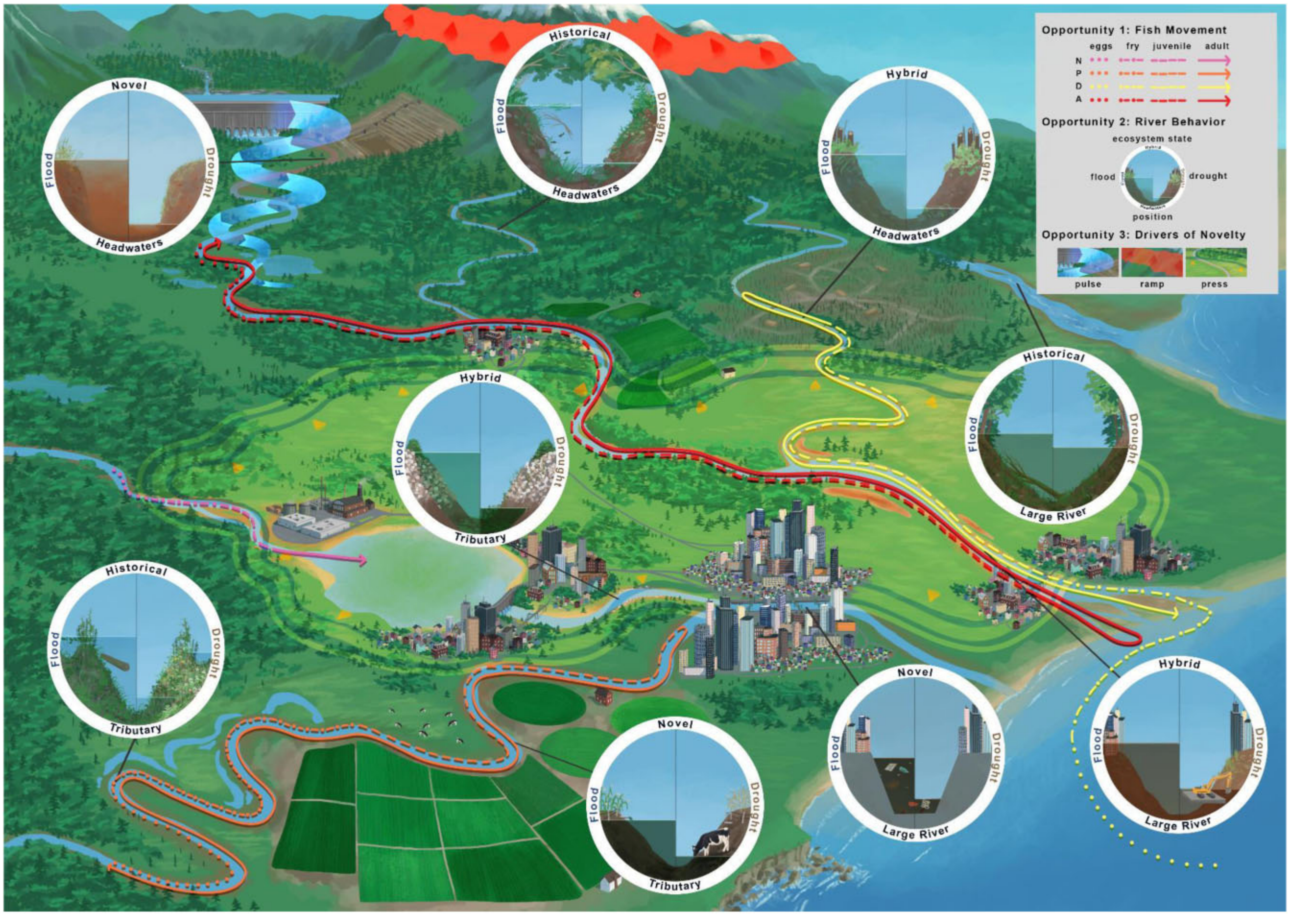


Figure 1. A hypothetical riverscape with historical, hybrid, and novel river reaches that highlight the three opportunities facing fish habitat models in rivers. Opportunity 1 concerns fish movement and how different life history strategies (nonmigratory, potamodromy, diadromy, and anadromy) all interact with riverscapes in different ways, given the distances travelled, life history stage, and location. Opportunity 2 concerns how the behavior of a river is influenced by its state, its stream order size, and the current hydrological regime. Opportunity 3 concerns drivers of novelty related to flow regimes: The pulse example shows hydropeaking, the ramp example shows reduced snowpack as a result of climate change, and the press example shows an expanding drought area. All three opportunities operate jointly in today's river systems to change the quality and quantity of fish habitat, but current models often neglect to incorporate such complexity.

recovery has informed fish movement and habitat expectations for decades. For example, dams have affected Chinese sturgeon (*Acipenser sinensis*) populations for all different life stages (Huang 2019). The novel riverscape concept highlights an alternative outcome, where a lentic-adapted lake sturgeon (*Acipenser fulvescens*), can thrive under vastly different geomorphic and hydraulic conditions in a hybrid river system altered by dams (Hrenchuk et al. 2017, McDougall et al. 2017). In both cases, heavily fragmented rivers affected movement and fish survival, but most fish habitat models would not be able to predict the success of lake sturgeon on one hand and the potential failure of Chinese sturgeon on the other hand. Recognizing how subtleties in the definition of fish movement could have profound impacts on the persistence of a fish population and is crucial for the success of potential restoration measures.

River behavior

The adage "no man steps in the same river twice," artfully describes the opportunity of river behavior, which we define as the progression of a river's flow in four dimensions (i.e., lateral, longitudinal, vertical, and temporal). The typical view of rivers concerns depth and velocity, but this view does not adequately address the complexity of fish habitat and ecological interactions as flows change (Tonkin et al. 2021). If we view rivers as moving targets for conservation that can change naturally or by human influence (Poff et al. 2010, Brierley and Fryirs 2016), we can better translate the ecosystem structure, biotic or abiotic processes, and ecosystem integrity to and from fish habitat models (river behavior opportunity; figure 1). The proliferation of gauging stations throughout global watersheds has now given us the capacity to study river behavior and its corresponding processes in ways that directly link process to ecosystem integrity and the organisms that depend on them (Palmer and Ruhi 2019). Stream gauging networks (i.e., multiple stations spanning multiple stream orders) provide continuous measurements on discharge and base flow statistics, often going back decades, but can also measure water depth, stage, water quality parameters, meteorological parameters, and physical parameters. Although future investments in stream gauging networks is needed to reduce geographical biases, the existing networks and regional hydrological models in many rivers provide unique fish habitat modeling opportunities at immense spatial and temporal scales that can also be combined with remote sensing to monitor flows (Krabbenhoft et al. 2022).

How this data informs our current understanding of river behavior has both theoretical and practical implications for fish habitat models. Updated perspectives on classical river theory such as the river continuum concept (Vannote et al. 1980, Stanford and Ward 2001, Doretto et al. 2020) demonstrate that a river's behavior serves as the environmental heterogeneity necessary to support complex requirements of biodiversity. Can our models distinguish good heterogeneity from bad for management? This is both a theoretical and a practical question worth investigating further. A functional flows approach to classifying heterogeneity offers a way to capture key components (e.g., pulses, baseflow, peak flow, recession) of historic flow regimes in order to recover natural heterogeneity (Yarnell et al. 2015, 2024). The practical value of understanding river behavior concerns the transferability of our research between riverscapes. Attempts to classify the natural progression of rivers and their behavior have often relied on geomorphic descriptions (Rosgen 1994, Brierley and Fryirs 2022). Only recently has a biome-based framework been developed to combine climatic gradients among other evolutionary processes into distinct regions of the world as a potential means to classify freshwater systems (Dodds et al. 2019). Combining a river behavior view within a biome framework could lend itself to enabling a much needed taxonomy of rivers that connects river behavior to fish habitat relationships and theory (Humphries et al. 2014, 2019). The hydrograph data pipelines available can help fish habitat modelers identify the theories most relevant for their own system, impacts, models, and target organisms, setting appropriate management expectations from the outset.

Drivers of novelty

Rivers naturally undergo disturbances, but the basis of novel riverscapes is the nature of irreversible disturbances of anthropogenic origin (Moyle 2014). A driver of novelty is any anthropogenic process (or natural process with anthropogenic influence), that affects desired ecosystem attributes and fish habitat such that they deviate further from the historical state. Some disturbances are natural processes (without direct or indirect human involvement) inherent to the historical state and would not be considered a driver of novelty. Understanding these drivers through their origin, spatial extent, interactions, and longevity is critical for model design and fish habitat restoration. Figure 1 shows how each of the three disturbance types might operate on a riverscape either independently or jointly. Recognizing that drivers of novelty can be of human origin or natural with direct or indirect human influence will help pinpoint cost-effective restoration measures (e.g., land-use policy changes versus invasive species control). The possibility of ecosystem state shifts opens the discussion to which type of drivers or removal of drivers of sufficient magnitudes could cause riverscapes to shift among states. Habitat changes during these state shifts can provide critical information on biological processes if fish habitat models can start accounting for ecosystem feedback loops rather than merely fitting linear relations of current conditions (Tonkin et al. 2019).

Remote-sensing (e.g., satellite, aerial, drone) data sets provide unique opportunities to relate these out-of-channel drivers to fish habitat. Not only is the data often freely available, but the spatial and temporal resolution becomes finer with every new satellite mission. For example, the Sentinel-2 mission provides nearly global coverage, with a monthly revisit time, measuring 13 spectral bands, which, in turn, provide multiple vegetation, soil, and water indices. Paid-for satellite services, although expensive, can provide daily revisit times with submeter resolution. To better understand historical circumstances of habitat, previously classified spy missions (e.g., CORONA missions) have now been made available to see watershed or landscape changes after World War II (Munteanu et al. 2020, 2024). Currently, most broad-scale disturbances (e.g., climate change–driven drought, nutrient runoff, landcover use, riparian removal) acting on riverscapes can be accurately mapped, quantified, and modeled using satellite remote-sensing products that go back more than 30 years for some missions, all of which can support fish habitat modeling needs (drivers of novelty; figure 1).

In-channel drivers require drone- and boat-based sensing technology for geomorphological insight. For example, one can purchase a commercially available transducer to map river bottoms with high resolution and georeferencing and can then consider using sonar to quantify fish abundance (Kaeser and Litts 2010). Aerial drones can also now map at river reach scale for elevation, riparian zones, waterfalls, thermal refugia, and other stream features using orthophotos, LiDAR, and infrared sensors (Allan and Lintermans 2021, Morgan and O'Sullivan 2023). Habitat and geomorphic features, as well as cross-sections of rivers that are too small for boats and that cannot be waded across, can be mapped with floating acoustic doppler profilers (Mueller and Wagner 2013).

A scalable approach to model design and application: The Stommel diagram

Even with immense data options, model development requires a scale-focused blueprint to ensure that the models are built and adapted properly to changing riverscape conditions and processes (Fausch et al. 2002, Kondolf et al. 2006, Yarnell et al. 2015). Fish habitat in lotic systems at small scales involves hydraulics, at large scales includes hydrology, and at both scales includes geomorphology, and it can encompass all levels of ecological organization (Nestler et al. 2016, Wegscheider et al. 2020). Our blueprint approach helps interpret and synthesize the novel ecosystems concept, current models, and the three opportunities. Current implementations of fish habitat models cannot incorporate all the synergistic opportunities presented in figure 1, but this issue can be addressed with good planning. To provide a more complete picture on our path forward for new fish habitat models, we have combined the previous sections into a collection of Stommel diagrams (figure 2). These diagrams can help modelers, researchers, and practitioners identify what processes could affect a system and its current state, which, in turn, could result in changes in both habitat quantity and quality for riverine fish.

The emphasis on the temporal and spatial scales of these impacts is intended to show the importance of scale-based thinking for future studies and model development. Our primary goal with these diagrams is to provide a context for how one may model fish habitat in rivers and then translate those findings into restoration recommendations or management actions. Figure 2 is a filled-out Stommel diagram for a hypothetical riverscape. Each opportunity has corresponding processes (color boxes) that change in relation to the ecosystem state. With each change, the processes overlap and provide the groundwork for new models. Depending on the spatial and temporal scale at which researchers start a study (e.g., mesoscale for a couple of years), they can then assess across the three ecosystem states what is likely changing within the modeling scale employed (e.g., micro, meso, macro, riverscape, river–sea connected), the overlap of processes, and whether anything can be done about the processes.

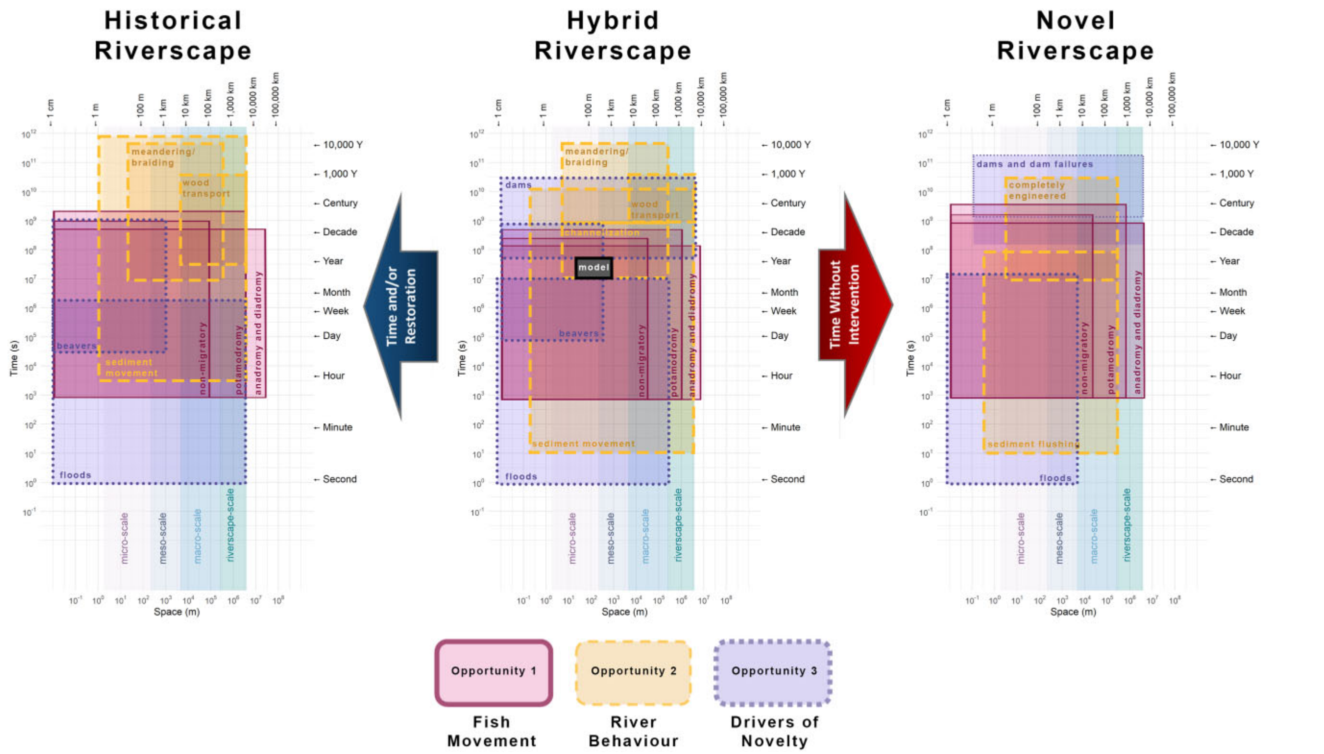


Figure 2. The key message of the figure is to help identify what processes (the colored boxes with textured borders) could influence habitat quantity and habitat quality for fish in relation to ecosystem state (i.e., historical, hybrid, novel). Stommel diagrams are scale-based depictions (temporal scales and spatial scales) of the riverscape where riverine processes corresponding to the three opportunities can be drawn (1, fish movement; 2, river behavior; 3, drivers of novelty). The shape and location of each opportunity is unique and changes with ecosystem state, which emphasizes how fish habitat models must either scale up or down (e.g., micro, meso, macro, riverscape) to overlap with the process or processes of interest. By forcing modelers to draw the spatial and temporal domain of their model (the black box), the Stommel diagrams provide a way to visualize the agreement of scales or lack thereof, indicating either potential bias or parameter uncertainty.

The Stommel diagrams are intended not merely as a theoretical depiction of processes but as a worksheet with straightforward restoration and management implications. How does one expand the spatial domain of native potamodromous fishes? How does one restrict the domain of invasive fishes? How does existing habitat and restored habitat drive these domain changes? Taking the time to show key processes acting on one's rivers is just the beginning, because one can also include human dimensions (e.g., laws, policies, management plans), observational coverage (e.g., satellites, genetic markers, animal tracking technology), and model capabilities (e.g., boundaries of model performance, area of interest for decision makers, regions of development) for a range of ecosystems (Fulton et al. 2019). To support readers in doing their own Stommel diagrams, either as a lab meeting or working group, we have attached a Stommel supplement (supplement S2) to work through the same exercise the authors of this article did.

Case study: Habitat modeling in the Republican River riverscape

The Republican River (Central Great Plains Region, in the United States) is an ideal case study to showcase the novel riverscape concept, because it represents a riverscape that has strong economic interests (i.e., agriculture) that introduces multiple stressors on fish habitat needs. It also serves as a warning for other hybrid riverscapes where past scientific evidence anticipated many of the problems it now faces.

Situated in the western Great Plains in the United States, the Republican River drains from eastern Colorado across western Kansas and Nebraska (figure 3). Much of the basin is west of the 100th meridian west where rainfall is less than the 51 centimeters needed to grow most crops. Overuse of groundwater in eastern Colorado resulted in legal action that requires the state to deliver water to the downstream states. This has been accomplished by purchasing irrigation wells and pumping groundwater that is delivered through a $60 million pipeline to the river channel at the state line. Since 1980, stream habitats have relied on minimum desirable streamflow standards, which have not been met for at least 6 of the years since 2000 (US Bureau of Reclamation 2016).

Old problems for a hybrid riverscape

The river and its tributaries provided insufficient flow to divert for agriculture, so large sprinklers fed by deep wells into the underlying High Plains Aquifer in the Ogallala Formation are used to irrigate crops, which are primarily corn to feed cattle and make ethanol. For example, in Yuma County, Colorado, irrigated acres increased rapidly during the early 1960s, and by 1980, the annual water withdrawals averaged 400 million cubic meters, which affected its major tributary, the Arikaree River (Falke et al. 2011). By 2000, groundwater levels in eastern Colorado had dropped 8 meters or more, and by 2002, they were dropping 0.3 meters per year. Flow in the Arikaree River was originally affected little by the regional aquifer level but crossed a threshold in 2000, after which no flow occurred at its mouth more than half the time.

Declines in flow have had strong effects on Arikaree River fish recolonization. Historical fish collections show that the river was originally 110 kilometers (km) long but, by 2005–2007, had been

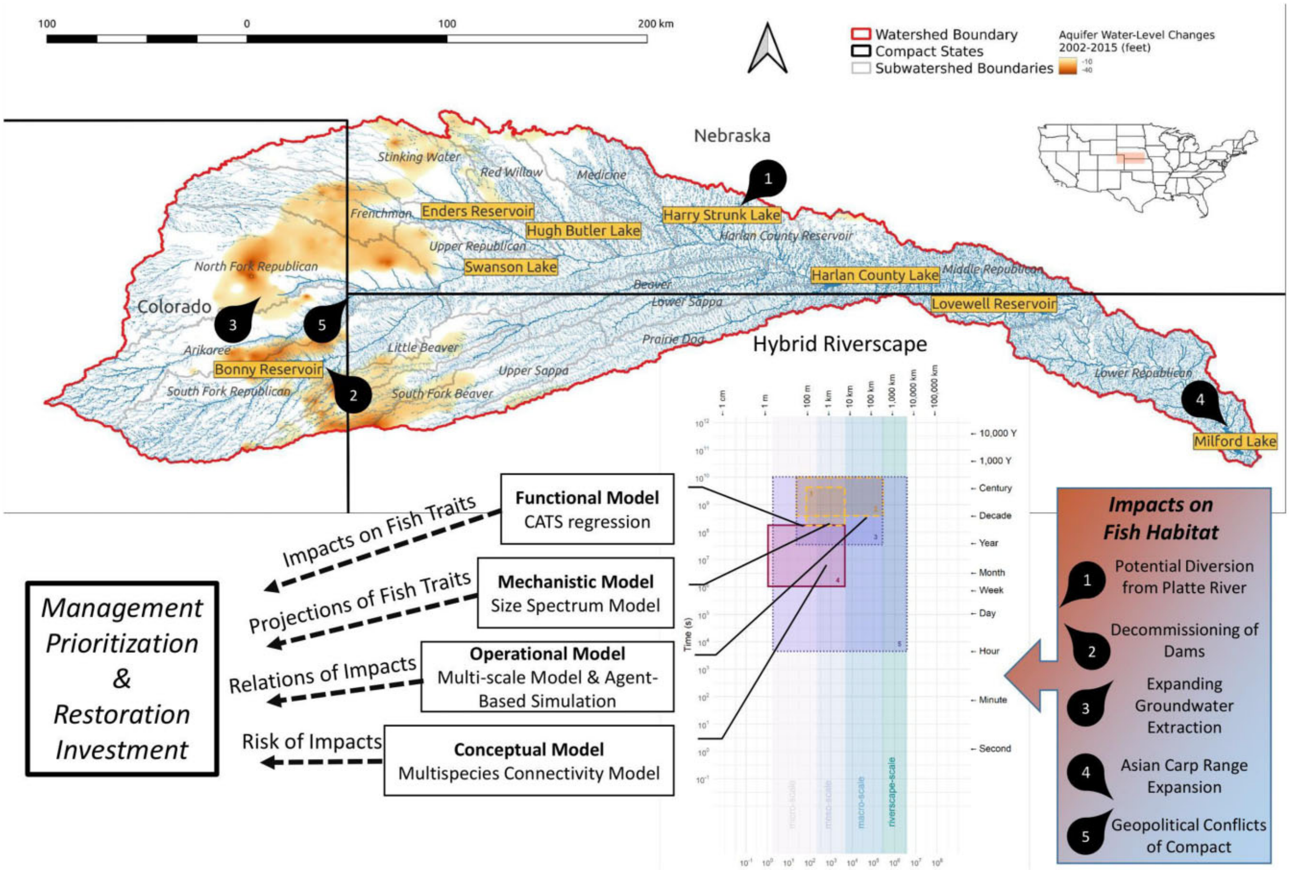


Figure 3. The Republican River watershed with lotic network and largest reservoirs in comparison to a decadal groundwater level change (McGuire 2017). The markers on map indicate select impacts that have or will affect fish habitat and the ecosystem state. Following the Stommel exercise in the supplement, impacts are drawn on to the spatial and temporal domains of primary interest. Once the impacts are mapped, modelers could use a variety of model types (box 1) or more advanced models (shown) to provide a comprehensive assessment of the impacts in relation to fish habitat and use this information to prioritize management and investments in restoration. Although there are a large number of models to choose from, the selected ones reflect a useful balance of appropriate scale and the uncertainty of estimates, and could make use of existing data.

reduced to only about 35–60 km of flowing segments during early summer peak flow. By late summer, only about 10–15 km were flowing during these years (Falke et al. 2011). Previous research on plains fishes of this region showed that groundwater-fed pools are critical to their survival during the dry season from late summer through winter and early spring, and that even small-body fishes such as minnows and darters move long distances to spawn and recolonize formerly dry segments (Labbe and Fausch 2000, Scheurer et al. 2003). Of the 16 native fish species, 5 had been extirpated by 2007, and 2 more were rare.

Coupling a regional groundwater model with pool levels showed that if pumping continued at rates as seen in 2007, by 2045, virtually all pools would be restricted to a 1 km river segment, leaving the remaining fish vulnerable to extirpation during dry years (Falke et al. 2011). Similar stream drying from groundwater pumping has been documented in many rivers of the western Great Plains in the three states (Falke et al. 2011, Perkin et al. 2017). A region-wide analysis that projected declining well levels into the future showed that between 1950 and 2010, 558 km of flowing streams supported by the High Plains aquifer were lost (21% of the total) in an area of eastern Colorado and western Kansas and Nebraska, approximately 300 × 300 km in area. A river once known for its large floods 100 years ago is now described as "not even deep enough to drown in" (Rayes 2022, p. 1).

New problems and new fish habitat models for a novel riverscape future

The models needed for this new ecosystem state must operate at the same time scale of typical integrated management plans used by local administrators (for 25 years or until 2044), leverage existing operations and groundwater modeling efforts, operate at the same spatial scale (individual districts), and must be in line with other water supplies and uses (Upper Republican Natural Resource District et al. 2019). Figure 3 highlights existing and new problems that are involved both on the map and on the Stommel diagram. Water transfer obligations have resulted in a proposed diversion from the Platte River, as well as a relatively recent partial decommissioning of Bonny Reservoir. Both decisions have unquantified impacts on local fish fauna and habitat, despite their strong influence (river behavior). This builds off the preexisting issue of expanding groundwater extraction (drivers of novelty). In addition, Asian carp have recently been detected just below the terminus of the Republican River and have the potential to move in and establish (fish movement). The whole fish community is the target organization unit for modeling and should be interpreted as a dynamic assemblage with frequent movements (Baxter 2002). Given these overlapping anthropogenic impacts and their related processes on fish habitat, how should one inform management and restoration with models? Our answer would be multiple scale appropriate models that have strong links not only to habitat and to each other but also to the underused data pipelines present (Nestler et al. 2016).

Starting with the Stommel, we notice that impacts 1, 2, 3, and 5 overlap but are centered at a meso to macro scale between a year and a century. A functional model (box 2), such as community assembly via trait selection regression (CATS [community assembly via trait selection] regression; Warton et al. 2015) or a similar trait based multilevel modeling approach (Kirk et al. 2022), could help set the stage of understanding these impacts on the fish traits (i.e., movement, growth, fecundity) of the community and the relations to environmental habitat variables from local gauge stations. With an understanding of existing traits and their sensitivities of impacts, one could feed these traits into a mechanistic model such as a size-spectrum approach (Scott et al. 2014), which would allow for projections of fish traits under different impact scenarios and for longer time scales. Probable scenarios could then be linked to the culmination of individual farmer impacts on groundwater (Noël and Cai 2017) and the resulting river condition (Gurnell et al. 2020), which spans multiple scales from meso to macro. Finally, a conceptual model such as a multispecies connectivity model (Wood et al. 2022) could be implemented to serve as a reality check for the previous models if Asian carp were to spread and establish. The resulting culmination of models could inform how water use could be adjusted to compromise fish habitat requirements at specific areas. More importantly, these models could give clear guidance on how to leverage existing policies intended to protect rivers, because they should be updated regularly. This includes water use fees, water regulation at water management structures, invasive species control, land-use planning, and groundwater management.

It is extremely important that this case study should not be interpreted as a sole endeavor by one individual or research group. In some respects, our discipline has typically relied on practitioners to do far too much with far too little. In this kind of environment, new models disappear as soon as a student graduates or an employee changes a job. The establishment of data pipelines, model development, and research needed to produce these tools requires a joint commitment from practitioners, modelers, and researchers, each with their respective roles that should establish channels of cooperation (supplement S3). Navigating fragmented data sources, finding historic primary and secondary literature, and creating links among partners with similar fish habitat goals are gateways for interdisciplinarity and interagency team building. To better address systemic river impacts from multiple fronts, we (all parties interested in rivers) must work together at the same time scale as the river impacts. The sum of our actions is meagre compared with a truly synchronized and interacting workforce that leverages each role's talent. Returning to our foundations of scale, this interdisciplinary, data-driven approach puts us in the position to apply multiple fish habitat models that are routinely updated and verified and then used to inform restoration and management. The time of one model, one person should become the exception not the norm for future fish habitat model development. Examples where data pipelines meet near-real-time modeling are all around us (e.g., weather forecasts, pandemic predictions, climate projections, flood warning systems, marketing ad suggestions, traffic predictions), and it is time for fish habitat models in riverscapes to do the same.

Conclusions

No single model will perfectly match the unique opportunities presented by all rivers, but exploring, exchanging, and communicating new developments that have shown success in other ecological disciplines may help us manage habitats in hybrid and novel ecosystems more effectively. A combination of theory, data pipelines, and scale-based thinking gives us a chance to explore habitat dynamics for higher organizational phenomena such as metapopulations, metacommunities, and metaecosystems to more comprehensively address the freshwater biodiversity crisis. Coordinating and building capacity for such a paradigm shift will not be easy but can be accelerated with strategic communication (i.e., fish habitat conferences) among all levels of research and practice and should be seen as a necessary step toward addressing rampant riverscape degradation.

Acknowledgments

A sincere thank you to Jennifer Clausen at jacdraws.com for providing the illustration support for the article. Kurt Fausch, Steve Railsback, Eric Higgs, Max Lindmark, and Mahboobeh Hajiesmaeili provided helpful comments. Many thanks also go to the other workshop attendees who contributed to the discussion. Thanks to Justin Tweet for providing permission to use the current St. Anthony Falls picture, Ianina Kopecki for the Badam River picture, Mahboobeh for the Elarm River picture, and Edem Srem for the Ankobra River picture. The research work presented in this article has received funding from the European Union Horizon 2020 Research and Innovation Programme under Marie Sklodowska-Curie grant agreement no. 860800.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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Received: November 27, 2023. **Revised:** July 2, 2024. **Accepted:** July 16, 2024