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## Identifying monitoring information needs that support the management of fish in large rivers --Manuscript Draft--

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| <b>Manuscript Number:</b>    | PONE-D-21-12444R1   |
| <b>Article Type:</b>         | Research Article  |
| <b>Full Title:</b>           | Identifying monitoring information needs that support the management of fish in large rivers  |
| <b>Short Title:</b>          | Identifying monitoring information needs that support the management of fish in large rivers  |
| <b>Corresponding Author:</b> | Timothy D. Counihan, MSc<br>US Geological Survey<br>Cook, WA UNITED STATES  |
| <b>Keywords:</b>             | large river; monitoring; long-term; information needs; fish; conceptual model, ecosystem  |
| <b>Abstract:</b>             | <p>Management actions intended to benefit fish in large rivers can directly or indirectly affect multiple ecosystem components. Without consideration of the effects of management on non-target ecosystem components, unintended consequences may limit management efficacy. Monitoring can help clarify the effects of management actions, including on non-target ecosystem components, but only if data are collected to characterize key ecosystem processes that could affect the outcome. Scientists from across the U.S. convened to develop a conceptual model that would help identify monitoring information needed to better understand how natural and anthropogenic factors affect large river fishes. We applied the conceptual model to case studies in four large U.S. rivers. The application of the conceptual model indicates the model is flexible and relevant to large rivers in different geographic settings and with different management challenges. By visualizing how natural and anthropogenic drivers directly or indirectly affect cascading ecosystem tiers, our model identified critical information gaps and uncertainties that, if resolved, could inform how to best meet management objectives. Despite large differences in the physical and ecological contexts of the river systems, the case studies also demonstrated substantial commonalities in the data needed to better understand how stressors affect fish in these systems. For example, in most systems information on river discharge and water temperature were needed and available. Conversely, information regarding trophic relationships and the habitat requirements of larval fishes were generally lacking. This result suggests that there may be a common need for a better understanding of certain factors across large-river systems.</p> |
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**Response to Reviewers:**

PONE-D-21-12444

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Reviewer 1 wonders about the utility of such conceptual models in the more realistic case of multiple species contexts. How could the model be expanded in this regard, besides the case of simple richness measures? In addition, how could the model help in actually prioritising or ranking the variables or interactions identified? Finally, reviewer 1 also noticed that an important stressor related to fragmentation and connectivity is only marginally discussed and included in the model. This is critical for meta-population dynamics and should be given more emphasis.

Reviewer 2, similarly raises the critical issue of the multi-species context, and how the needs of different species could be simultaneously identified. Therefore, I advice to expand the Discussion in this regard, eventually acknowledging limitations and suggesting future research needs. Reviewer 2 also wonders how such models could effectively guide restoration and decision-making beyond monitoring needs; if the relative importance of data gaps and interactions is not quantified (e.g. via a cost-benefit analysis), how could it help prioritise the focus of monitoring and action?

Besides carefully responding to each reviewers' comments and modify the manuscript accordingly, I also suggest to simplify the manuscript, which feels rather long. Perhaps some of the background information from each case study could be included as supplementary or shortened. Also, caption from Fig.5 (and sister-figures) is rather hard to digest for the reader. I wonder if this could be simplified as well.

Response: Thank you for the opportunity to revise our manuscript. We have tried to address comments of Reviewer 1 and 2 below and in the revised manuscript. To shorten and simplify the manuscript, we relocated some of the contextual information from the case studies and moved it to an Appendix in Supplemental Information. With respect to Fig 5 and sister figures, we have discussed trying to simplify the figure captions but have not come up with a good solution. There is a lot of information contained within the figures and feel that further generalizations would not be clarifying. We do, however, acknowledge that the figure caption format is awkwardly long. What we propose is that we retain Fig 5 in the main body of the text as an example, and then move subsequent sister figures to Supplemental Materials. Please let us know if this satisfies your and the reviewer's comments to reduce the length of the manuscript.

Comments to the Author

5. Review Comments to the Author

Reviewer #1: In this study a conceptual model is used to aid the development of best practices of large river monitoring programs. The model was developed based on former scientific works and during scientist's workshop negotiations. Case study applications prove that the application of this complex conceptual model can be useful to identify critical information gaps, which can then be used to develop management and monitoring objectives.

I like the approach of developing such conceptual models, which can reveal information gaps, and think that the model in general can be useful to adopt across large river systems with some refinements and local adaptations. Consequently, I believe showing such an approach can provide useful information for the readers. 1)What I lack is to show more convincingly how such complex models can be used for multispecies systems, where not only the requirements of a single species is evaluated, which in fact the more realistic situation. How can individual species level models be put together to provide meaningful information for management? It would be useful to discuss this in more detail in the Discussion section.

Response: Thank you for this comment. We have added text in the discussion that describes how the CM could contribute to our understanding of the need for a multi-

species context in management activities. Please see: L645-691

2)Also a critical issue which should be briefly discussed is how the identified critical target variables should be prioritized, especially in a multispecies systems, where several variables will appear. Development of this section could convince the reader and could clearly show the applicability of such conceptual models by management.

Response: Thank you for this insight. We have provided language in the discussion that describes how the CM could be used to identify critical target variables in a multispecies context. Please see: L650-668

3)Although channel morphology/hydraulics may contain fragmentation/connectivity issues this should be made more clear in the material, because this is one of the most critical issue, which determine fish (meta)population or metacommunity dynamics. In fact fragmentation is often used as one of the most critical variable of anthropogenic drivers and as such is a critically important target to mitigate by management. However, it does not appear either in Fig 2 or Fig 3, but only on the case study figures belonging to morphology/hydraulics TIER1 components.

Response: Thank you. We agree with your assessment. We have further emphasized the importance of fragmentation by specifically mentioning it in the manuscript section describing the CM form. Please see: L223-234. Also, in Table 2, habitat fragmentation is emphasized as affecting multiple facets of the CM in multiple river systems and is mentioned in the text describing Table 2. This result indicates the need to better study the effects of habitat fragmentation on multiple biotic components.

Reviewer #2: Dear Editor,

This study demonstrates how a conceptual model can be used to identifying knowledge gaps in the mechanisms by which Essential Ecosystem Characteristics influence large-river fish species in the USA. These gaps should then be filled to improve the effectiveness of restoration and management.

I agree on the value of these conceptual models to identify knowledge gaps and inform decisions on what to monitor to fill them and allow a better understanding of the system and, therefore, enhance our capacity to manage them adequately. However, I disagree with some of the arguments:

1)The conceptual model represents potential interactions across different structural element of the river system but does not allow quantitative evaluations of strength of those interaction. As such, the value of is conceptual model is limited to identifying knowledge gaps and cannot be used to evaluate the relative importance of each interaction. Therefore, this conceptual model should only be used for identifying knowledge gaps and not for decision-making, as argued (see L771-773), beyond monitoring.

Response: This is an excellent point and we have removed the statement in L771-773 and elaborated on the considerations that need to be accounted for, and the difficulties with, assessing benefit:cost ratios. Please see: L692-726. Also, you are correct that the CM does not provide quantitative evaluations of the strength of the relations. We do acknowledge this and suggest that the CM could provide a basis for developing quantitative assessments in L749-754 and have added language that describes how the CMs could be the basis for Structural Decision Making and Adaptive Management processes (see L727-741).

2)The conceptual model lacks a cost analysis to evaluate the most efficient way of filling knowledge gaps. Some of the gaps might be more difficult/ costly or even feasible to fill. Without such analysis we can only identify the gaps but cannot prioritise where to focus monitoring on a cost-effective way and just confirm where gaps exist.

Response: Thank you for this comment. In addition to addressing the benefit:cost issue above, we have provided language in the discussion that describes how the CM could be used to identify critical target variables in a multispecies context but that there are critical uncertainties that need to be considered. See: L650-668. We agree with you about prioritizing based on cost effectiveness but respectfully suggest that the CM could provide information that would suggest where to focus monitoring effort.

|  |   |
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|  | <p>3) Three of the case studies present conceptual models for individual species. While I see the value of developing these conceptual models for charismatic endangered species, I wonder how feasible/ useful it would be this method when facing management needs for many species simultaneously. One of the case studies does present a conceptual model for the full fish community, but focused on diversity, rather than individual species, so no information of particular species issues are addressed. Would it be feasible to elaborate a conceptual model that addressed all individual species needs/ issues simultaneously? This would allow identifying knowledge gaps common to multiple species simultaneously.</p> <p>Response: Thank you for this comment. We have added text in the discussion that describes how the CM could contribute to our understanding of the need for a multi-species context in management activities. Please see: Please see: L645-691</p> <p>4) Minor comments:<br/>- L304 &amp; 369. What does ATV stand for?</p> <p>Response: Thank you for bringing this to our attention. ATV stands for all-terrain vehicle. We have removed the acronym from the revision.</p> <p>- The manuscript is quite long, especially because of the description of each case study. It would be good to present the information of these case studies in a more synthetic way (maybe on a table?).</p> <p>Response: Thank you for the comment. Per your and the Associate Editor's recommendation we have pulled out some of the contextual information from the case studies and moved the information to an Appendix in Supplemental Information. We have also moved three figures and associated captions to the supplemental information section.</p> <hr/> |
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**Additional Information:**

| Question | Response |
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| <p><b>Financial Disclosure</b></p> <p>Enter a financial disclosure statement that describes the sources of funding for the work included in this submission. Review the <a href="#">submission guidelines</a> for detailed requirements. View published research articles from <a href="#">PLOS ONE</a> for specific examples.</p> <p>This statement is required for submission and <b>will appear in the published article</b> if the submission is accepted. Please make sure it is accurate.</p> | <p>This work was funded in part by U.S. Geological Survey's Core Science Systems Mission Area. This research also was conducted using in-kind contributions of the Ball State University, Illinois Natural History Survey, Oregon Department of Fish and Wildlife, Pacific Northwest Aquatic Monitoring Partnership, the Oklahoma and Alabama Cooperative Fish and Wildlife Research Units, and the U.S. Geological Survey Columbia Environmental Research Center, Grand Canyon Monitoring and Research Center, Oregon Water Science Center, Upper Midwest Environmental Sciences Center, and Western Fisheries Research Center.</p> |
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30 **Abstract** – Management actions intended to benefit fish in large rivers can directly or indirectly  
31 affect multiple ecosystem components. Without consideration of the effects of management on  
32 non-target ecosystem components, unintended consequences may limit management efficacy.  
33 Monitoring can help clarify the effects of management actions, including on non-target  
34 ecosystem components, but only if data are collected to characterize key ecosystem processes  
35 that could affect the outcome. **Scientists from across the U.S. convened to develop** a conceptual  
36 model that would help identify monitoring information needed to better understand how natural  
37 and anthropogenic factors affect large river fishes. We applied the conceptual model to case  
38 studies in four large U.S. rivers. The application of the conceptual model indicates the model is  
39 flexible and relevant to large rivers in different geographic settings and with different  
40 management challenges. By visualizing how natural and anthropogenic drivers directly or  
41 indirectly affect cascading ecosystem tiers, our model identified critical information gaps and  
42 uncertainties that, if resolved, could inform how to best meet management objectives. Despite  
43 large differences in the physical and ecological contexts of the river systems, the case studies  
44 also demonstrated substantial commonalities in the data needed to better understand how  
45 stressors affect fish in these systems. For example, in most systems information on river  
46 discharge and water temperature were needed and available. Conversely, information regarding  
47 trophic relationships and the habitat requirements of larval fishes were generally lacking. This  
48 result suggests that there **may be** a common need for a better understanding of certain factors  
49 across large-river systems.

50

## 51 **Introduction**

52 Long-term monitoring has benefited a variety of ~~marine and~~ freshwater ecosystems,  
53 including large rivers like the Ohio [1, 2] and Illinois rivers [3]. Large-river systems are  
54 complex, making the development of effective monitoring programs especially difficult. Large  
55 rivers are dynamic systems with high variability in spatio-temporal physicochemical  
56 characteristics and biotic assemblages [4]. The inherent complexity of large rivers makes biotic  
57 assemblages logistically difficult to sample [5] and the mechanisms of change difficult to  
58 understand. Large rivers represent the culmination of vast stream networks and, thus, integrate  
59 and accumulate the effects of multiple stressors at varying spatial scales [6]. The spatial and  
60 temporal complexity associated with large rivers has hindered the identification of mechanisms  
61 driving declining populations of aquatic species [7-10]. To exacerbate the complexity, large  
62 rivers commonly have within-channel structural alterations (e.g., dams, river training structures,  
63 [11]) and often exhibit legacy effects from historical land uses [12]. To deal with the complexity,  
64 some areas of aquatic science recommend monitoring be used to test the linkages developed first  
65 through conceptual models (e.g., environmental flows, [13-15]).

66 Conceptual models are useful tools to help guide the design of monitoring programs [16].  
67 The identification of questions relevant to conservation and management efforts requires some  
68 foresight and knowledge of the complexities of the system being monitored. For example, it is  
69 generally well accepted that the native range of the federally-listed Arkansas River Shiner  
70 (*Notropis girardi*) is truncated [17], though there is uncertainty surrounding the multiple threats  
71 affecting the species [18]. Reducing the uncertainty associated with the decline of the Arkansas  
72 River Shiner through the implementation of a hypothesis-driven monitoring program would

73 facilitate confidence in moving forward with a recovery plan. This is where conceptual models  
74 are quite useful; they can serve as the foundation to guide hypothesis-driven monitoring  
75 programs [14, 16] and identify key ecosystem processes and factors that may directly or  
76 indirectly affect management outcomes [19-22].

77         Understanding factors affecting the status and trends of fishes is of interest to ~~multiple~~  
78 stakeholder groups across multiple jurisdictions. Fishes provide economic benefits to businesses  
79 that serve recreational interests, commercial and recreational fishers, tribal members for whom  
80 fish are an integral part of their cultural identity [23], and to local and state governments who  
81 derive revenue from these activities. Fish populations are affected by the integration of physical  
82 habitat, water quality, environmental contamination, habitat fragmentation, and overall  
83 ecosystem productivity [24-27]. Consequently, fish are often the focus of management and  
84 monitoring programs (e.g., [28]). However, because fish integrate the effects of so many  
85 components of the ecosystem, the success of efforts to manage fishes can be affected by  
86 unintended consequences of mitigation on factors not directly targeted by the actions. Without  
87 consideration of the effects of management on non-target ecosystem components, unintended  
88 consequences may limit management efficacy.

89         Our goal is to demonstrate how a structured, yet flexible, conceptual model (CM) can be  
90 used to identify the types of monitoring information needed to understand the range of factors  
91 affecting large-river fishes. Our CM includes a hierarchically structured conceptualization of  
92 ecosystem characteristics based on CMs originally developed by Harwell, Myers (29) and  
93 elaborated by Jacobson and Berkley (30). We chose to incorporate the tiered conceptualization of  
94 ecosystem characteristics proposed by Jacobson and Berkley (30) in part because it allows users  
95 to define their own biotic or abiotic interests. In this paper, we discuss the structure and

96 development of the CM. We apply the CM to case studies to illustrate the flexibility and  
97 applicability of this approach and use it to identify monitoring information needs specific to  
98 disparate management goals. More specifically, for each case study, we use the CM to  
99 hypothesize how human activities affect fish populations and then identify information needs  
100 required to evaluate the hypothesized relationships. We then posit the spatial and temporal scales  
101 of the management goal addressed in the conceptual model, inferences needed to inform the  
102 management goal, and data collection requirements needed to make the inferences.

## 103 **Conceptual Model**

### 104 **Overview of Approach**

105 Since 2012, scientists working on large rivers across the United States have participated  
106 in a forum intended to improve our understanding of large-river ecosystems. The collaborative  
107 forum has worked to identify best practices of long-term monitoring programs [31] and evaluate  
108 trends in fish assemblages across rivers [32]. As this group of scientists moved toward linking  
109 changes in fish populations and assemblages to human activities, there was a need to develop a  
110 process to help identify and prioritize the information needed to assess trends in large river  
111 fishes. To that end, a workshop was convened in Hood River, Oregon in May 2017, to jointly  
112 adapt, apply, and qualitatively evaluate a conceptual model for developing hypotheses that detail  
113 stressors affecting fishes arising from natural and anthropogenic sources [33].

114 **Our general approach** was to first identify human activities that affect large-river fishes  
115 and then hypothesize how the activities related to physical and chemical factors and biological  
116 communities. Prior to the workshop, we elicited opinion from experts that comprise a U.S.

117 Geological Survey (USGS) led forum on large river monitoring about important anthropogenic  
118 activities that could affect fish populations or communities in the river basins they work in. (Fig  
119 1). We summarized the information from this exercise and grouped the anthropogenic activities  
120 into driver categories (Fig 2) and proposed a general form of the CM. We then disseminated the  
121 information to the experts prior to the workshop.

122 Fig 1. Map of rivers and watersheds represented by scientists that convened to develop a  
123 conceptual model that depicts how natural and anthropogenic drivers interact with habitats,  
124 biological systems, and fish in large rivers. River segments where we conducted case studies that  
125 applied the conceptual model to identify monitoring information needs associated with  
126 management goals are highlighted in red.

127 Fig 2. The results of a query to scientists from the Canadian, Colorado, Columbia, Hudson,  
128 Illinois, Ohio, Missouri, Red, Tallapoosa, Upper Mississippi, and Wabash Rivers, U.S to identify  
129 anthropogenic activities that affect large-river fishes in the river systems they represent.  
130 Anthropogenic activities were classified into five driver categories.

131 **During the workshop we discussed** and refined the CM form (Fig 3). We then had  
132 representatives from each river system represented at the workshop choose a management goal  
133 to address. Then, through a facilitated discussion led primarily by the representative of the river  
134 system being addressed, we 1) elaborated tiered conceptualizations of ecosystem characteristics  
135 to reflect the large-river systems and management goals being examined, 2) used knowledge of  
136 the fish species' life history and population bottlenecks to relate biological ecosystem  
137 characteristics to habitat requirements, 3) hypothesized pathways describing how anthropogenic



138 and natural drivers affect large-river fish populations either indirectly (e.g., effects on flow  
139 regime, habitat, trophic resources, etc.) or directly (e.g., competition with invasive species), and  
140 4) hypothesized interactions within ecosystem characteristic tiers that could affect the  
141 management goal. Based on this exercise, we chose four case studies to refine for use in this  
142 manuscript (Fig 1).

143 Fig 3. Tiered hierarchical conceptualization of how anthropogenic and natural drivers relate to  
144 physical and biological components of large-river ecosystems. Essential ecosystem  
145 characteristics (EECs) are groupings of ecosystem components. Tier 1 EECs represent physical  
146 and chemical effects; fundamental measures of process that are directly affected by  
147 anthropogenic and natural drivers. Tier 2 EECs represent a broad habitat category that is  
148 intended to encompass the physical, chemical, and biological components of the riverine habitats  
149 that influence reproduction, growth, and survival of biotic communities. The Tier 3 EEC  
150 represent components of the biological systems that respond to changes in the hierarchical  
151 components of the conceptual model.

152 **After the workshop**, we held a series of conference calls with workshop participants with  
153 expertise in the selected case studies to refine all aspects of the CMs and associated information.  
154 During the calls, we started with the CM from the workshop and discussed and clarified CM  
155 components, pathways, and inter-tier interactions. We then characterized whether, based on the  
156 expert knowledge of workshop participants, there was a strong, moderate, or weak understanding  
157 of the pathways and interactions. A list of the information needed to understand the relationships  
158 described in the CM was developed. We then had the case study leader classify whether the data

159 required to understand the information needs were available, insufficient, or not available. For  
160 information needs that were classified as insufficient or not available, we characterized the  
161 spatial and temporal scales at which data should be collected to make inferences that support the  
162 evaluation of management goals.

163 We then encouraged representatives from each basin to share the CM and the case study  
164 narrative with other experts familiar with the river system and management goal. This outreach  
165 took several forms including sharing the CM with working groups tasked with implementing the  
166 management goal, discussions with peers familiar with the management goal, and presenting the  
167 CM at regional conferences. The intent was to garner opinions from outside the workshop  
168 participants. ~~If needed, the CMs incorporated the feedback received.~~

### 169 **Hierarchical structure of Conceptual Model**

170 Our CM is a hierarchical conceptualization of how anthropogenic and natural drivers  
171 relate to multiple tiers representing the physical and biological components of large-river  
172 ecosystems (Fig 3). Natural drivers included in the CM were physiographic, climatic, and  
173 biogeographic factors that control fluxes of water, mass, energy, and genetic information in a  
174 watershed [30]. The physiographic factors, such as lithology, soils, and watershed topography,  
175 exert control on water, sediment, and geochemical fluxes (e.g., nutrients) into the river corridor.  
176 Physiography is generally static over time frames of decades to centuries. Climate controls fluxes  
177 of atmospheric energy and moisture into the watershed. Unlike physiography, climate is more  
178 likely to vary over relatively shorter temporal scales. Biogeography describes the native  
179 organism assemblage in the watershed (e.g., [34]) and the natural flux of genetic information due

180 to immigrations, emigrations, mutations, and extinctions. Changes arising from the biogeography  
181 driver includes altered spatial distribution of organisms within the watershed, which, in turn, may  
182 alter the effects of natural system regimes on the river corridor. For example, natural variation of  
183 the type and distribution of vegetation can affect the time series and magnitude of runoff events  
184 [30].

185 We created five categories of anthropogenic drivers to characterize a range of human  
186 activities that affect large rivers: land use, commercial use, biological community alteration,  
187 water use, and recreation (Fig 2). The land-use category is intended to reflect different ways  
188 humans use landscape resources that affect large rivers. We defined commercial use as the use of  
189 river resources for marketable enterprises that did not involve water removal or transfer. We  
190 included biological community alteration to represent the intentional or non-intentional human  
191 alteration or manipulation of the river's biological community (e.g., introductions of non-native  
192 fish). Recreational use was defined as the use of river resources for leisure activities (e.g.,  
193 fishing, boating). We considered water use a direct commercial or non-commercial use of river  
194 water that involved the removal or transfer of water.

195 Our CM includes hierarchically structured essential ecosystem characteristics (EEC),  
196 originally developed by Harwell, Myers (29) and described in detail by Jacobson and Berkley  
197 (30). Briefly, EECs are characteristics that can be classified into similar groups based on the way  
198 they link to biological endpoints [30]. Tier 1 EECs are measurable characteristics that describe  
199 processes that can significantly alter the morphological or chemical characteristics within a river  
200 channel. The Tier 1 categories we considered were 1) hydrology, 2) channel  
201 morphology/hydraulics, 3) sediment transport, and 4) biogeochemistry/thermodynamics. Tier 2  
202 EECs are broadly described as physicochemical or biological components of "habitat" that are

203 hypothesized to affect (e.g., growth, survival, reproduction, [35]) fish populations or  
204 assemblages. Lastly, Tier 3 EECs represent components of the hypothesized biological system  
205 that are affected by the cascading (e.g., degradation of egg quality caused by increases in  
206 sediment deposition) or direct (e.g., predation by invasive species) effects of anthropogenic and  
207 natural drivers. Tier 2 characteristics are particularly important because these are the factors that  
208 can be examined at scales most often sampled by fisheries managers [36]. The specific  
209 components that comprise Tier 2 and 3 EECs are flexible and can be adapted and elaborated  
210 depending on the river system and specific management goal being addressed.

211         We retained aspects of the approach taken by Jacobson and Berkley (30) with respect to  
212 how our model represents interactions between drivers and EECs, but with key differences.  
213 Since we were interested in representing how human activities affect large river ecosystems, our  
214 approach acknowledges that anthropogenic and natural drivers interact and alter the expected  
215 characteristics of Tier 1 EECs. Similar to Jacobson and Berkley (30), our model depicts a stress  
216 associated with a natural or anthropogenic driver to Tier 1 EECs as fluxes in natural system  
217 regimes that alter the frequency, magnitude, duration, timing, or rate of change in natural  
218 systems or by the imposition of a hard-structural constraint on channel form. The natural system  
219 regimes considered in our CM were hydraulic, hydrologic, sediment, temperature, light, and  
220 biogeochemistry. Graphically, the natural system fluxes were represented by arrows connecting  
221 anthropogenic and natural drivers to Tier 1 EECs. Similarly, hypothesized pathways between  
222 EECs, that depict the expression of the cascading effects of anthropogenic and natural drivers,  
223 and interaction within EECs were depicted as arrows. For example, fragmentation of river  
224 systems resulting from altered hydrologic and/or hydraulic regimes caused by dams, weirs,  
225 levees, and other factors are frequently cited sources of stress to large-river fishes [37].

226 Fragmentation can prevent fish from migrating and/or dispersing through their natural  
227 reproductive ranges and from accessing critical habitats [38]. To depict a scenario where the  
228 presence of a dam is altering hydrologic and/or hydraulic regimes resulting in habitat  
229 fragmentation, the CM would show an arrow from an anthropogenic stress (i.e., dam as a  
230 commercial activity) to a Tier 1 EEC (e.g., channel morphology/hydraulics) that would depict a  
231 natural system flux (e.g., altered hydrologic and/or hydraulic regime) that would then manifest as  
232 a stress caused by habitat fragmentation depicted by an arrow between the Tier 1 EEC and a Tier  
233 2 EEC (e.g. habitat) that would then manifest as an effect on a Tier 3 component, shown by an  
234 arrow between Tier 2 and Tier 3. All stress pathways and interactions were classified with  
235 respect to the strength of understanding of the relationships based on expert opinion. Arrows  
236 with solid blue lines depict a strong understanding of the relationship, dotted-dashed blue lines  
237 represent a moderate understanding of the relationship, and with a black dashed line represent a  
238 weak understanding of the relationship.

### 239 **Spatial and temporal context**

240 The successful characterization of how human activities influence large-river fishes is  
241 dependent upon integrated concepts of scale. Fish distributions in rivers can vary spatially within  
242 river basins in relation to naturally occurring and human induced landscape characteristics [32].  
243 Fish distributions can also vary seasonally, annually, and over longer times in response to  
244 changing environmental conditions [39]. Consequently, the spatial and temporal scope of fish  
245 management goals often varies within and between large-river systems and agencies. For data  
246 collected by monitoring programs to have the highest relevance, the spatial and temporal scales

247 appropriate for scientific investigation and management must also be time and geographic-  
248 context specific. For example, the management of White Sturgeon (*Acipenser transmontanus*) in  
249 the Columbia River varies by reservoir or river segment and season [40, 41]. The effects of  
250 hydropower development on White Sturgeon vary spatially and temporally as well, so the spatial  
251 and temporal context of the data needed to understand the effects needs to be considered. For  
252 instance, hydropower peaking operations, that can vary by dam and season, affect river discharge  
253 in a river reach on a diel and even hourly basis [42], whereas water storage and other  
254 management actions can affect seasonal discharges over a broader geographic scale [40].  
255 Understanding the spatial and temporal context needed to inform management will help ensure  
256 relevant information is collected.

257         We considered spatial and temporal resolution in our CMs. We defined spatial extent as :  
258 local network – synonymous with Hydrologic Unit Code (HUC) 2 basins [43, 44]; segment – the  
259 portion of a river between two major tributary confluences [45] or other hydrogeomorphic  
260 features [46]; reach - the length of river occurring between breaks in channel slope caused by  
261 man-made dams or other hydrogeomorphic features [45]; patch – an area used by an organism  
262 (e.g., for reproduction or resource attainment) that can vary both spatially and temporally  
263 depending on the species of interest [47, 48]. For our purposes, the spatial scales considered are  
264 nested such that segments occur within local networks, reaches occur within segments, and  
265 patches occur at the sub-reach scale. Temporal units considered were daily, seasonal, annual, and  
266 decadal. The temporal units were used to denote both the scale of inferences needed to support  
267 the management goal and the scale at which data should be collected to inform the inferences.

## 268 **Case Studies**

269 We applied the CM to four case studies. For each, we followed the pathways of stress  
270 from Tier 1 EECs to the biological endpoint associated with the management goal to identify  
271 information needs. We then characterized the spatial and temporal scales of the management  
272 goal, the scientific inferences needed to inform the management goal, and that data collection  
273 needs to occur to support the inferences for monitoring information needs identified as requiring  
274 additional data for each of the case studies. To summarize similarities across case studies, we  
275 generalized the stressors and inter- tier interactions identified in the case studies and then  
276 summarize the similarities by EEC tier. More context for the river systems characterized in the  
277 case studies can be found in Appendix S1.

#### 278 **South Canadian River**

279 Native populations of the federally-threatened Arkansas River Shiner are believed to be  
280 restricted to two fragmented portions of the South Canadian River [49]. The Arkansas River  
281 Shiner is hypothesized to be affected by several anthropogenic activities that primarily affect  
282 water quality and quantity (Fig 4). Three reservoirs on the South Canadian River have altered  
283 discharge patterns (Fig S1), and fragmented river habitats. Two known native populations of  
284 Arkansas River Shiner occupy the two remaining river segments of sufficient length and  
285 complexity to allow eggs to drift the time required to successfully complete their early life  
286 history. Small impoundments for agriculture use, road crossings, groundwater pumping and other  
287 local water extractions (e.g., oil and gas) threaten to further fragment existing habitat.  
288 Fragmentation could also be problematic for upstream fish migrations; there is some evidence  
289 that Arkansas River Shiners migrate upstream to spawn to achieve adequate drift distances for

290 their offspring [50]. It has also been speculated that this species might benefit from access to  
291 floodplain habitats [51], but we are unaware of efforts to examine that hypothesis. Changes in  
292 the flow patterns may also relate to the expansion of salt cedar *Tamarix* spp. and other non-  
293 native riparian species that constrain the channel and inhibit channel habitat complexity [52, 53].  
294 Changes to the riparian corridor can also alter the availability of drifting invertebrates for  
295 Arkansas River Shiner feeding (i.e., Coleoptera, Hymenoptera; [54]). Channel complexity acts to  
296 slow the transport of eggs [49] and may prevent eggs from being washed into downstream  
297 reservoirs where survival is hypothesized to be extremely low. Climate change is expected to  
298 increase the intensity and frequency of drought events within this region [55, 56], which may  
299 exacerbate habitat fragmentation, promote all-terrain vehicle traffic within the river channel  
300 causing direct mortality on stranded fish (Gene Wilde, Texas Tech University, Personal Comm.),  
301 and concentrate contaminants and salinity [57]. The tolerances of Arkansas River Shiner to  
302 salinity concentrations and many other contaminants are unknown (see Table S1; [18]). Lastly,  
303 introductions of non-native fishes have occurred within the basin. The primary concern is the  
304 presence of Red River Shiner (*Notropis bairdi*) because it is suspected to reproduce in a similar  
305 manner and be a possible competitor to the Arkansas River Shiner [57].

306 **Fig 4.** Conceptual model describing the relationship of natural and anthropogenic drivers to  
307 essential ecosystem characteristics (EECs) affecting the recruitment of the Arkansas River  
308 Shiner in the South Canadian River in New Mexico, Texas, and Oklahoma. Essential ecosystem  
309 characteristics are groupings of ecosystem components. Tier 1 EECs represent physical and  
310 chemical effects; fundamental measures of process that are directly affected by anthropogenic  
311 and natural drivers. Tier 2 EECs represent a broad habitat category that is intended to encompass



312 the physical, chemical, and biological components of the riverine habitats that influence  
313 reproduction, growth, and survival of biotic communities. The Tier 3 EECs represent  
314 components of the biological systems that respond to changes in the hierarchical components of  
315 the conceptual model. The strength of our understanding of how natural and anthropogenic  
316 drivers interact with habitats, biological systems, and fish in large rivers is represented by the  
317 different types of lines in the figure. Solid blue lines depict a strong understanding of the  
318 relationship, the dotted-dashed blue line represents a moderate understanding of the relationship,  
319 and the black dashed line represents a weak understanding of the relationship. The different  
320 types of lines also represent the strength of our understanding of within EEC-tier relationships.

321         The results of the CM exercise that characterized factors affecting the Arkansas River  
322 Shiner in the South Canadian River suggested the critical life-history bottlenecks for the  
323 Arkansas River Shiner are successful spawning and recruitment to the first year. Impediments  
324 that limit our understanding of factors that lead to successful spawning and recruitment included  
325 the effects of channel morphology and hydraulics on the quality and quantity of larval rearing  
326 habitat, and subsequent effects on larval production (Table S1). Water use and other drivers  
327 occurring at relatively coarse spatial and temporal scales are the hypothesized drivers related to  
328 degradation of reproductive habitat for the Arkansas River Shiner (Fig 5). A temporal lag in  
329 responses at finer scales (i.e., improved habitat) would be anticipated with management actions  
330 at these coarser spatial scales (e.g., water releases from dams); though, providing connectivity  
331 via minimal water releases would occur relatively quickly. Although there are gages on the  
332 South Canadian River, the spacing of the gages is not sufficient to have a full understanding of  
333 flow patterns between the gages given the semi-arid nature of the basin and potential for reaches

334 to be affected by water withdrawals such as groundwater pumping. Our understanding of the  
335 species life history is well established; however, the effects of human pressures on the species  
336 and associated habitat has not been well studied (i.e., production, survival). As stressors  
337 propagate through Tier 1 to Tier 2 and Tier 3, the level of uncertainty increased such that it is not  
338 possible to define a preferred hypothesis for Arkansas River Shiner recruitment failure. The  
339 status of information needed to understand the hypothesized stress pathways and interactions was  
340 mostly characterized as insufficient or not available (Table S1).

341 **Fig 5.** The spatial and temporal scales of the management goal, the scientific inferences needed  
342 to inform the management goal, and that data collection needs to occur to support the inferences  
343 for monitoring information needs identified as requiring additional data in the case study  
344 addressing the recruitment of the Arkansas River Shiner in the Canadian River, Oklahoma (see  
345 Table S1 for additional detail). A: Tier 1 EEC=channel morphology/hydraulics; Stressor=altered  
346 hydraulic regime; B: Tier 1 EEC=biogeochemistry/thermodynamics; Stressor=altered water  
347 temperature regime; C: Tier 1 EEC=biogeochemistry/thermodynamics; Stressor=altered  
348 biogeochemical regime; D: Tier 2 EEC=Arkansas River Shiner spawning habitat;  
349 Stressors=contaminants, water temperature, habitat fragmentation; E: Tier 2 EEC=larval  
350 Arkansas River Shiner habitat, Stressors=water temperature, habitat fragmentation and Tier 2  
351 EEC=invertebrate habitat, Stressors=altered riparian plant community, discharge, sediment  
352 deposition; F: Tier 3 EEC=primary production, Stressor = nutrient flux; G: Tier 3  
353 EEC=invertebrate production; Stressor=invertebrate habitat quantity and quality and Tier 3  
354 EEC=Arkansas River Shiner larvae production, Stressor=predation by invasive species; H: Tier 1  
355 EEC= biogeochemistry/thermodynamics; Inter-tier interaction= Sediment adsorption of

356 contaminants and nutrients and Tier 3 EEC=Arkansas River Shiner larvae production,  
357 Stressors=Arkansas River Shiner larvae habitat quantity and quality and Tier 3 EEC=Arkansas  
358 River Shiner age-0 recruitment; Inter-tier interaction=Arkansas River Shiner larvae mortality and  
359 Tier 3 EEC=Arkansas River Shiner age-1+ recruitment, Inter-tier interaction= Arkansas River  
360 Shiner age-0 mortality and Tier 3 EEC=all, Inter-tier interaction=trophic level interactions;  
361 I:Arkansas River Shiner larvae production; Stressor= direct mortality from recreational use (i.e.,  
362 all-terrain vehicle and in-river traffic); J:Tier 3 EEC=Arkansas River Shiner egg quality and  
363 production; Stressor=Arkansas River Shiner spawning habitat quantity and quality; K:Tier 3  
364 EEC=Arkansas River Shiner larvae production; Inter-tier interaction=Arkansas River Shiner egg  
365 mortality.

## 366 **Colorado River**

367 The Humpback Chub (*Gila cypha*), a fish native to the Colorado River, was listed as  
368 endangered by the U.S. Fish and Wildlife Service in 1967 and given full protection under the  
369 Endangered Species Act of 1973 (ESA). To mitigate the effects of anthropogenic changes to the  
370 river on Humpback Chub, an understanding of the mechanisms by which Glen Canyon Dam and  
371 non-native species affect Humpback Chub is needed. A critical life-history bottleneck for  
372 Humpback Chub is recruitment into the first year class (Fig 6). Temperature, light, and seasonal  
373 high river discharge from snowmelt are thought to cue spawning behavior [58]. Hydropower  
374 development has dampened the range of river discharges of the Lower Colorado River within  
375 Grand Canyon. Historically, river discharge varied between 15 and 3400 m<sup>3</sup>/s, however  
376 discharge was greater in large flood events; current dam operations limit flows to a range of 140

377 to 1000 m<sup>3</sup>/s (Fig S2). Resulting changes in turbidity and water temperature create risks to  
378 endangered Humpback Chub, and other endemic fish. For example, the quantity and quality of  
379 habitat is reduced through changes in turbidity, biogeochemistry, and the temperature regime.  
380 Hypolimnetic water releases from Lake Powell maintain cold temperatures in the Colorado River  
381 downstream from Glen Canyon Dam; currently, spawning is limited to a single tributary, the  
382 Little Colorado River. As embryos survive into the larval stage, nursery habitats to support  
383 growth and foraging are essential [59-61]. A secondary risk to juvenile survival post-larval stage  
384 is predation by non-native species including Rainbow Trout (*Oncorhynchus mykiss*) and Channel  
385 Catfish (*Ictalurus punctatus*) [62]. Temperatures for well over 100 km downstream of Lake  
386 Powell are excellent for non-native, cold water species, including a closely managed world-class  
387 Rainbow Trout fishery at Lees Ferry. Rainbow and Brown Trout (*Salma trutta*) are currently  
388 managed as an invasive species downstream of the confluence of the Colorado and Little  
389 Colorado River, approximately 97 km downstream of Glen Canyon Dam, to mitigate predation  
390 upon native fishes including the endangered Humpback Chub.

391 Fig 6. Conceptual model describing the relationship of anthropogenic drivers to essential  
392 ecosystem characteristics (EECs) affecting the recruitment of Humpback Chub in the Colorado  
393 River between Glen Canyon Dam and Lake Mead, Arizona. Essential ecosystem characteristics  
394 (EECs) are groupings of ecosystem components. Tier 1 EECs represent physical and chemical  
395 effects; fundamental measures of process that are directly affected by anthropogenic and natural  
396 drivers. Tier 2 EECs represent a broad habitat category that is intended to encompass the  
397 physical, chemical, and biological components of the riverine habitats that influence  
398 reproduction, growth, and survival of biotic communities. The Tier 3 EECs represent

399 components of the biological systems that respond to changes in the hierarchical components of  
400 the conceptual model. The strength of our understanding of how natural and anthropogenic  
401 drivers interact with habitats, biological systems, and fish in large rivers is represented by the  
402 different types of lines in the figure. Solid blue lines depict a strong understanding of the  
403 relationship, the dotted-dashed blue line represents a moderate understanding of the relationship,  
404 and the black dashed line represents a weak understanding of the relationship. The different  
405 types of lines also represent the strength of our understanding of within EEC-tier relationships.

406         The CM exercise documented a high understanding of the relationships of anthropogenic  
407 drivers to Tier 1 EECs, cascading to multiple, less-understood hypotheses about how these  
408 factors would combine to affect habitats at Tier 2 (Fig 6). High confidence in the linkages from  
409 Tier 2 invertebrate habitat to Tier 3 insect production is followed by a lesser understanding of  
410 how insect production is linked to larval production. The uncertainty of the relations between  
411 food resources stands in contrast to high certainty that was ascribed to the linkages from larval  
412 chub habitat to larval chub production, and from spawning habitat to larval chub production and  
413 then to recruitment. Since 1997, the Glen Canyon Dam Adaptive Management Program has  
414 supported extensive monitoring and research across the spatial and temporal landscape of the  
415 Colorado River. As a result, the information needed to characterize some of the stressors is  
416 readily available (Table S2). However, the status of some existing information was characterized  
417 as insufficient or not available. For the information needs characterized as being insufficient or  
418 not available, we identified the spatial and temporal scales at which data collection would  
419 facilitate the inferences needed to inform the management goal (Fig S3). Understanding how

420 these knowledge gaps affect Humpback Chub recruitment could identify strategies that will help  
421 achieve the management goal of improving Humpback Chub recruitment in the Colorado River.

## 422 **Columbia River**

423 White Sturgeon is the largest freshwater fish in North America [63]. Like other sturgeon  
424 species, anthropogenic stressors have negatively affected White Sturgeon productivity. Our  
425 knowledge of factors affecting White Sturgeon productivity remain poorly understood [40].  
426 Therefore, we used the CM to identify knowledge gaps associated with the hypotheses that dam  
427 construction and operation, land-use practices, and invasive species, in some combination, affect  
428 the recruitment of age-0 White Sturgeon (Fig 7). Within the basin, development of hydroelectric  
429 and water-storage dams have changed the magnitude and seasonality of the natural river  
430 discharge (Fig S4) and thermal regimes [64], reduced the quantity and quality of spawning  
431 habitats [65, 66], and disrupted historical migration patterns [67]. Prior to hydropower  
432 development, White Sturgeon experienced a hydrograph that peaked during June-July due to  
433 snowmelt [64]. However, from 1949 to 1993 the average discharge in June decreased from  
434 14,000 m<sup>3</sup>/s to 6,000 m<sup>3</sup>/s and the maximum water temperature has increased by 1.8°C [64].  
435 White Sturgeon likely used the natural hydrograph and thermal regime as cues to seek out  
436 optimal spawning habitats and initiate spawning [65, 68].

437 Fig 7. Conceptual model describing the relationship of anthropogenic drivers to essential  
438 ecosystem characteristics (EECs) affecting the recruitment of White Sturgeon in the Columbia  
439 River, U.S. Essential ecosystem characteristics (EECs) are groupings of ecosystem components.  
440 Tier 1 EECs represent physical and chemical effects; fundamental measures of process that are

441 directly affected by anthropogenic and natural drivers. Tier 2 EECs represent a broad habitat  
442 category that is intended to encompass the physical, chemical, and biological components of the  
443 riverine habitats that influence reproduction, growth, and survival of biotic communities. The  
444 Tier 3 EECs represent components of the biological systems that respond to changes in the  
445 hierarchical components of the conceptual model. The strength of our understanding of how  
446 natural and anthropogenic drivers interact with habitats, biological systems, and fish in large  
447 rivers is represented by the different types of lines in the figure. Solid blue lines depict a strong  
448 understanding of the relationship, the dotted-dashed blue line represents a moderate  
449 understanding of the relationship, and the black dashed line represents a weak understanding of  
450 the relationship. The different types of lines also represent the strength of our understanding of  
451 within EEC-tier relationships.

452           Factors other than river discharge and water temperature may also be affecting age-0  
453 White Sturgeon recruitment [40]. In areas of the Columbia and Snake Rivers with hydropower  
454 development, White Sturgeon populations are functionally isolated by dams. Consequently,  
455 White Sturgeon depend on conditions within restricted reaches to sustain production. In some  
456 reaches, suitable rearing habitat exists, and individual growth rates are high, but spawning habitat  
457 is limited and recruitment of fish is poor [65]. In other reaches, favorable spawning conditions  
458 exist but growth of young fish may be density limited [69]. How the availability of food  
459 resources for larval and juvenile White Sturgeon varies among reservoirs may affect age-0 White  
460 Sturgeon recruitment. Research has also suggested that contaminants may affect White Sturgeon  
461 reproductive biology [70]. The introduction of non-native fishes has clearly affected the native  
462 fish assemblage in the Columbia River [32, 71]. Channel Catfish, Smallmouth Bass *Micropterus*

463 *dolomieu*, and Walleye (*Sander vitreus*) that have been introduced into the Columbia River have  
464 all been shown to prey upon or compete with native fish species [71, 72] and may also affect  
465 White Sturgeon.

466 The CM (Fig 7) provides structure to the multiple competing hypotheses and indicates  
467 how anthropogenic drivers may be affecting Tier 1, 2, and 3 EEC's. Not surprisingly, the  
468 strength of our understanding of the effects of stressors on White Sturgeon was greater for  
469 relationships between life stages that are more easily sampled (e.g., adults) and that rely on data  
470 that are readily accessible as part of monitoring associated with hydropower development (e.g.,  
471 discharge and water temperature) or metrics that are from combinations of these variables (e.g.,  
472 estimates of White Sturgeon spawning habitat; Table S3). However, for relationships between  
473 harder to sample White Sturgeon life stages (e.g., larvae), biota that require expertise and  
474 equipment atypical of traditional fisheries assessments in large rivers (e.g., benthic  
475 macroinvertebrates), or stressors that are described by metrics that require specialized modeling  
476 expertise (e.g., sediment transport dynamics), the existing information was insufficient or not  
477 available. For example, we identified the need to better understand the effects of channel  
478 morphology and hydraulics on benthic macroinvertebrate habitat, invertebrate production, and  
479 subsequent larval White Sturgeon production. The most certain pathways connected changes in  
480 hydrology, hydraulics, and temperature regimes to reduced spawning habitat in Tier 2, then to  
481 decreased egg quality and production at Tier 3.

482 Our results suggest there are stressors that can affect the management goal of increasing  
483 age-0 White Sturgeon recruitment that are poorly understood and that could confound efforts to  
484 manage White Sturgeon in the Columbia River. Our characterization of the spatial and temporal  
485 scales that data should be collected at could help guide future efforts to fill data gaps to support



486 the inferences needed to address the goal of improving recruitment of age-0 White Sturgeon (Fig  
487 S5).

## 488 **Upper Mississippi and Illinois Rivers**

489 In the agricultural Midwest, basin-wide land uses affect the delivery of sediments,  
490 nutrients, and runoff to the Upper Mississippi and Illinois rivers [73-76]. Within the floodplain of  
491 these two large rivers, agriculture and residential land uses often rely upon the use of levees to  
492 isolate productive or developed lands during seasonal high-flow events. Within the channel,  
493 these rivers support commercial navigation with locks and dams and river-training structures,  
494 which have dramatically altered channel morphology and hydraulics throughout the system.  
495 Together, the cumulative effects of these modifications to the basin, floodplain, and river have  
496 implications for habitat diversity and native fish biodiversity [77]. Additionally, recent invasion  
497 and expansion of non-native species, namely Silver Carp (*Hypophthalmichthys molitrix*) and  
498 Bighead Carp (*H. nobilis*), have direct and indirect effects on native fishes that likely compound  
499 or confound stress pathways on native fish biodiversity [78, 79]. Therefore, we used the CM to  
500 explore how these primary anthropogenic drivers have likely influenced fish habitats and  
501 associated life stages (Fig 8).

502 Fig 8. Conceptual model of how anthropogenic drivers in the upper Mississippi and Illinois  
503 Rivers influence native fish habitats and recruitment. Essential ecosystem characteristics (EECs)  
504 are groupings of ecosystem components. Tier 1 EECs represent physical and chemical effects;  
505 fundamental measures of process that are directly affected by anthropogenic and natural drivers.  
506 Tier 2 EECs represent a broad habitat category that is intended to encompass the physical,

507 chemical, and biological components of the riverine habitats that influence reproduction, growth,  
508 and survival of biotic communities. The Tier 3 EECs represent components of the biological  
509 systems that respond to changes in the hierarchical components of the conceptual model. The  
510 strength of our understanding of the relationships of how natural and anthropogenic drivers  
511 interact with habitats, biological systems, and fish in large rivers is represented by the different  
512 types of lines in the figure. Solid blue lines depict a strong understanding of the relationship, the  
513 dotted-dashed blue line represents a moderate understanding of the relationship, and the black  
514 dashed line represents a weak understanding of the relationship. The different types of lines also  
515 represent the strength of our understanding of within EEC-tier relationships.

516           Increased sediment loads in combination with altered hydraulics and morphology have  
517 resulted in high rates of sedimentation, homogeneity of depth, and loss of low-velocity, off-  
518 channel areas [80, 81]. A diversity of off-channel habitat conditions (i.e., increased residence  
519 time, low velocity, warm temperatures, availability of food resources) support growth and  
520 development of larval and juvenile fishes [82, 83] and often provide important food resources for  
521 adult fishes [84-88]. Further, deep, low-velocity off-channel habitats are recognized as important  
522 refugia for a wide range of fishes during high-flow events and seasonal periods of low  
523 temperatures [89-92]. Loss of floodplain connectivity has eliminated the seasonal exchange of  
524 nutrients, organisms and organic matter between river and floodplain environments that support  
525 biological diversity and productivity [93, 94]. Reduced availability of spawning, nursery,  
526 foraging, or overwintering habitat conditions can serve as bottlenecks to fish populations through  
527 limited larval production, reduced growth, and increased overwinter mortality. For example, high  
528 sedimentation rates have been filling backwaters in the Illinois River for decades, thus limiting

529 the availability of overwintering conditions for fishes that bioenergetically need a deep refuge  
530 with slow water velocities. Missing year-classes in this reach, represented by truncated size  
531 structure in the Largemouth Bass (*Micropterus salmoides*) population are hypothesized to be a  
532 result of periodic winter mortality (Fig S6).

533         The application of our CM makes clear that while the general effects of anthropogenic  
534 drivers on hydrology, sediment transport, biogeochemistry, ~~and~~ hydraulics and morphology are  
535 well understood, there is much less known about how those effects influence the quality and  
536 availability of required habitat conditions (Tier 2, Fig 8). Although there is likely overlap of  
537 habitat requirements among species with similar life histories, the diversity of habitat conditions  
538 necessary to support a native and diverse fish community has not been explored. Consequently,  
539 the existing information needed to assess the relationship between habitat quality and quantity,  
540 and egg production, juvenile recruitment, and adult survival of fish populations within the Upper  
541 Mississippi and Illinois rivers was categorized as insufficient to not available (Tier 3 Inter-tier  
542 interaction, Fig 8; Table S4). Addressing these knowledge gaps could improve the effectiveness  
543 of habitat restoration efforts focused on maintaining a diverse native fish community. The spatial  
544 and temporal scales of data collection that would support needed inferences to address restoring  
545 and maintaining native fish biodiversity and habitat quantity and quality are characterized in Fig  
546 S7.

#### 547         **Similarities across case studies**

548         We observed similarities in the stressors and interactions within EEC tiers across the four  
549 case studies. For Tier 1, an altered hydrologic regime was identified as a stressor to the

550 hydrology EEC in all four rivers (Table 1). Presumably this is due to the ubiquitous effects of  
551 dams on the systems examined. However, in some rivers the altered hydrologic regime  
552 originated from other anthropogenic (e.g., water use, land use, biological community alteration)  
553 and natural (e.g., climate) drivers. Similarly, all four case studies listed an altered water  
554 temperature regime as a stressor to the biogeochemistry/thermodynamics EEC with linkages to  
555 several anthropogenic drivers (Fig 4, 6-8; Tables S1-S4). There were also similarities across case  
556 studies with respect to the identification of interactions between Tier 1 EECs with all four case  
557 studies noting interactions between Tier 1 EEC components.

558 Table 1. Stressors or inter-tier interactions affecting Tier 1 Essential Ecosystem Characteristics (EEC) identified as an information  
 559 need in the application of the conceptual model to case studies in the Canadian River (1), Colorado River (2), Columbia River (3), and  
 560 Upper Mississippi and Illinois rivers (4). Tier 1 EECs are measurable characteristics that describe processes that can significantly alter  
 561 the morphological or chemical characteristics within a river channel.

| Stressor or inter-tier interaction                   | Tier 1 EEC |                               |                    |                                    |
|--|------------|-------------------------------|--------------------|------------------------------------|
|  | Hydrology  | Channel Morphology/Hydraulics | Sediment Transport | Biogeochemistry/<br>Thermodynamics |
| Altered Hydrologic Regime                            | 1, 2, 3, 4 | 1                             | 1, 2               |                                    |
| Altered Hydraulic Regime                             |            | 1, 3, 4                       | 3                  |                                    |
| Altered Sediment Regime                              |            |                               | 3, 4               |                                    |
| Altered Water Temperature Regime                     |            |                               |                    | 1, 2, 3, 4                         |
| Altered Biogeochemical Regime                        |            |                               |                    | 1, 3, 4                            |
| Channel forming processes                            |            | 1, 2, 3, 4                    |                    |                                    |
| Sediment transport dynamics                          |            | 1, 2, 3, 4                    | 1, 2, 3, 4         |                                    |
| Sediment adsorption of<br>contaminants and nutrients |            |                               |                    | 1, 2, 3, 4                         |

562

563

564 For Tier 2, there were similarities across case studies; however, the adaptation and  
565 elaboration of the components to the management goal in the case studies was apparent (Table  
566 2). The management goal associated with the case study for the Upper Mississippi and Illinois  
567 Rivers resulted in Tier 2 EEC components (e.g., overwintering habitat) and stressors (e.g.,  
568 dissolved oxygen) that were unique. Spawning habitat was identified as a Tier 2 EEC component  
569 in all the case studies and multiple stressors were identified as affecting this component in two or  
570 more of the case studies. Larval fish and invertebrate habitat were noted as Tier 2 EEC  
571 components with some similarities in stressors across case studies. Habitat fragmentation,  
572 sediment deposition, and water temperature were listed as stressors to Tier 2 EECs in all four  
573 case studies. No interactions between Tier 2 EEC components were listed for the case studies.

574 Table 2. Stressors affecting Tier 2 Essential Ecosystem Characteristics (EEC) identified in the application of the conceptual model to  
 575 case studies in the Canadian River (1), Colorado River (2), Columbia River (3), and Upper Mississippi and Illinois rivers (4). Tier 2  
 576 EECs are broadly described as physical, chemical, or biological components of “habitat” that are hypothesized to have overall fitness  
 577 consequences.

| Stressor                   | Tier 2 EEC (habitat) |               |               |             |              |
|----------------------------|----------------------|---------------|---------------|-------------|--------------|
|                            | Spawning             | Overwintering | Juvenile fish | Larval fish | Invertebrate |
| Altered riparian community |                      |               |               |             | 1            |
| Channel stability          |                      |               |               |             | 2, 3         |
| Contaminants               | 1, 3, 4              |               | 4             |             |              |
| Discharge                  |                      |               |               |             | 1            |
| Dissolved oxygen           | 4                    | 4             | 4             |             |              |
| Habitat fragmentation      | 1, 3, 4              |               |               | 1, 2, 3     | 2, 3         |
| Sediment deposition        | 3, 4                 | 4             | 4             | 3           | 1, 2, 3      |
| Turbidity                  |                      |               |               | 2           |              |
| Water Depth                | 4                    |               | 4             |             |              |
| Water temperature          | 1, 2, 3, 4           | 4             | 4             | 1, 3        |              |
| Water velocity             | 3, 4                 | 4             | 4             |             |              |

578

579           The adaptation of Tier 3 EECs and elaboration of the biological system related to the  
580 management goal addressed by the case studies resulted in EECs that were comprised of fish life  
581 stages ranging from eggs to adult fish, primary and invertebrate production, and biodiversity  
582 (Table 3). All Tier 3 EEC components, except biodiversity, were present in the four case studies.  
583 Not surprisingly, habitat quantity and quality were listed as stressors to all the EECs related to  
584 fish and invertebrates. Six of eight stressors or inter-tier interactions were listed as affecting fish  
585 larvae and five of eight were noted as affecting egg quantity and quality. In contrast to Tier 2,  
586 interactions were extensively noted between Tier 3 EECs and trophic level interspecific  
587 interactions were listed in all four case studies.



588 Table 3. Stressors or inter-tier interactions affecting Tier 3 Essential Ecosystem Characteristics (EEC) identified in the application of  
 589 the conceptual model to case studies in the Canadian River (1), Colorado River (2), Columbia River (3), and Upper Mississippi and  
 590 Illinois rivers (4). Tier 3 EECs represent components of the hypothesized biological system upon which the cascading effects of  
 591 anthropogenic and natural drivers act, and interactions occur.

| Stressor or inter-tier interaction        | Tier 3 EEC             |                           |                        |                             |                         |                    |              |
|---|------------------------|---------------------------|------------------------|-----------------------------|-------------------------|--------------------|--------------|
|   | Adult fish recruitment | Juvenile fish recruitment | Larval fish production | Fish egg quality/production | Invertebrate production | Primary production | Biodiversity |
| Direct mortality                          |                        |                           | 1                      |                             |                         |                    |              |
| Predation/competition by invasive species |                        |                           | 1, 2, 3                | 3                           |                         |                    | 4            |
| Habitat quantity/quality                  | 4                      | 4                         | 1, 2, 3                | 1, 2, 3, 4                  | 1, 2, 3                 |                    |              |
| Nutrient flux                             |                        |                           |                        |                             |                         | 1, 2, 3            |              |
| Trophic level interspecific interactions  | 1, 2, 3, 4             | 1, 2, 3, 4                | 1, 2, 3, 4             | 1, 2, 3, 4                  | 1, 2, 3, 4              | 1, 2, 3, 4         | 4            |
| Predation                                 |                        |                           | 3                      | 3                           |                         |                    |              |
| Mortality                                 | 1, 3, 4                | 1, 2, 3, 4                | 1, 2, 3                |                             |                         |                    |              |
| Fish condition                            |                        |                           |                        | 1, 3, 4                     |                         |                    |              |

592

## 593 **Discussion**

594           The main objective of our exploration of CMs was to impose some structure on the  
595 complex ecosystems found in large rivers and from that structure, identify gaps in monitoring  
596 information that could inform the management of fish. Comparison across our four case studies  
597 provides some insights into large rivers and the utility of the CM to identify gaps in our  
598 understanding of factors affecting fish in large rivers.

599           Despite large differences in the physical and ecological contexts of the river systems, the  
600 case studies demonstrated substantial commonalities in the data needed to better understand how  
601 human activities affect these systems and ~~in the application of the~~ CM. The general tiered  
602 structure of drivers and cascading responses through EECs worked well with the four examples.  
603 Each of the four rivers could be placed in the tiered CM to illustrate current perceptions about  
604 drivers and responses. The hierarchical CM generally increased in complexity from top to  
605 bottom. Among all rivers, there tended to be greater understanding of links from drivers to Tier 1  
606 and Tier 2 EECs, and less understanding about linkages to Tier 3.

607           The strength of understanding of interactions between anthropogenic and natural drivers  
608 and EECs, and between and within EECs, varied considerably among river systems, however,  
609 resulting from both variable complexity and existing knowledge. For example, linkages from  
610 drivers to Tier 1 EECs were considered strong in the case of the Humpback Chub in the Grand  
611 Canyon, but between Tier 1 and Tier 2 only moderate. This is probably indicative of the  
612 substantial research investments in examination of physical processes in this river system [95].

613           Although we did not prescribe a specific approach to the CM process, the case studies  
614 employed similar strategies. Our modelling exercises started with the definition of a management

615 goal. In all our case studies, the management goals pertained to a desired biological endpoint  
616 represented in Tier 3. After the definition of the management goal, we conceptualized  
617 interactions between drivers and EECs and between EECs with a combination of top-down and  
618 bottom-up approaches. A top-to-bottom approach to working with these models is generally  
619 consistent with a management perspective wherein anthropogenic drivers that are most directly  
620 managed in a large-river system (e.g., land and water use, etc.) cascade from top to bottom  
621 through fluxes to physical and chemical habitats, and then to biological responses. While this is  
622 generally true for anthropogenic drivers, a notable exception to the top-to-bottom management  
623 approach would be that in the U.S., there are few actions currently directed at reducing emissions  
624 affecting climate [96] which is a natural driver in our CM. Climate was hypothesized to be a  
625 stressor in the case study application of the CM to Arkansas River Shiner management in the  
626 South Canadian River and is hypothesized to be affecting hydrologic regimes elsewhere [97, 98],  
627 but was not specifically mentioned in other case studies. The CMs can readily be modified to  
628 incorporate other factors or pathways (e.g., climate effects) as new information or perspectives  
629 become available. A bottom to top approach is equally or more valuable as it starts with the  
630 foundation of understanding about the species or community, and then seeks to identify which  
631 stressors affect population or community responses. A bottom-up approach can readily identify  
632 information gaps in linkages from ecological processes to demographic parameters [99].

633         The top-to-bottom and bottom-up approaches meet in the middle in Tier 2 in the concept  
634 of habitat: the resources and conditions present in an area that produce occupancy [100]. Tier 2 is  
635 critical as it has little value if it is not defined based on biological requirements or if managers  
636 lack understanding on how habitat is formed. Among our examples, the Upper Mississippi River  
637 is notable for asserting strong understanding of the linkages from land-use stressors to sediment

638 regime to diminished overwintering habitat for native adult fishes. After that, interactions with  
639 other processes and life stages combine to increase uncertainty about whether overwintering  
640 habitat is a limiting factor in biodiversity. In contrast, the high confidence in understanding how  
641 White Sturgeon egg quality and production are linked to spawning habitat in the Columbia River  
642 Basin, provides a strong linkage upward through Tier 1 EECs and potential management actions  
643 (Fig 7). Although at times elusive, the concept of habitat is critical for linking management to  
644 biotic endpoints [101].

645         Large rivers are typically managed for multiple objectives, including fisheries, multi-  
646 species, or ecosystem objectives. Management decisions typically require an understanding of  
647 how management actions propagate through a river ecosystem. Although the emphasis may be  
648 on a biological endpoint (among other objectives), understanding the intermediate steps and the  
649 processes linking them, and potential interactions between processes or EEC components, can  
650 help formulate effective management strategies; especially as multiple objectives compete. In a  
651 multi-species context, the conceptual models can help identify commonalities and differences in  
652 in how stressors propagate to biota and therefore provide a basis for prioritizing monitoring  
653 efforts. In the case where species or guilds have similar habitat affinities and life histories, a  
654 dominant anthropogenic stress pathway may be hypothesized and focus on a single or few  
655 monitoring components may be justified. An example may be multiple large-river species that  
656 are known to be cued to spawn by spring flow pulses. In such a case, the characteristics of the  
657 annual hydrograph would be a dominant physical monitoring variable and biological monitoring  
658 could focus on reproductive success of one or more of the species. In the case where multiple  
659 species of concern have different reproductive strategies – for example, rheophilic species like  
660 sturgeon that may require in-channel dispersion of young to flowing habitats compared to

661 invasive carp whose young thrive when they can disperse to lentic floodplain pools – pathways  
662 and monitoring strategies will diverge. In the latter case, it would probably not be sufficient to  
663 monitor and assess the characteristics of the annual hydrograph; instead, hydrologic metrics  
664 would need to be integrated with hydraulic and geomorphic metrics to assess where and when  
665 the different habitats would be available and could be targeted for young-of-the-year sampling.  
666 Effectively addressing multiple species would rely on detailed knowledge of life histories and  
667 how they play out on the landscape – such information is missing for many species and may  
668 need to be developed for effective design of monitoring and management actions.

669 Management actions intended to benefit fish in large rivers can directly or indirectly  
670 affect multiple ecosystem components. Without consideration of the effects of management on  
671 non-target ecosystem components, unintended consequences may limit management efficacy.  
672 Hypothesizing inter-tier interactions in the Tier 3 EEC (e.g., see Fig 7), can provide insight on  
673 the potential interactions among fish species and other biological components in the context of  
674 the hierarchical CM. In all our case studies, the lumping of multiple biological interactions in  
675 Tier 3 resulted in a simplification of complex trophic interactions. For example, as Tier 3  
676 encompasses all biological responses, it includes multiple life stages of many interacting species  
677 at varying trophic levels. Because of this, the four CMs diverged significantly at Tier 3 as  
678 components were expanded to accommodate existing understanding. Even as the Tier 3  
679 components were expanded in complexity, they remained highly simplified views of the  
680 ecosystem. Simplification was based, in part, on the importance of key species in management  
681 goals and the experts' existing knowledge. Even though the hypothesized Tier 3 interactions in  
682 our case studies conveyed a simplification of the trophic interactions, the hypothesized  
683 interactions do suggest the need for information that clarifies the trophic interactions and effects

684 of Tier 3 EEC components on the biological endpoint. If desired or warranted, the Tier 3 EEC  
685 could be elaborated to capture more complexity. For example, in Fig 7, the Tier 3 inter-tier  
686 interaction between anadromous and resident fishes and white sturgeon larvae could expanded to  
687 include interactions with specific fish species. Monitoring can help clarify the effects of  
688 management actions, including on non-target ecosystem components, but only if data are  
689 collected to characterize key ecosystem processes that could affect the outcome. The process of  
690 considering and elucidating Tier 3 EEC interactions can help identify the non-target ecosystem  
691 components that could be affected when managing for a specific biological endpoint.

692 The CMs explored here also provide a framework for considering return on science  
693 investments. The knowledge needed for effective management of large rivers can be gained by  
694 monitoring intermediate endpoints along the cascade, but the type of information and costs vary  
695 widely. Costs for monitoring Tier 1 EECs can be high but some programs are already in place.  
696 For example, large rivers are likely to have monitoring infrastructure installed for Tier 1  
697 monitoring of discharge and temperature regimes, with varying potential for monitoring  
698 sediment transport and water quality. Investment at Tier 2 may emphasize physical processes and  
699 habitats that can be measured at relatively low cost, assuming that habitats are adequately  
700 defined based on biological criteria. In larger rivers, Tier 2 habitat assessments can be more cost  
701 effective compared to smaller rivers because they can rely on automated data collection through  
702 hydroacoustics and remote sensing [101]. As discussed above, habitat assessments have value  
703 only to the extent that they are based on well-defined biological requirements; it is notable that  
704 some large-river management efforts have found that relatively simple habitat models are useful  
705 to predict biological responses [102]. At Tier 3, costs can increase substantially because of  
706 structural uncertainties (i.e., which life stages, which species are most important to monitor) and

707 because of the inherent uncertainties of monitoring fish in large river systems where detection  
708 probability can be low and highly variable [36, 103]. Generally, the cost of monitoring increases  
709 from Tier 1 to Tier 3 in the CM hierarchy; at the same time, the relevance of information to  
710 decision making is typically greater for biological responses depicted in Tier 3 [104].

711 Because both costs and information benefits increase from Tier 1 to Tier 3 in the CM  
712 hierarchy, it is difficult to generalize about where the benefit:cost ratio would be optimized.  
713 Indeed, as discussed by Jacobson and Berkley [30], the decision about where in the hierarchy  
714 monitoring resources would get the highest return on investment may depend more directly on  
715 managers' and stakeholders' perceptions about risks of acting with incomplete information. For  
716 example, the details of how a fish's reproductive strategy depends on the nuances of a seasonal  
717 hydrograph may not be known, but stakeholders may believe strongly that the natural  
718 hydrograph was functional for the species and therefore monitoring of the flow regime will have  
719 the highest return on investment and, by extension, restoration of the flow regime is likely to  
720 have the most positive effects. On the other hand, in systems where stakeholders' opinions are  
721 divided or socio-economic values would be compromised by a return to a natural flow regime,  
722 managers may be required to demonstrate more precisely how elements of the flow regime  
723 propagate to species' benefits [105]. Thus, once information needs are identified and there is an  
724 assessment of the availability of data identified as information needs, there needs to be a process  
725 whereby the costs of collecting the information need to be placed in a socioeconomic context  
726 (e.g., see [30]).

727 The development of the CMs described in this manuscript can be a first step in  
728 application of structured decision-making (SDM) and its iterative form-adaptive management  
729 (AM) processes [106, 107]. Structured decision-making is a stakeholder driven process by which

730 a problem can be defined with conceptual models and decomposed into decision components  
731 that include the problem context, stakeholder objectives, potential management actions,  
732 consequences of those actions on the objectives, and trade-offs related to different decisions  
733 (actions) [107-109]. One primary focus of SDM is the identification of uncertainties such as  
734 those identified in the CMs for the case studies in this paper [110]. Quantification of the  
735 influence of decision relevant uncertainties can be modeled using sensitivity analysis and other  
736 techniques and ranked [107, 109, 111]. In addition, the quantitative techniques available to assist  
737 in solving complex ecological problems are robust and range in complexity from consequences  
738 tables to Bayesian models to dynamic optimization models [107-109, 112, 113]. The SDM  
739 process is often used as the set-up phase for adaptive management which includes monitoring  
740 over time to reduce uncertainty related to how management will influence important outcomes  
741 (e.g. fish population status; [109, 112]).

742         The CM may also help to identify which processes or components are amenable to a field  
743 monitoring effort and which are more aptly addressed through laboratory or mesocosm  
744 experiments. For example, if it is hypothesized that the condition of age 1+ Arkansas Shiners is a  
745 critical determining factor in egg quality or production (Fig 4), it could be determined that the  
746 best approach to developing a quantitative relation between condition and eggs is through a  
747 controlled laboratory experiment rather than field-based monitoring. The CM helps to visualize  
748 where different types of information may be applied within a decision-making framework.

749         A large-river CM may also serve as a precursor to computational ecological or population  
750 models [30]. Similar questions about how monitoring and other science efforts should be  
751 distributed among EECs and processes can be addressed iteratively by carrying out sensitivity  
752 analyses in a modeling framework. Indeed, given substantial uncertainties associated with



753 monitoring data, computation modeling can be considered a necessary component of large-river  
754 monitoring and evaluation systems [99, 114].

## 755 **Conclusions**

756         We found the process of conceptualizing the relationships between and within EECs  
757 fostered a critical assessment of what we know about factors affecting the management endpoint.  
758 By visualizing how EEC drivers directly and indirectly affect management endpoints, our CM  
759 identified critical information gaps and uncertainties that, if resolved, could improve our  
760 understanding of how to best meet management objectives. The process of conceptualizing the  
761 EEC relationships affecting fish in large rivers could help to structure, or restructure, monitoring  
762 programs around scientifically sound monitoring questions, promote the selection of relevant  
763 ecological indicators that characterize resource condition or management outcomes, and  
764 facilitate communication and information sharing within and between organizations managing or  
765 researching management endpoints. Ultimately, understanding the mechanisms by which EECs  
766 influence large-river fishes will improve the effectiveness of restoration and management  
767 actions.

768         As shown with our case studies, our CM is flexible and applicable to a wide range of  
769 river systems with different anthropogenic drivers and management objectives. We feel our CM  
770 provides a generic structure that scientists can adapt to their management goals and needs. By  
771 not being overly prescriptive, for example, with respect to the components of the Tier 2 and 3  
772 EEC components, scientists can adapt the CM to different biological communities and

773 management endpoints. By doing so, we feel that users have the flexibility to place their  
774 management questions in the context of EECs that are specific to their large-river system.

775         Although the case studies addressed management issues that were river or basin specific,  
776 there were similarities relative to information needs and data availability. For example, in most  
777 systems information on river discharge and water temperature were needed and available.  
778 Conversely, information regarding trophic relationships and the habitat requirements of larval  
779 fishes were generally lacking. This result suggests that there may be a common need for a better  
780 understanding of certain factors across large-river systems.

## 781 **Acknowledgements**

782 We thank Megan Dethloff of the Pacific Northwest Aquatic Monitoring Partnership for her role  
783 in organizing the logistics associated with the workshop and conference calls needed to develop  
784 this manuscript. David Ward from the U.S. Geological Survey's Grand Canyon Monitoring and  
785 Research Center provided many valuable comments and suggestions that improved the  
786 manuscript. This work was funded in part by U.S. Geological Survey, Science Synthesis,  
787 Analysis, and Research Program. This research is a contribution of the Ball State University,  
788 Illinois Natural History Survey, Oregon Department of Fish and Wildlife, Pacific Northwest  
789 Aquatic Monitoring Partnership, the Alabama Cooperative Fish and Wildlife Research Unit, and  
790 the U.S. Geological Survey Columbia Environmental Research Center, Grand Canyon  
791 Monitoring and Research Center, Oregon Water Science Center, Upper Midwest Environmental  
792 Sciences Center, and Western Fisheries Research Center. Any use of trade, firm, or product

793 names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

794 An animal care and use protocol was not required for this research.

795

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1141 **Supporting Information Captions**

1142 Fig S1. Discharge ( $\text{m}^3/\text{s}$ ) patterns over time in the Canadian River, Oklahoma near Canadian, TX  
1143 (USGS 2019; USGS Gage 07228000).

1144 Fig S2. Hydrograph showing pre- and post-Glen Canyon Dam closure in 1964 (dashed line)  
1145 mean monthly discharge ( $\text{m}^3/\text{s}$ ), which transitions from seasonally stochastic to a more  
1146 homogeneous regime focusing on anthropogenic interests.

1147 Fig S3. The spatial and temporal scales of the management goal, the scientific inferences needed  
1148 to inform the management goal, and that data collection needs to occur to support the inferences  
1149 for monitoring information needs identified as requiring additional data in the case study  
1150 addressing Humpback Chub recruitment in the Colorado River between Glen Canyon Dam and  
1151 Lake Mead, Arizona (see Table S2 for additional detail). A: Tier 2 EEC= larval Humpback Chub  
1152 habitat; Stressors=habitat fragmentation, turbidity and Tier 2 EEC= Humpback Chub spawning  
1153 habitat; Stressor= water temperature and Tier 3 EEC=insect production; Stressor=benthic  
1154 macroinvertebrate habitat quantity and quality and Tier 3 EECs=all; Inter-tier interaction=trophic  
1155 level interactions; B: Tier 3 EEC=larval Humpback Chub production; Stressor= larval Humpback  
1156 chub habitat quantity and quality; C: Tier 3 EEC=Humpback Chub egg quality and production;  
1157 Stressors= Humpback Chub spawning habitat quantity and quality; D:Larval Humpback Chub  
1158 production; Inter-tier interaction=mortality of Humpback Chub eggs; E: Tier 3 EEC= larval  
1159 Humpback Chub production; Stressor=predation by invasive species and Tier 3 EEC=Primary  
1160 production; Stressor=nutrient flux; F: Tier 1 EEC= biogeochemistry/thermodynamics; Inter-tier  
1161 interaction=sediment adsorption of contaminants and nutrients; G: Tier 3 EEC=Humpback Chub  
1162 age-0 recruitment; Inter-tier interaction=mortality of larval Humpback Chub.

1163 Fig S4. Proportion of total annual Columbia River discharge at The Dalles, OR occurring in the  
1164 month of June from 1879 to 2015.

1165 Fig S5. The spatial and temporal scales of the management goal, the scientific inferences needed  
1166 to inform the management goal, and that data collection needs to occur to support the inferences  
1167 for monitoring information needs identified as requiring additional data in the case study  
1168 addressing White Sturgeon recruitment in the Columbia River (see Table S3 for additional  
1169 detail). A: Tier 1 EEC= biogeochemistry/thermodynamic; Stressor= altered biogeochemical  
1170 regime and Tier 2 EEC= benthic macroinvertebrate habitat; Stressors=channel stability, sediment  
1171 deposition, fragmentation and Tier 2 EEC=Larval White Sturgeon habitat; Stressors=habitat  
1172 fragmentation sediment deposition, water temperature and Tier 2 EEC=White Sturgeon  
1173 spawning habitat; Stressors=contaminants, sediment deposition and Tier 3 EEC=White Sturgeon  
1174 egg quality and production; Stressor=predation by invasive species and Tier 3 EEC=White  
1175 Sturgeon larvae production; Stressor=predation by invasive species and Tier 3 EEC=benthic  
1176 macroinvertebrate production; Stressor=benthic macroinvertebrate habitat quantity and quality;  
1177 B: Tier 1 EEC=sediment transport; Stressors=altered sediment regime, altered hydraulic regime  
1178 and Tier 1 EECs=channel morphology/hydraulics, sediment transport; Stressor=altered hydraulic  
1179 regime and Tier 3 EEC=primary production; Stressor=nutrient fluxes; C: Tier 1 EEC=channel  
1180 morphology/hydraulics, sediment transport; Stressor=altered hydraulic regime and Tier 1 EEC =  
1181 channel morphology/hydraulics, sediment transport; Inter-tier interaction=sediment transport  
1182 dynamics; D: Tier 1 EEC=channel morphology/hydraulics, sediment transport; Stressor=altered  
1183 hydraulic regime and Tier 1 EEC=channel morphology/hydraulics, sediment transport; Inter-tier  
1184 interaction=sediment transport dynamics; E: Tier 1 EEC=biogeochemistry/thermodynamics;  
1185 Inter-tier interaction=sediment adsorption of contaminants and nutrients; F: Tier 3 EEC=White

1186 Sturgeon larvae production; Stressors=larval White Sturgeon habitat quantity and quality and  
1187 Tier 3 EEC=White Sturgeon larvae production, age-0 White Sturgeon recruitment; Inter-tier  
1188 interaction=mortality and White Sturgeon egg quality and production; Inter-tier  
1189 interaction=predation of White Sturgeon eggs by native fish and Tier 3 EECs=White Sturgeon  
1190 larvae production; Inter-tier interaction=predation of White Sturgeon larvae by native fish and  
1191 Tier 3 EECs=all; Inter-tier interactions=trophic level interactions.

1192 Fig S6. Largemouth bass (*Micropterus salmoides*) data from the Pool 13 of the Upper  
1193 Mississippi River (A, B) and the La Grange Pool of the Illinois River (C, D). The two river  
1194 reaches are roughly the same latitude, but the La Grange Pool is more limited in overwintering  
1195 habitat. Population abundance is presented in panels A and C where each point is an individual  
1196 fish cumulatively caught with standardized day time electrofishing (Ratcliff et al. 2014) in a  
1197 specific year. The dashed triangle highlights ‘missing’ >400 mm size classes since 2000 in the  
1198 La Grange Pool. Population size structure is indexed by proportional stock density (PSD) is  
1199 presented in panels B and D with the dashed line showing trends in the largest size classes over  
1200 time. Data and methodology were downloaded from the publicly available databases via the  
1201 Upper Mississippi River Restoration’s Long Term Resource Monitoring Graphical Fish Browser  
1202 [115].

1203 Fig S7. The spatial and temporal scales of the management goal, the scientific inferences needed  
1204 to inform the management goal, and that data collection needs to occur to support the inferences  
1205 for monitoring information needs identified as requiring additional data in the case study  
1206 addressing native fish biodiversity and habitat diversity in the Mississippi and Illinois rivers (see  
1207 Table S4 for additional detail). A: Tier 1 EEC=sediment transport; Stressor=altered hydraulic  
1208 regime and Tier 1 EEC=biogeochemistry/thermodynamics; Stressor=altered biogeochemical

1209 regime and Tier 1 EEC=biogeochemistry/thermodynamics; Inter-tier interaction=sediment  
1210 adsorption of contaminants and nutrients; B: Tier 2 EEC=adult native fish overwintering habitat;  
1211 Stressors=water velocity, water temperature, dissolved oxygen, sediment deposition and Tier 2  
1212 EEC=juvenile native fish habitat; Stressors=water depth, water velocity, water temperature,  
1213 dissolved oxygen, contaminants, sediment deposition and Tier 2 EEC=adult native fish spawning  
1214 habitat; Stressors=water depth, water velocity, habitat fragmentation, sediment deposition, water  
1215 temperature, dissolved oxygen, contaminants and Tier 3 EEC=adult and juvenile native fish  
1216 recruitment; Inter-tier interaction=mortality and Tier 3 EEC=all; Stressors=invasive species and  
1217 Tier 3 EEC=all; Inter-tier interaction=trophic level interactions; C: Tier 1 EEC=channel  
1218 morphology/hydraulics; Inter-tier interaction=channel forming processes; D: Tier 1 EEC=channel  
1219 morphology/hydraulics, sediment transport; Inter-tier interaction=sediment transport dynamics;  
1220 E: Tier 3 EEC=adult native fish recruitment; Stressor=adult native fish overwintering habitat  
1221 quantity and quality and Tier 3 EEC=juvenile native fish recruitment; Stressor=juvenile native  
1222 fish habitat quantity and quality and Tier 3 EEC=native fish egg quality and production;  
1223 Stressor=spawning habitat quantity and quality.

1224 Table S1. Summary of information needs identified in the Conceptual Model describing factors  
1225 affecting the recruitment of the Arkansas River Shiner in the South Canadian River, OK (Fig 4;  
1226 this publication) by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or within  
1227 Tier interactions and an assessment of the status of existing information that could be used to  
1228 address the information needs.

1229 Table S2. Summary of information needs identified in the Conceptual Model describing factors  
1230 affecting the recruitment of the Humpback Chub in the Colorado River, Arizona (Fig 6; this  
1231 publication) by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier

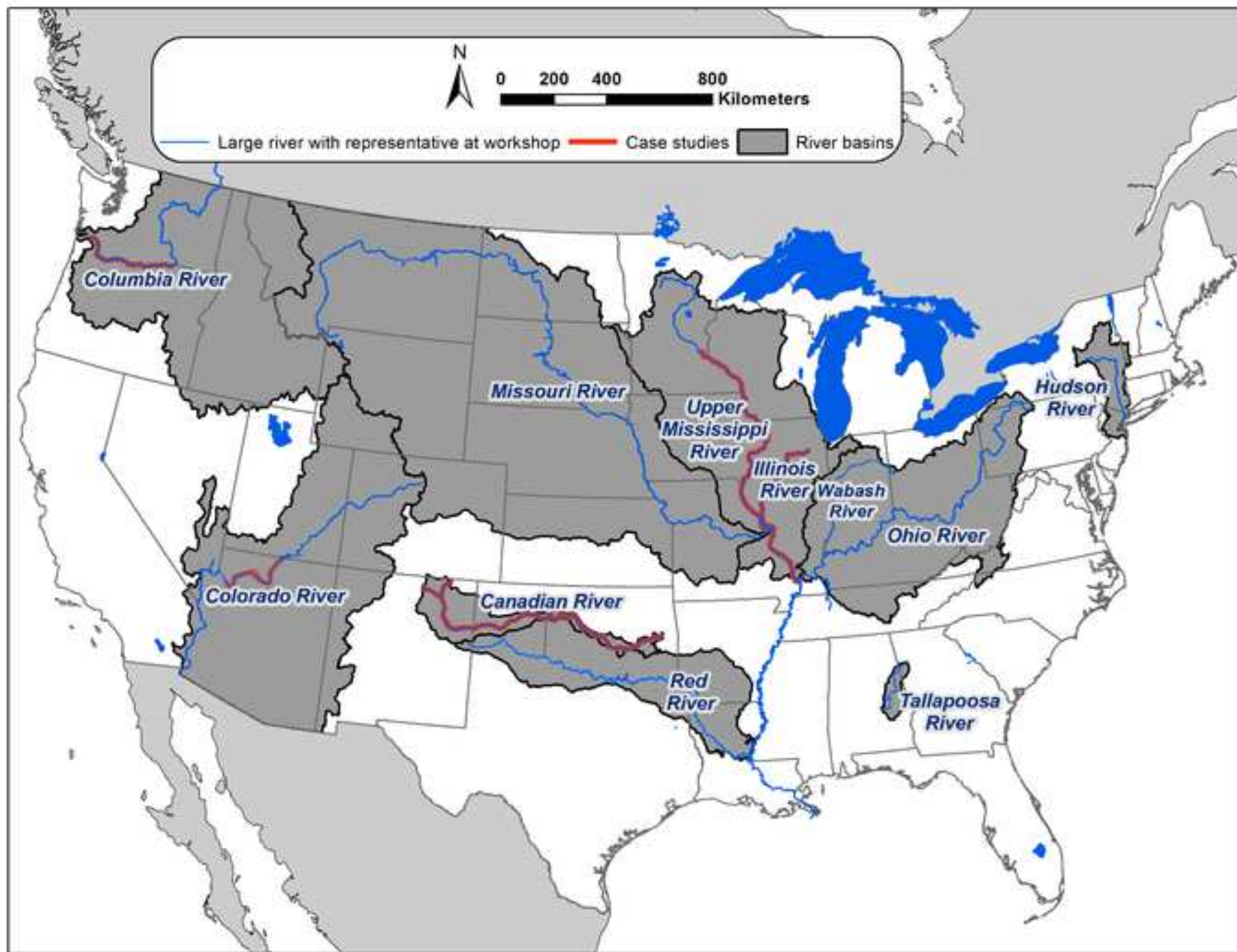
1232 interactions and an assessment of the status of existing information that could be used to address  
1233 the information needs.

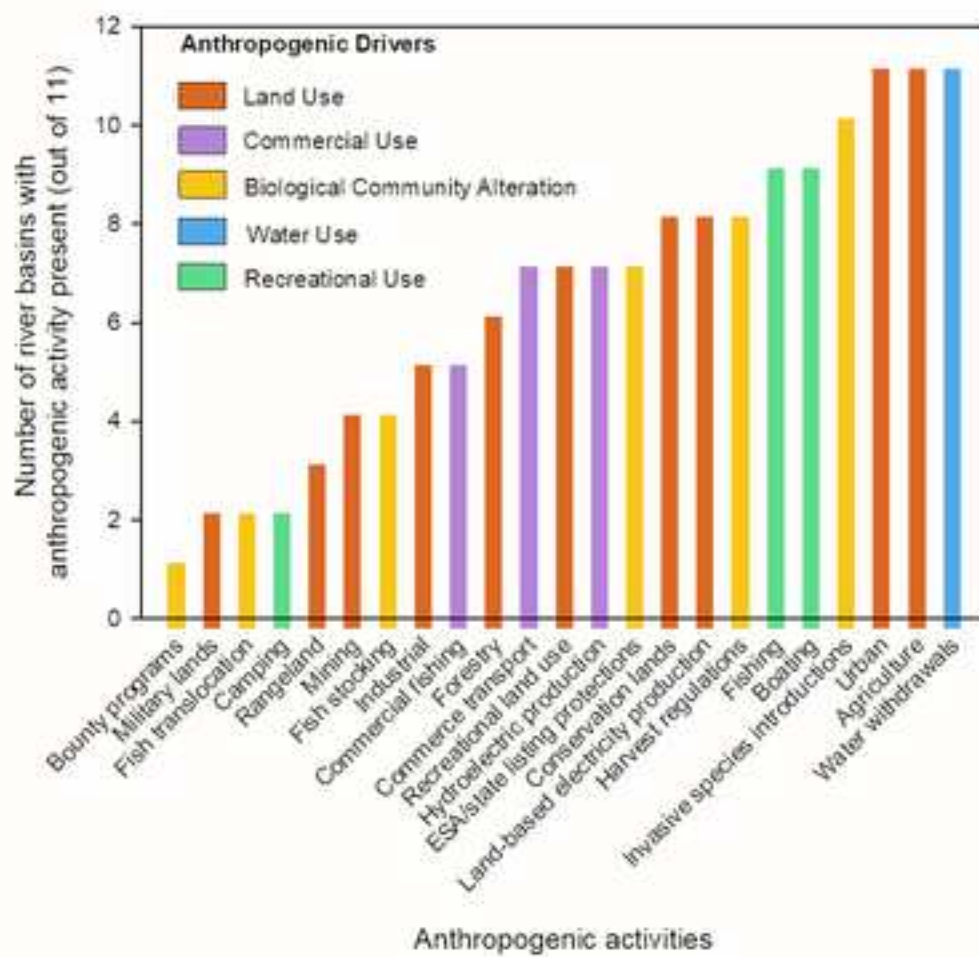
1234 Table S3. Summary of information needs identified in the Conceptual Model describing factors  
1235 affecting the recruitment of age-0 White Sturgeon in the Columbia River (Fig 7; this  
1236 publication), by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier  
1237 interactions and an assessment of the status of existing information that could be used to address  
1238 the information needs.

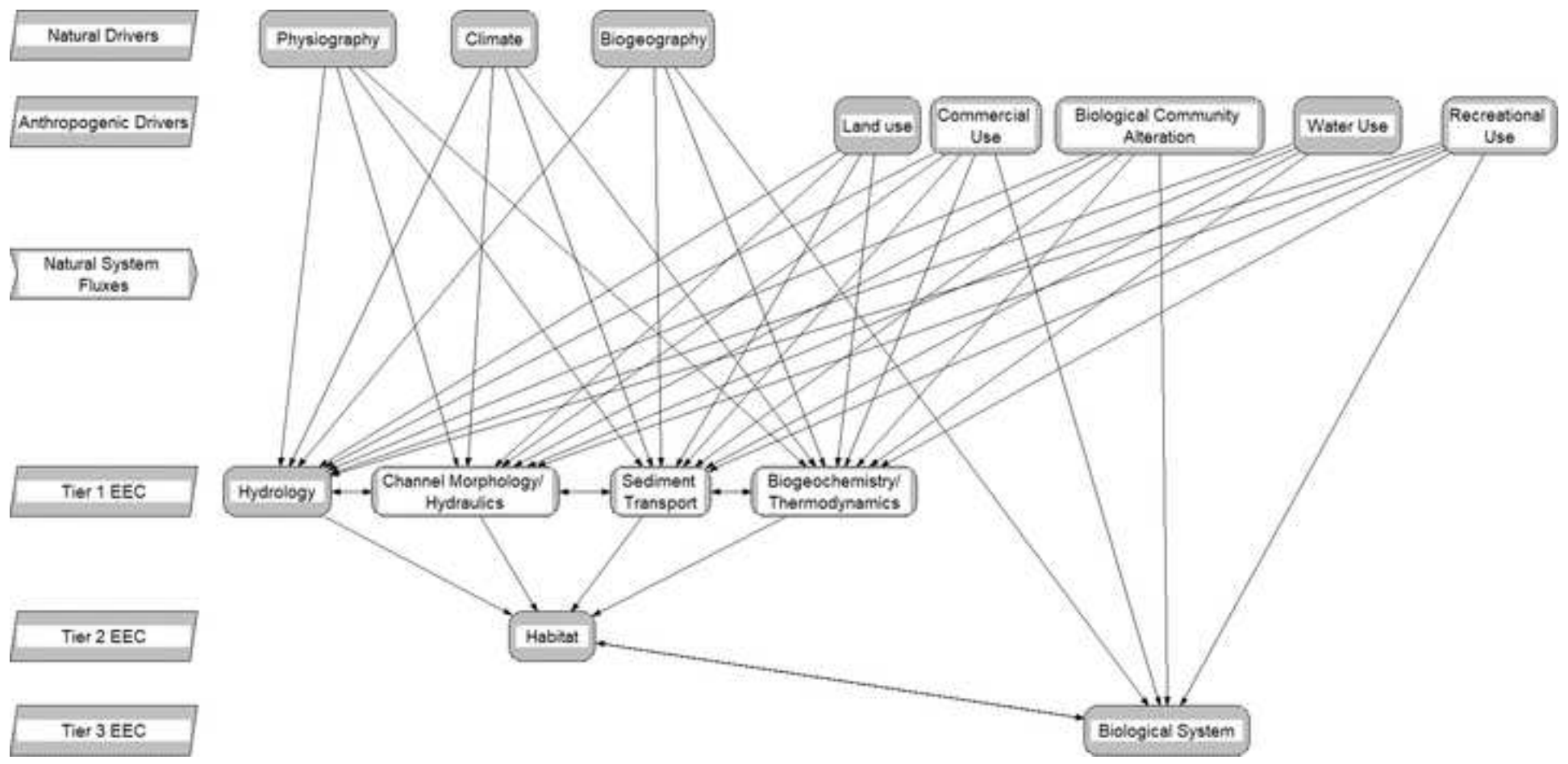
1239 Table S4. Summary of information needs identified in the Conceptual Model describing factors  
1240 affecting the restoration and maintenance of native fish biodiversity and habitat quantity and  
1241 quality in the Upper Mississippi and Illinois rivers (Fig 8; this publication), by Essential  
1242 Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier interactions and an  
1243 assessment of the status of existing information that could be used to address the information  
1244 needs.

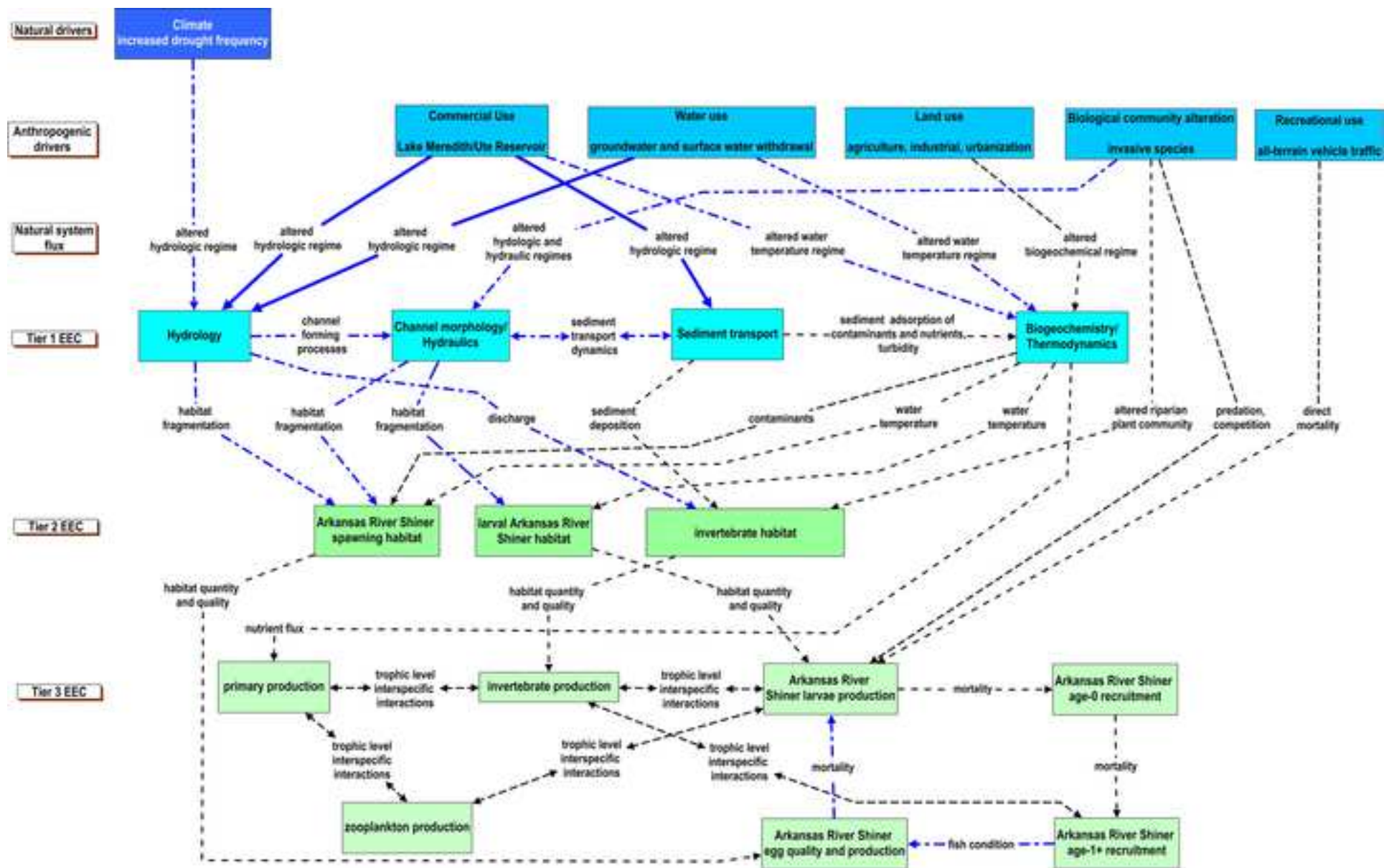
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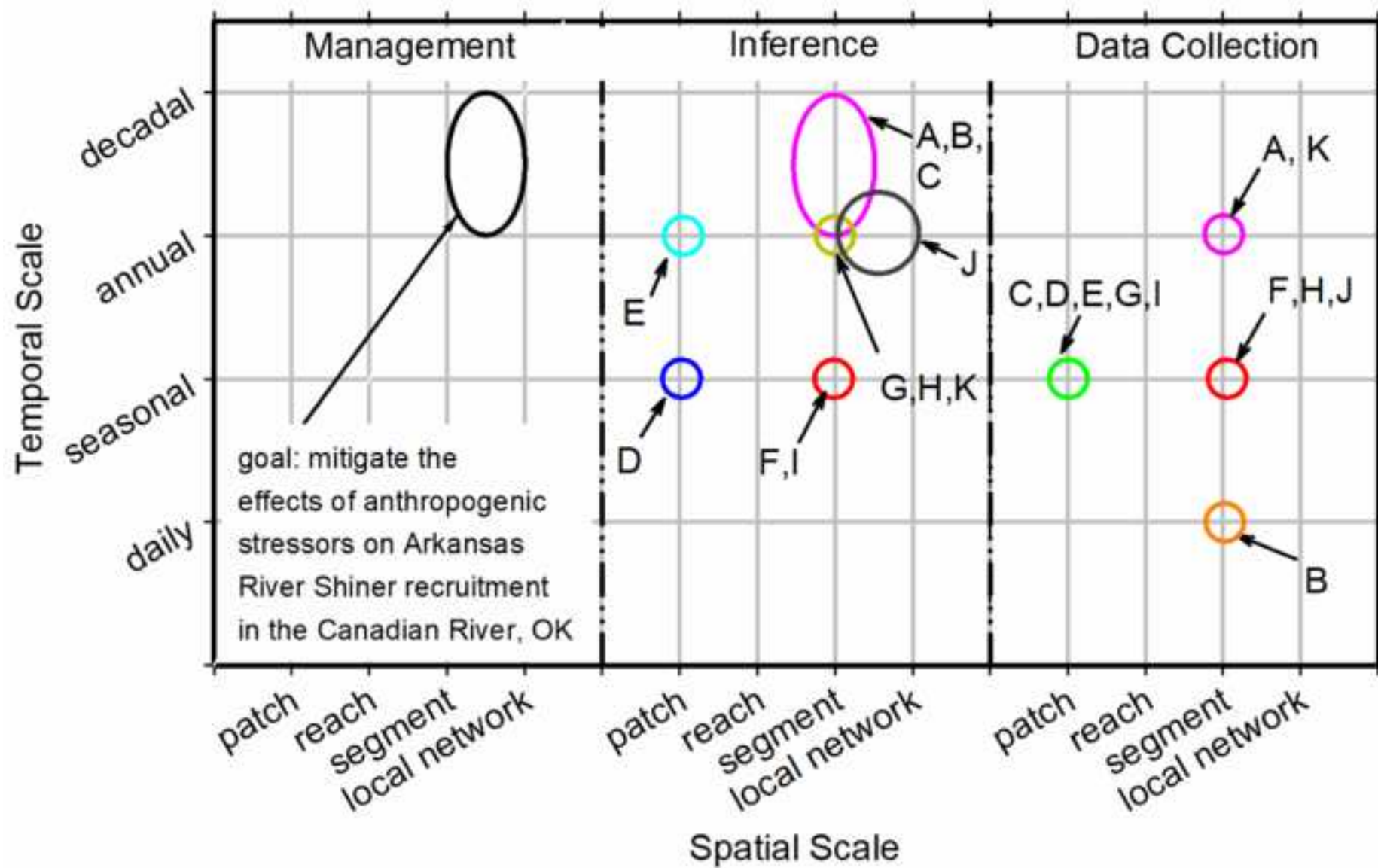


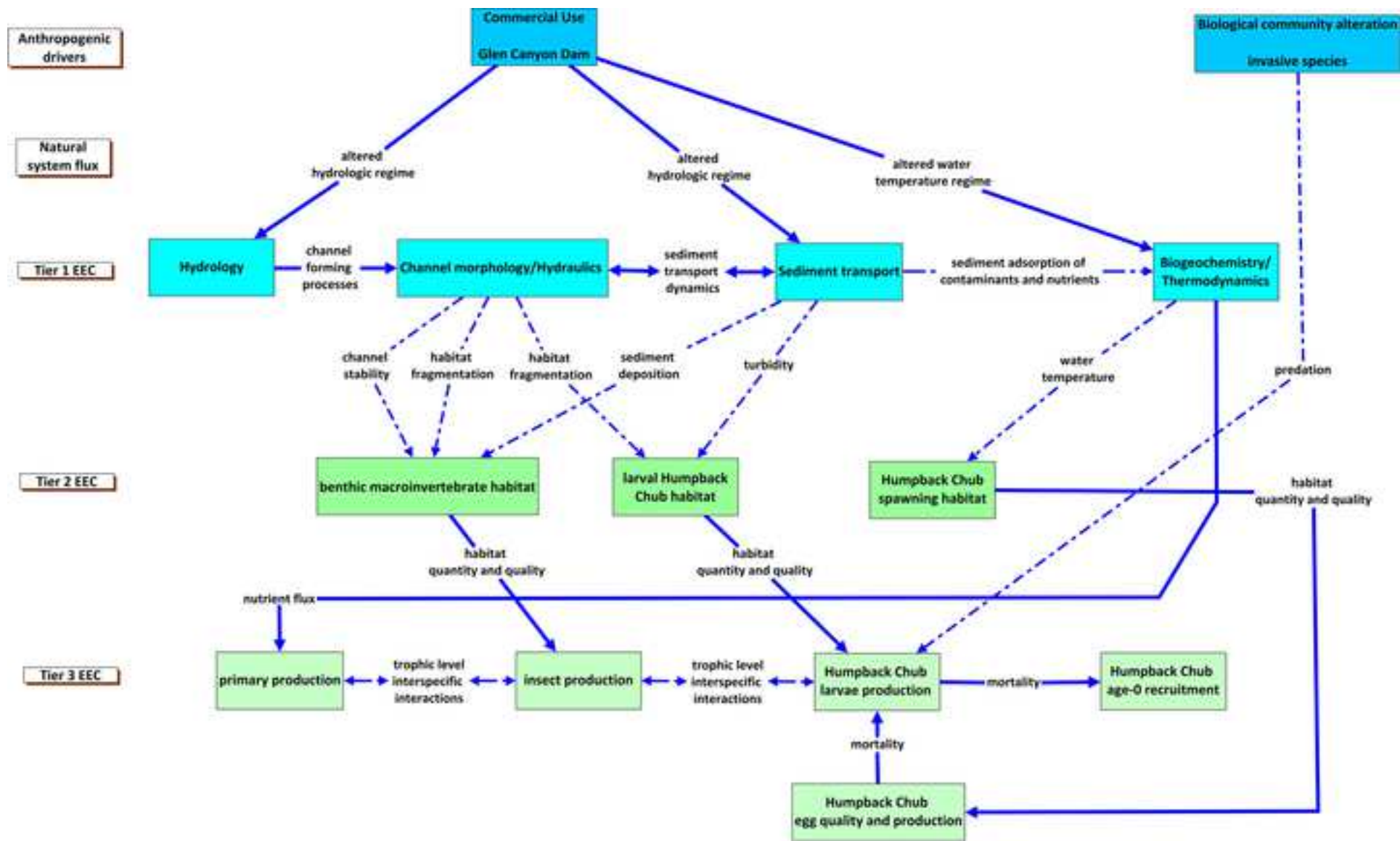


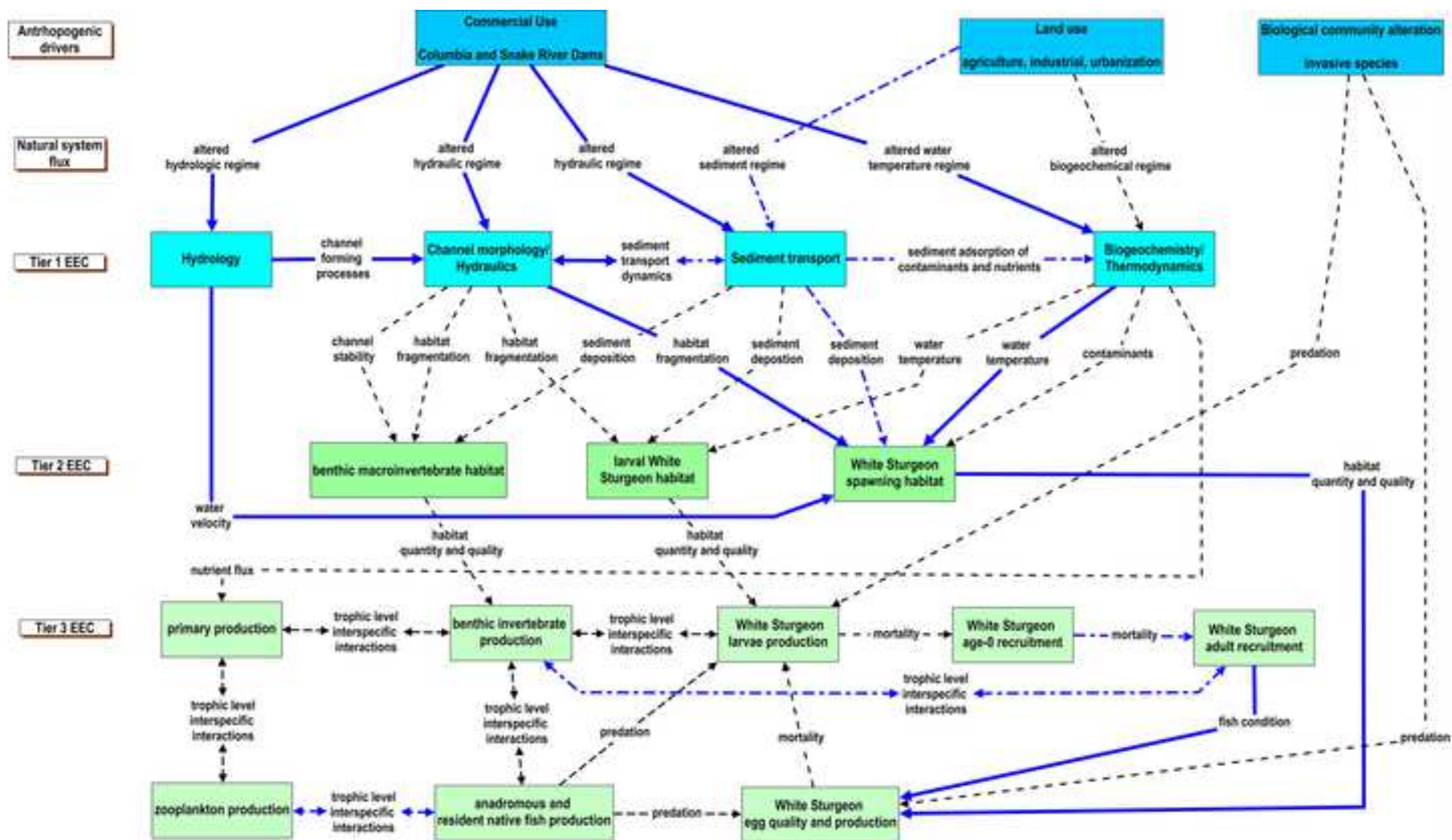


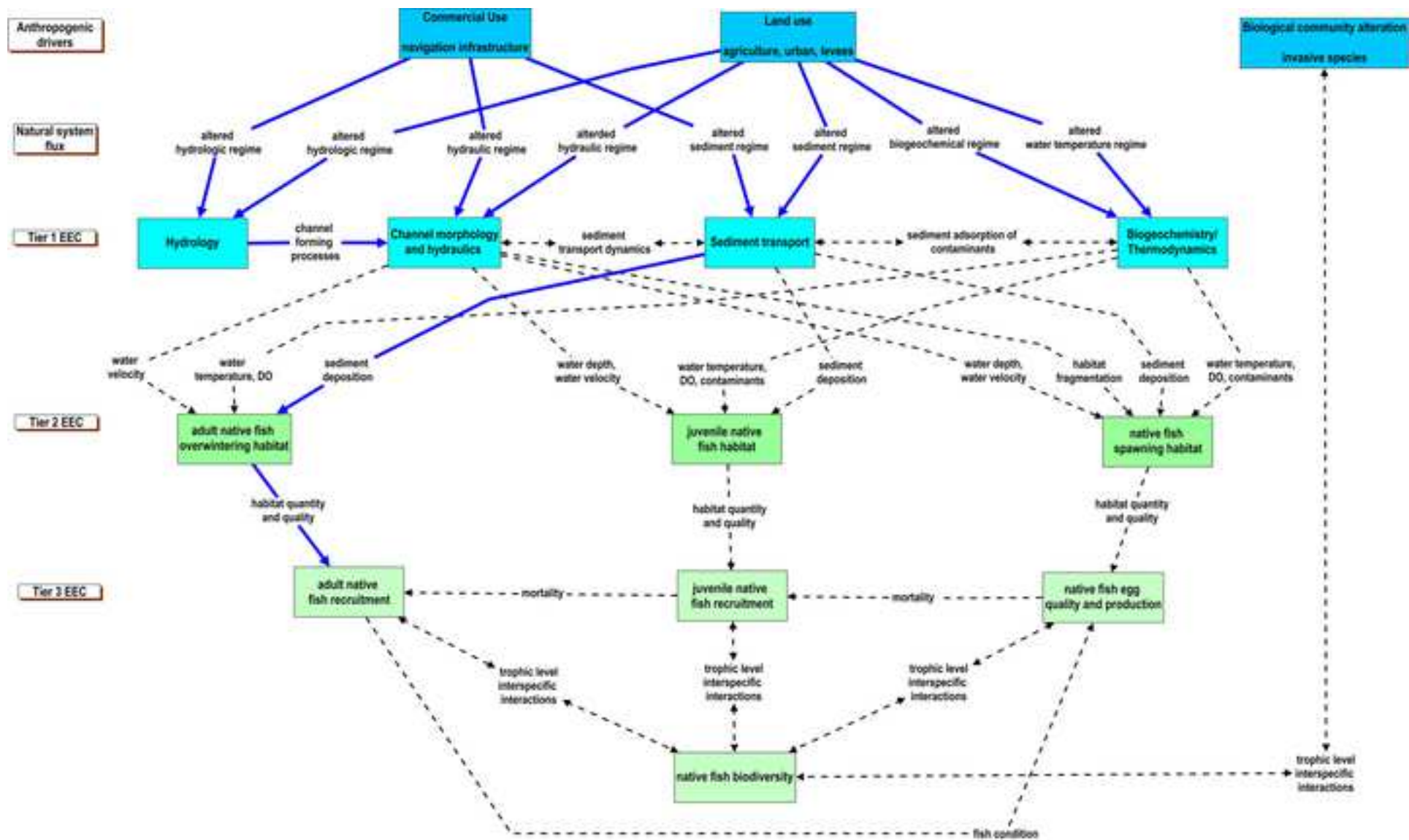
















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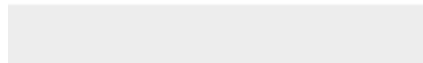




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**Supporting Information**

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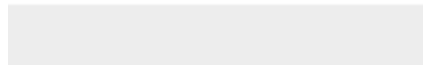




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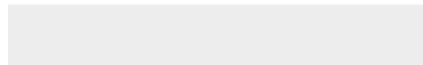




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1 Title: Identifying monitoring information needs that support the management of fish in large  
2 rivers

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31 **Abstract** – Management actions intended to benefit fish in large rivers can directly or indirectly  
32 affect multiple ecosystem components. Without consideration of the effects of management on  
33 non-target ecosystem components, unintended consequences may limit management efficacy.  
34 Monitoring can help clarify the effects of management actions, including on non-target  
35 ecosystem components, but only if data are collected to characterize key ecosystem processes  
36 that could affect the outcome. Scientists from across the U.S. convened to develop a conceptual  
37 model that would help identify monitoring information needed to better understand how natural  
38 and anthropogenic factors affect large river fishes. We applied the conceptual model to case  
39 studies in four large U.S. rivers. The application of the conceptual model indicates the model is  
40 flexible and relevant to large rivers in different geographic settings and with different  
41 management challenges. By visualizing how natural and anthropogenic drivers directly or  
42 indirectly affect cascading ecosystem tiers, our model identified critical information gaps and  
43 uncertainties that, if resolved, could inform how to best meet management objectives. Despite  
44 large differences in the physical and ecological contexts of the river systems, the case studies  
45 also demonstrated substantial commonalities in the data needed to better understand how  
46 stressors affect fish in these systems. For example, in most systems information on river  
47 discharge and water temperature were needed and available. Conversely, information regarding  
48 trophic relationships and the habitat requirements of larval fishes were generally lacking. This  
49 result suggests that there may be a common need for a better understanding of certain factors  
50 across large-river systems.

51

52 **Introduction**

53 ~~Long-term monitoring has benefited a variety of marine and freshwater ecosystems,~~  
54 ~~including large rivers like the Ohio [1, 2] and Illinois rivers [3]. Large river systems are~~  
55 ~~complex, making the development of effective monitoring programs especially difficult. Large~~  
56 ~~rivers are dynamic systems with high variability in spatio-temporal physicochemical~~  
57 ~~characteristics and biotic assemblages [4]. The inherent complexity of large rivers makes biotic~~  
58 ~~assemblages logistically difficult to sample [5] and the mechanisms of change difficult to~~  
59 ~~understand. Large rivers represent the culmination of vast stream networks and, thus, integrate~~  
60 ~~and accumulate the effects of multiple stressors at varying spatial scales [6]. The spatial and~~  
61 ~~temporal complexity associated with large rivers has hindered the identification of mechanisms~~  
62 ~~driving declining populations of aquatic species.~~Long-term monitoring has benefited a variety of  
63 marine and freshwater ecosystems, including large rivers like the Ohio [1, 2] and Illinois rivers  
64 [3]. Large-river systems are complex, making the development of effective monitoring programs  
65 especially difficult. Large rivers are dynamic systems with high variability in spatio-temporal  
66 physicochemical characteristics and biotic assemblages [4]. The inherent complexity of large  
67 rivers makes biotic assemblages logistically difficult to sample [5] and the mechanisms of  
68 change difficult to understand. Large rivers represent the culmination of vast stream networks  
69 and, thus, integrate and accumulate the effects of multiple stressors at varying spatial scales [6].  
70 The spatial and temporal complexity associated with large rivers has hindered the identification  
71 of mechanisms driving declining populations of aquatic species [7-10].~~To exaeerbate the~~  
72 ~~complexity, large rivers commonly have within-channel structural alterations (e.g., dams, river~~  
73 ~~training structures, [11]) and often exhibit legacy effects from historical land uses [12]. To deal~~



74 ~~with the complexity, some areas of aquatic science recommend monitoring be used to test the~~  
75 ~~linkages developed first through conceptual models (e.g., environmental flows, . To exacerbate~~  
76 ~~the complexity, large rivers commonly have within-channel structural alterations (e.g., dams,~~  
77 ~~river training structures, [11]) and often exhibit legacy effects from historical land uses [12]. To~~  
78 ~~deal with the complexity, some areas of aquatic science recommend monitoring be used to test~~  
79 ~~the linkages developed first through conceptual models (e.g., environmental flows, [13-15]).~~

80 Conceptual models are useful tools to help guide the design of monitoring programs  
81 ~~[16]~~[16]. The identification of questions relevant to conservation and management efforts  
82 requires some foresight and knowledge of the complexities of the system being monitored. For  
83 example, it is generally well accepted that the native range of the federally-listed Arkansas River  
84 Shiner (*Notropis girardi*) is truncated ~~[17]~~[17], though there is uncertainty surrounding the  
85 multiple threats affecting the species [18]. Reducing the uncertainty associated with the decline  
86 of the Arkansas River Shiner through the implementation of a hypothesis-driven monitoring  
87 program would facilitate confidence in moving forward with a recovery plan. This is where  
88 conceptual models are quite useful; they can serve as the foundation to guide hypothesis-driven  
89 monitoring programs [14, 16] and identify key ecosystem processes and factors that may directly  
90 or indirectly affect management outcomes [19-22].

91 Understanding factors affecting the status and trends of fishes is of interest to multiple  
92 stakeholder groups across multiple jurisdictions. Fishes provide economic benefits to businesses  
93 that serve recreational interests, commercial and recreational fishers, tribal members for whom  
94 fish are an integral part of their cultural identity ~~[23]~~[23], and to local and state governments who  
95 derive revenue from these activities. Fish populations are affected by the integration of physical  
96 habitat, water quality, environmental contamination, habitat fragmentation, and overall

97 ecosystem productivity [24-27]. Consequently, fish are often the focus of management and  
98 monitoring programs (e.g., [28]). However, because fish integrate the effects of so many  
99 components of the ecosystem, the success of efforts to manage fishes can be affected by  
100 unintended consequences of mitigation on factors not directly targeted by the actions. Without  
101 consideration of the effects of management on non-target ecosystem components, unintended  
102 consequences may limit management efficacy.

103 Our goal is to demonstrate how a structured, yet flexible, conceptual model (CM) can be  
104 used to identify the types of monitoring information needed to understand the range of factors  
105 affecting large-river fishes. Our CM includes a hierarchically structured conceptualization of  
106 ecosystem characteristics based on CMs originally developed by Harwell, Myers (29) and  
107 elaborated by ~~Jacobson and Berkley (30)~~, Jacobson and Berkley (30). We chose to incorporate  
108 the tiered conceptualization of ecosystem characteristics proposed by ~~Jacobson and Berkley~~  
109 ~~(30)~~ Jacobson and Berkley (30) in part because it allows users to define their own biotic or abiotic  
110 interests. In this paper, we discuss the structure and development of the CM. We apply the CM to  
111 case studies to illustrate the flexibility and applicability of this approach and use it to identify  
112 monitoring information needs specific to disparate management goals. More specifically, for  
113 each case study, we use the CM to hypothesize how human activities affect fish populations and  
114 then identify information needs required to evaluate the hypothesized relationships. We then  
115 posit the spatial and temporal scales of the management goal addressed in the conceptual model,  
116 inferences needed to inform the management goal, and data collection requirements needed to  
117 make the inferences.

118

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119 **Conceptual Model**

120 **Overview of Approach**

121 Since 2012, scientists working on large rivers across the United States have participated  
122 in a forum intended to improve our understanding of large-river ecosystems. The collaborative  
123 forum has worked to identify best practices of long-term monitoring programs [31] and evaluate  
124 trends in fish assemblages across rivers [32]. As this group of scientists moved toward linking  
125 changes in fish populations and assemblages to human activities, there was a need to develop a  
126 process to help identify and prioritize the information needed to assess trends in large river  
127 fishes. To that end, a workshop was convened in Hood River, Oregon in May 2017, to jointly  
128 adapt, apply, and qualitatively evaluate a conceptual model for developing hypotheses that detail  
129 stressors affecting fishes arising from natural and anthropogenic sources ~~[33]~~[33].

130 Our general approach was to first identify human activities that affect large-river fishes  
131 and then hypothesize how the activities related to physical and chemical factors and biological  
132 communities. Prior to the workshop, we elicited opinion from experts that comprise a U.S.  
133 Geological Survey (USGS) led forum on large river monitoring about important anthropogenic  
134 activities that could affect fish populations or communities in the river basins they work in. (Fig  
135 1). We summarized the information from this exercise and grouped the anthropogenic activities  
136 into driver categories (Fig 2) and proposed a general form of the CM. We then disseminated the  
137 information to the experts prior to the workshop.

138 Fig 1. Map of rivers and watersheds represented by scientists that convened to develop a  
139 conceptual model that ~~would depict~~depicts how natural and anthropogenic drivers interact with

140 habitats, biological systems, and fish in large rivers. River segments where we conducted case  
141 studies that applied the conceptual model to identify monitoring information needs associated  
142 with management goals are highlighted in red.

143 ~~Fig 2. The types of anthropogenic activities affecting large river fishes across 11 river systems as~~  
144 ~~identified from a query to expert participants of a workshop convened to develop a conceptual~~  
145 ~~model that would depict how natural and anthropogenic drivers interact with habitats, biological~~  
146 ~~systems, and fish in large rivers. Meeting participants included researchers~~ Fig 2. The results of a  
147 query to scientists from the Canadian, Colorado, Columbia, Hudson, Illinois, Ohio, Missouri,  
148 Red, Tallapoosa, Upper Mississippi, and Wabash Rivers, U.S. to identify anthropogenic  
149 activities that affect large-river fishes in the river systems they represent. Anthropogenic  
150 activities were classified into five ~~anthropogenic~~ driver categories.

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151 During the workshop we discussed and refined the CM form (Fig 3). We then had  
152 representatives from each river system represented at the workshop choose a management goal  
153 to address. Then, through a facilitated discussion led primarily by the representative of the river  
154 system being addressed, we 1) elaborated tiered conceptualizations of ecosystem characteristics  
155 to reflect the large-river systems and management goals being examined, 2) used knowledge of  
156 the fish species' life history and population bottlenecks to relate biological ecosystem  
157 characteristics to habitat requirements, 3) hypothesized pathways describing how anthropogenic  
158 and natural drivers affect large-river fish populations either indirectly (i.e.g., effects on flow  
159 regime, habitat, trophic resources, etc.) or directly (e.g., competition with invasive species), and  
160 4) hypothesized interactions within ecosystem characteristic tiers that could affect the

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161 management goal. Based on this exercise, we chose four case studies to refine for use in this  
162 manuscript (Fig 1).

163 Fig 3. Tiered hierarchical conceptualization of how anthropogenic and natural drivers relate to  
164 physical and biological components of large-river ecosystems. Essential ecosystem  
165 characteristics (EECs) are groupings of ecosystem components. Tier 1 EECs represent physical  
166 and chemical effects; fundamental measures of process that are directly affected by  
167 anthropogenic and natural drivers. Tier 2 EECs represent a broad habitat category that is  
168 intended to encompass the physical, chemical, and biological components of the riverine habitats  
169 that influence reproduction, growth, and survival of biotic communities. The Tier 3 EEC  
170 represent components of the biological systems that respond to changes in the hierarchical  
171 components of the conceptual model.

172 After the workshop, we held a series of conference calls with workshop participants with  
173 expertise in the selected case studies to refine all aspects of the CMs and associated information.  
174 During the calls, we started with the CM from the workshop and discussed and clarified CM  
175 components, pathways, and inter-tier interactions. We then characterized whether, based on the  
176 expert knowledge of workshop participants, there was a strong, moderate, or weak understanding  
177 of the pathways and interactions. ~~We then developed a~~ list of the information needed to  
178 understand the relationships described in the CM ~~was developed~~. We then had the case study  
179 leader classify whether the data required to understand the information needs were available,  
180 insufficient, or not available. For information needs that were classified as insufficient or not

181 available, we ~~then~~ characterized the spatial and temporal scales at which data should be collected  
182 to make inferences that support the evaluation of management goals.

183 We then encouraged representatives from each basin to share the CM and the case study  
184 narrative with other experts familiar with the river system and management goal. This outreach  
185 took several forms including sharing the CM with working groups tasked with implementing the  
186 management goal, discussions with peers familiar with the management goal, and presenting the  
187 CM at regional conferences. The intent was to garner opinions from outside the workshop  
188 participants. If needed, the CMs incorporated the feedback received.

### 189 **Hierarchical structure of Conceptual Model**

190 Our CM is a hierarchical conceptualization of how anthropogenic and natural drivers  
191 relate to multiple tiers representing the physical and biological components of large-river  
192 ecosystems (Fig 3). Natural drivers included in the CM were physiographic, climatic, and  
193 biogeographic factors that control fluxes of water, mass, energy, and genetic information in a  
194 watershed [30][30]. The physiographic factors, such as lithology, soils, and watershed  
195 topography, exert control on water, sediment, and geochemical fluxes (e.g., nutrients) into the  
196 river corridor. Physiography is generally static over time frames of decades to centuries. Climate  
197 controls fluxes of atmospheric energy and moisture into the watershed. Unlike physiography,  
198 climate is more likely ~~variable to vary~~ over relatively shorter temporal scales. Biogeography  
199 describes the native organism assemblage in the watershed (e.g., [34][34]) and the natural flux of  
200 genetic information due to immigrations, emigrations, mutations, and extinctions. Changes  
201 arising from the biogeography driver includes altered spatial distribution of organisms within the

202 watershed, which, in turn, may alter the effects of natural system regimes on the river corridor.  
203 For example, natural variation of the type and distribution of vegetation can affect the time series  
204 and magnitude of runoff events ~~{30}~~[30].

205 We created five categories of anthropogenic drivers to characterize a range of human  
206 activities that affect large rivers: land use, commercial use, biological community  
207 ~~manipulation~~alteration, water use, and recreation (Fig 2). The land-use category is intended to  
208 reflect different ways humans use landscape resources that affect large rivers. We defined  
209 commercial use as the use of river resources for marketable enterprises that did not involve water  
210 removal or transfer. We included biological community alteration to represent the intentional or  
211 non-intentional human alteration or manipulation of the river’s biological community (e.g.,  
212 introductions of non-native fish). Recreational use was defined as the use of river resources for  
213 leisure activities (e.g., fishing, boating). We considered water use a direct commercial or non-  
214 commercial use of river water that involved the removal or transfer of water.

215 Our CM includes hierarchically structured essential ecosystem characteristics (EEC),  
216 originally developed by Harwell, Myers (29) and described in detail by ~~Jacobson and Berkley~~  
217 ~~(30)~~Jacobson and Berkley (30). Briefly, EECs are characteristics that can be classified into  
218 similar groups based on the way they link to biological endpoints ~~{30}~~[30]. Tier 1 EECs are  
219 measurable characteristics that describe processes that can significantly alter the morphological  
220 or chemical characteristics within a river channel. The Tier 1 categories we considered were 1)  
221 ~~Hydrology~~hydrology, 2) ~~Channel Morphology/Hydraulics~~channel morphology/hydraulics, 3)  
222 ~~Sediments~~sediment transport, and 4)  
223 ~~Biogeochemistry/Thermodynamics~~biogeochemistry/thermodynamics. Tier 2 EECs are broadly  
224 described as physicochemical or biological components of “habitat” that are hypothesized to

225 affect (e.g., growth, survival, reproduction, ~~{35}~~[35]) fish populations or assemblages. Lastly,  
226 Tier 3 EECs represent components of the hypothesized biological system that are affected by the  
227 cascading (e.g., degradation of egg quality caused by increases in sediment deposition) or direct  
228 (e.g., predation by invasive species) effects of anthropogenic and natural drivers. Tier 2  
229 characteristics are particularly important because these are the factors that can be examined at  
230 scales most often sampled by fisheries managers (~~e.g., Smallmouth Bass *Micropterus dolomieu*,~~  
231 ~~{36}~~[36]). The specific components that comprise Tier 2 and 3 EECs are flexible and can be  
232 adapted and elaborated depending on the river system and specific management goal being  
233 addressed.

234 We retained aspects of the approach taken by ~~Jacobson and Berkley (30)~~Jacobson and  
235 Berkley (30) with respect to how our model represents interactions between drivers and EECs,  
236 but with key differences. Since we were interested in representing how human activities affect  
237 large river ecosystems, our approach acknowledges that anthropogenic and natural drivers  
238 interact and alter the expected characteristics of Tier 1 EECs. ~~Similar to Jacobson and Berkley~~  
239 ~~(30)~~Similar to Jacobson and Berkley (30), our model depicts a stress associated with a natural or  
240 anthropogenic driver to Tier 1 EECs as fluxes in natural system regimes that alter the frequency,  
241 magnitude, duration, timing, or rate of change in natural systems or by the imposition of a hard-  
242 structural constraint on channel form. The natural system regimes considered in our CM were  
243 hydraulic, hydrologic, sediment, temperature, light, and biogeochemistry. Graphically, the  
244 natural system fluxes were represented by arrows connecting anthropogenic and natural drivers  
245 to Tier 1 EECs. Similarly, hypothesized pathways between EECs, that depict the expression of  
246 the cascading effects of anthropogenic and natural drivers, and interaction within EECs were  
247 depicted as arrows. ~~A~~For example, fragmentation of river systems resulting from altered



248 hydrologic and/or hydraulic regimes caused by dams, weirs, levees, and other factors are  
249 frequently cited sources of stress to large-river fishes [37]. Fragmentation can prevent fish from  
250 migrating and/or dispersing through their natural reproductive ranges and from accessing critical  
251 habitats [38]. To depict a scenario where the presence of a dam is altering hydrologic and/or  
252 hydraulic regimes resulting in habitat fragmentation, the CM would show an arrow from an  
253 anthropogenic stress (i.e., dam as a commercial activity) to a Tier 1 EEC (e.g., channel  
254 morphology/hydraulics) that would depict a natural system flux (e.g., altered hydrologic and/or  
255 hydraulic regime) that would then manifest as a stress caused by habitat fragmentation depicted  
256 by an arrow between the Tier 1 EEC and a Tier 2 EEC (e.g. habitat) that would then manifest as  
257 an effect on a Tier 3 component, shown by an arrow between Tier 2 and Tier 3. All stress  
258 pathways and interactions were classified with respect to the strength of understanding of the  
259 relationships based on expert opinion. Arrows with solid blue lines depict a strong understanding  
260 of the relationship, dotted-dashed blue lines represent a moderate understanding of the  
261 relationship, and with a black dashed line represent a weak understanding of the relationship.

## 262 **Spatial and temporal context**

263 The successful characterization of how human activities influence large-river fishes is  
264 dependent upon integrated concepts of scale. Fish distributions in rivers can vary spatially within  
265 river basins in relation to naturally occurring and human induced landscape characteristics [32].  
266 Fish distributions can also vary seasonally, annually, and over longer times in response to  
267 changing environmental conditions [37,39]. Consequently, the spatial and temporal scope of fish  
268 management goals often varies within and between large-river systems and agencies. For data

269 collected by monitoring programs to have the highest relevance, the spatial and temporal scales  
270 appropriate for scientific investigation and management must also be time and geographic-  
271 context specific. For example, the management of White Sturgeon (*Acipenser transmontanus*) in  
272 the Columbia River varies by reservoir or river segment and season [38, 39, 40, 41]. The effects of  
273 hydropower development on White Sturgeon vary spatially and temporally as well, so the spatial  
274 and temporal context of the data needed to understand the effects needs to be considered. For  
275 instance, hydropower peaking operations, that can vary by dam and season, affect river discharge  
276 in a river reach on a diel and even hourly basis [40, 42], whereas water storage and other  
277 management actions can affect seasonal discharges over a broader geographic scale [38], [40].  
278 Understanding the spatial and temporal context needed to inform management will help ensure  
279 relevant information is collected.

280 We considered spatial and temporal resolution in our CMs. We defined spatial extent as :

281 ~~Local Network~~local network – synonymous with Hydrologic Unit Code (HUC) 2 basins [41,  
282 42, 43, 44]; ~~Segment~~segment – the portion of a river between two major tributary confluences  
283 [43], [45] or other hydrogeomorphic features [44]; ~~Reach – the length of river occurring between~~  
284 ~~breaks in channel slope caused by man-made dams or other hydrogeomorphic features~~ [43];  
285 ~~Patch~~[46]; reach - the length of river occurring between breaks in channel slope caused by man-  
286 made dams or other hydrogeomorphic features [45]; patch – an area used by an organism (e.g.,  
287 for reproduction or resource attainment) that can vary both spatially and temporally depending  
288 on the species of interest [45, 46, 47, 48]. For our purposes, the spatial scales considered are  
289 nested such that segments occur within local networks, reaches occur within segments, and  
290 patches occur at the sub-reach scale. Temporal units considered were daily, seasonal, annual, and

291 decadal. The temporal units were used to denote both the scale of inferences needed to support  
292 the management goal and the scale at which data should be collected to inform the inferences.

### 293 **Case Studies**

294 We applied the CM to four case studies. For each, we followed the pathways of stress  
295 from Tier 1 EECs to the biological endpoint associated with the management goal to identify  
296 information needs. We then characterized the spatial and temporal scales of the management  
297 goal, the scientific inferences needed to inform the management goal, and that data collection  
298 needs to occur to support the inferences for monitoring information needs identified as requiring  
299 additional data for each of the case studies. To summarize similarities across case studies, we  
300 generalized the stressors and inter- tier interactions identified in the case studies and then  
301 summarize the similarities by EEC tier. More context for the river systems characterized in the  
302 case studies can be found in Appendix S1.

### 303 **South Canadian River**

304 ~~The South Canadian River is the mainstem river of the Canadian River basin (south-~~  
305 ~~central U.S., Fig 1). The basin occupies a significant west-east climate gradient with~~  
306 ~~precipitation ranging from 40 to 145 cm/yr [47]. Land use in the basin is primarily cropland or~~  
307 ~~pasture that transitions to the urban area near Oklahoma City. Three major reservoirs on the~~  
308 ~~South Canadian River have significantly altered the river flow patterns, particularly the~~  
309 ~~frequency and magnitude of high flow events, and the number of zero flow days (Fig S1).~~  
310 ~~Multiyear to decadal droughts are not uncommon in the region [48], and groundwater pumping,~~

311 particularly in the upper basin, has severed groundwater connections in many areas transforming  
312 the fish assemblage [49]. Further, groundwater pumping in the alluvial aquifer has decreased  
313 stream baseflows within this region [50, 51]. The rivers of the Great Plains are characterized  
314 by extreme physicochemical conditions (i.e., water temperatures 4–40°C; salinities greater than  
315 ocean water) and extensive flooding and extended periods of drought, and native fishes are well  
316 adapted to those extremes. Pelagic broadcast spawning minnows (i.e., pelagophils) belong to a  
317 reproductive guild of diminutive fishes that are emblematic of these stream systems. Of the  
318 approximately 20 species in this reproductive guild, 13 are of conservation concern; the status of  
319 the remaining seven species is poorly understood [18, 52]. Native populations of the federally-  
320 threatened Arkansas River Shiner are believed to be restricted to two fragmented portions of the  
321 South Canadian River [53,49].

322 The Arkansas River Shiner is hypothesized to be affected by several anthropogenic  
323 activities that primarily affect water quality and quantity (Fig 4). Three reservoirs on the South  
324 Canadian River have altered discharge patterns (Fig S1), and fragmented river habitats. Two  
325 known native populations of Arkansas River Shiner occupy the two remaining river segments of  
326 sufficient length and complexity to allow eggs to drift the time required to successfully complete  
327 their early life history. Small impoundments for agriculture use, road crossings, groundwater  
328 pumping and other local water extractions (e.g., oil and gas) threaten to further fragment existing  
329 habitat. Fragmentation could also be problematic for upstream fish migrations; there is some  
330 evidence that Arkansas River Shiners migrate upstream to spawn to achieve adequate drift  
331 distances for their offspring [54],[50]. It has also been speculated that this species might benefit  
332 from access to floodplain habitats [55][51], but we are unaware of efforts to examine that  
333 hypothesis. Changes in the flow patterns may also relate to the expansion of salt cedar *Tamarix*

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334 spp. and other non-native riparian species that constrain the channel and inhibit channel habitat  
335 complexity [~~56, 57~~52, 53]. Changes to the riparian corridor can also alter the availability of  
336 drifting invertebrates ~~available~~ for Arkansas River Shiner feeding (i.e., Coleoptera,  
337 Hymenoptera; ~~58~~54). Channel complexity acts to slow the transport of eggs [5349] and may  
338 prevent eggs from being washed into downstream reservoirs where survival is hypothesized to be  
339 extremely low. Climate change is expected to increase the intensity and frequency of drought  
340 events within this region [~~59, 60~~55, 56], which may exacerbate habitat fragmentation, promote  
341 ATV all-terrain vehicle traffic within the river channel causing direct mortality on stranded fish  
342 (Gene Wilde, Texas Tech University, Personal Comm.), and concentrate contaminants and  
343 salinity [6457]. The tolerances of Arkansas River Shiner to salinity concentrations and many  
344 other contaminants are unknown (see Table 3S1; [18]). Lastly, introductions of non-native fishes  
345 ~~via bait buckets~~ have occurred within the basin. The primary concern ~~has related to~~ the  
346 presence of Red River Shiner (*Notropis bairdi*) because it is suspected to reproduce in a similar  
347 manner and be a possible competitor to the Arkansas River Shiner [6457].

348 Fig 4. Conceptual model describing the relationship of natural and anthropogenic drivers to  
349 essential ecosystem characteristics (EECs) affecting the recruitment of the Arkansas River  
350 Shiner in the South Canadian River in New Mexico, Texas, and Oklahoma. Essential ecosystem  
351 characteristics are groupings of ecosystem components. Tier 1 EECs represent physical and  
352 chemical effects; fundamental measures of process that are directly affected by anthropogenic  
353 and natural drivers. Tier 2 EECs represent a broad habitat category that is intended to encompass  
354 the physical, chemical, and biological components of the riverine habitats that influence  
355 reproduction, growth, and survival of biotic communities. The Tier 3 EECs represent

356 components of the biological systems that respond to changes in the hierarchical components of  
357 the conceptual model. The strength of our understanding of how natural and anthropogenic  
358 drivers interact with habitats, biological systems, and fish in large rivers is represented by the  
359 different types of lines in the figure. Solid blue lines depict a strong understanding of the  
360 relationship, the dotted-dashed blue line represents a moderate understanding of the relationship,  
361 and the black dashed line represents a weak understanding of the relationship. The different  
362 types of lines also represent the strength of our understanding of within EEC-tier relationships.

363         The results of the CM exercise that characterized factors affecting the Arkansas River  
364 Shiner in the South Canadian River suggested the critical life-history bottlenecks for the  
365 Arkansas River Shiner are successful spawning and recruitment to the first year. Impediments  
366 that limit our understanding of factors that lead to successful spawning and recruitment included  
367 the effects of channel morphology and hydraulics on the quality and quantity of larval rearing  
368 habitat, and subsequent effects on larval production (Table S1). Water use and other drivers  
369 occurring at relatively coarse spatial and temporal scales are the hypothesized drivers related to  
370 degradation of reproductive habitat for the Arkansas River Shiner (Fig 5). A temporal lag in  
371 responses at finer scales (i.e., improved habitat) would be anticipated with management actions  
372 at these coarser spatial scales (i.e.g., water releases from dams); though, providing connectivity  
373 via minimal water releases would occur relatively quickly. Although there are gages on the  
374 South Canadian River, the spacing of the gages is not sufficient to have a full understanding of  
375 flow patterns between the gages given the semi-arid nature of the basin and potential for reaches  
376 to be affected by water withdrawals such as groundwater pumping. Our understanding of the  
377 species life history is well established; however, the effects of human pressures on the species

378 and associated habitat has not been well studied (i.e., production, survival). ~~As indicated in Fig 4,~~  
379 ~~the only stress pathway that was characterized as being well understood was from land use~~  
380 ~~stressors to Tier 1 processes. As those~~As stressors propagate through Tier ~~1 to Tier 2~~ and Tier 3,  
381 the level of uncertainty ~~increases~~increased such that it is not possible to define a preferred  
382 hypothesis for Arkansas River Shiner recruitment failure. The status of ~~much existing~~  
383 information ~~was needed to understand the hypothesized stress pathways and interactions was~~  
384 mostly characterized as insufficient or not available (Table S1).

385 Fig 5. The spatial and temporal scales of the management goal, the scientific inferences needed  
386 to inform the management goal, and that data collection needs to occur to support the inferences  
387 for monitoring information needs identified as requiring additional data in the case study  
388 addressing the recruitment of the Arkansas River Shiner in the Canadian River, Oklahoma (see  
389 Table S1 for additional detail). A: Tier 1 EEC=~~Channel~~channel  
390 morphology/~~Hydraulics~~hydraulics; Stressor=altered hydraulic regime; B: Tier 1  
391 EEC=~~Biogeochemistry/Thermodynamics~~biogeochemistry/thermodynamics; Stressor=altered  
392 water temperature regime; C: Tier 1  
393 EEC=~~Biogeochemistry/Thermodynamics~~biogeochemistry/thermodynamics; Stressor=altered  
394 biogeochemical regime; D: Tier 2 EEC=Arkansas River Shiner spawning habitat;  
395 Stressors=contaminants, water temperature, habitat fragmentation; E: Tier 2 EEC=larval  
396 Arkansas River Shiner habitat, Stressors=water temperature, habitat fragmentation and Tier 2  
397 EEC=invertebrate habitat, Stressors=altered riparian plant community, discharge, sediment  
398 deposition; F: Tier 3 EEC=primary production, Stressor = nutrient flux; G: Tier 3  
399 EEC=invertebrate production; Stressor=invertebrate habitat quantity and quality and Tier 3

400 EEC=Arkansas River Shiner larvae production, Stressor=predation by invasive species; H:Tier 1  
401 EEC= ~~Biogeochemistry/Thermodynamics~~biogeochemistry/thermodynamics; Inter-tier  
402 interaction= Sediment adsorption of contaminants and nutrients and Tier 3 EEC=Arkansas River  
403 Shiner larvae production, Stressors=Arkansas River Shiner larvae habitat quantity and quality  
404 and Tier 3 EEC=Arkansas River Shiner age-0 recruitment; Inter-tier interaction=Arkansas River  
405 Shiner larvae mortality and Tier 3 EEC=Arkansas River Shiner age-1+ recruitment, Inter-tier  
406 interaction= Arkansas River Shiner age-0 mortality and Tier 3 EEC=all, Inter-tier  
407 interaction=trophic level interactions; I:Arkansas River Shiner larvae production; Stressor=  
408 direct mortality from recreational use (i.e., ~~ATV~~all-terrain vehicle and in-river traffic); J:Tier 3  
409 EEC=Arkansas River Shiner egg quality and production; Stressor=Arkansas River Shiner  
410 spawning habitat quantity and quality; K:Tier 3 EEC=~~Larval~~-Arkansas River Shiner larvae  
411 production; Inter-tier interaction=Arkansas River Shiner egg mortality.

## 412 **Colorado River**

413 ~~The Colorado River flows 2,330 km from its origin in Colorado to its confluence with the~~  
414 ~~Gulf of California in Mexico draining parts of seven U.S. and two Mexican states; our~~  
415 ~~assessment focused on the portion of the Colorado River that flows through the Grand Canyon in~~  
416 ~~Arizona (Fig 1). Water storage associated with the allocation of water in the Colorado River for~~  
417 ~~human consumption and hydroelectric power generation has altered the hydrologic regime (Fig~~  
418 ~~S2) in the Colorado River between Glen Canyon Dam and Lake Mead. Most fish species native~~  
419 ~~to the Colorado River have declined in abundance and distribution while numerous non-native~~  
420 ~~species have become established [62]. The Humpback Chub (*Gila cypha*), a fish native to the~~



421 ~~Colorado River, was listed as endangered by~~The Humpback Chub (*Gila cypha*), a fish native to  
422 ~~the Colorado River, was listed as endangered by the~~ U.S. Fish and Wildlife Service in 1967 and  
423 given full protection under the Endangered Species Act of 1973 (ESA). To mitigate the effects of  
424 anthropogenic changes to the river on Humpback Chub, an understanding of the mechanisms by  
425 which Glen Canyon Dam and non-native species affect Humpback Chub is needed.

426 A critical life-history bottleneck for Humpback Chub is recruitment into the first year  
427 class- (Fig 6). Temperature, light, and seasonal high river discharge from snowmelt are thought  
428 to cue spawning behavior [63]-[58]. Hydropower development has dampened the range of river  
429 discharges of the Lower Colorado River within Grand Canyon. Historically, river discharge  
430 varied between 15 and 3400 m<sup>3</sup>/s, however discharge was greater in large flood events; current  
431 dam operations limit flows to a range of 140 to 1000 m<sup>3</sup>/s (Fig S2). Resulting changes in  
432 turbidity and water temperature create risks to endangered Humpback Chub, and other endemic  
433 fish. For example, the quantity and quality of habitat is reduced through changes in turbidity,  
434 biogeochemistry, and the temperature regime. Hypolimnetic water releases from Lake Powell  
435 maintain cold temperatures in the Colorado River downstream from Glen Canyon Dam;  
436 currently, spawning is limited to a single tributary, the Little Colorado River. As embryos  
437 survive into the larval stage, nursery habitats to support growth and foraging are essential [64-  
438 6659-61]. A secondary risk to juvenile survival post-larval stage is ~~piscivory from~~predation by  
439 non-native species including Rainbow Trout (*Oncorhynchus mykiss*) and Channel Catfish  
440 (*Ictalurus punctatus*) [67]-[62]. Temperatures for well over 100 km downstream of Lake Powell  
441 are excellent for non-native, cold water species, including a closely managed world-class  
442 Rainbow Trout fishery at Lees Ferry. Rainbow and Brown Trout (*Salma trutta*) are currently  
443 managed as an invasive species downstream of the confluence of the Colorado and Little

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444 Colorado River, approximately 97 km downstream of Glen Canyon Dam, to mitigate predation  
445 upon native fishes including the endangered Humpback Chub.

446 ~~The CM exercise documented a generally high understanding of the relationships of~~  
447 ~~anthropogenic drivers to Tier 1 EECs, cascading to multiple, less understood hypotheses about~~  
448 ~~how these factors would combine to affect habitats at Tier 2 (Fig 6). High confidence in the~~  
449 ~~linkages from Tier 2 invertebrate habitat to Tier 3 insect population is followed by a lesser~~  
450 ~~understanding of how insect populations are linked to larval production. The uncertainty of the~~  
451 ~~relations between food resources stands in contrast to high certainty that was ascribed to the~~  
452 ~~linkages from larval chub habitat to larval chub production, and from spawning habitat to larval~~  
453 ~~chub production and thence to recruitment. Since 1997, the Glen Canyon Dam Adaptive~~  
454 ~~Management Program has supported extensive monitoring and research across the spatial and~~  
455 ~~temporal landscape of the Colorado River. As a result, the information needed to characterize~~  
456 ~~some of the stressors is readily available (Table S2). However, the status of some existing~~  
457 ~~information was characterized as insufficient or not available. For the information needs~~  
458 ~~characterized as being insufficient or not available, we identified the spatial and temporal scales~~  
459 ~~at which data collection would facilitate the inferences needed to inform the management goal~~  
460 ~~(Fig 7). Understanding how these knowledge gaps affect Humpback Chub recruitment could~~  
461 ~~identify strategies that will help achieve the management goal of improving Humpback Chub~~  
462 ~~recruitment in the Colorado River.~~

463 Fig 6. Conceptual model describing the relationship of anthropogenic drivers to essential  
464 ecosystem characteristics (EECs) affecting the recruitment of Humpback Chub in the Colorado

465 River between Glen Canyon Dam and Lake Mead, Arizona. Essential ecosystem characteristics  
466 (EECs) are groupings of ecosystem components. Tier 1 EECs represent physical and chemical  
467 effects; fundamental measures of process that are directly affected by anthropogenic and natural  
468 drivers. Tier 2 EECs represent a broad habitat category that is intended to encompass the  
469 physical, chemical, and biological components of the riverine habitats that influence  
470 reproduction, growth, and survival of biotic communities. The Tier 3 EECs represent  
471 components of the biological systems that respond to changes in the hierarchical components of  
472 the conceptual model. The strength of our understanding of how natural and anthropogenic  
473 drivers interact with habitats, biological systems, and fish in large rivers is represented by the  
474 different types of lines in the figure. Solid blue lines depict a strong understanding of the  
475 relationship, the dotted-dashed blue line represents a moderate understanding of the relationship,  
476 and the black dashed line represents a weak understanding of the relationship. The different  
477 types of lines also represent the strength of our understanding of within EEC-tier relationships.

478 Fig 7. The CM exercise documented a high understanding of the relationships of  
479 anthropogenic drivers to Tier 1 EECs, cascading to multiple, less-understood hypotheses about  
480 how these factors would combine to affect habitats at Tier 2 (Fig 6). High confidence in the  
481 linkages from Tier 2 invertebrate habitat to Tier 3 insect production is followed by a lesser  
482 understanding of how insect production is linked to larval production. The uncertainty of the  
483 relations between food resources stands in contrast to high certainty that was ascribed to the  
484 linkages from larval chub habitat to larval chub production, and from spawning habitat to larval  
485 chub production and then to recruitment. Since 1997, the Glen Canyon Dam Adaptive  
486 Management Program has supported extensive monitoring and research across the spatial and

487 temporal landscape of the Colorado River. As a result, the information needed to characterize  
488 some of the stressors is readily available (Table S2). However, the status of some existing  
489 information was characterized as insufficient or not available. For the information needs  
490 characterized as being insufficient or not available, we identified the spatial and temporal scales  
491 at which data collection would facilitate the inferences needed to inform the management goal  
492 (Fig S3). Understanding how these knowledge gaps affect Humpback Chub recruitment could  
493 identify strategies that will help achieve the management goal of improving Humpback Chub  
494 recruitment in the Colorado River.

495 ~~The spatial and temporal scales of the management goal, the scientific inferences needed to~~  
496 ~~inform the management goal, and that data collection needs to occur to support the inferences for~~  
497 ~~monitoring information needs identified as requiring additional data in the case study addressing~~  
498 ~~Humpback Chub recruitment in the Colorado River between Glen Canyon Dam and Lake Mead,~~  
499 ~~Arizona (see Table S2 for additional detail). A: Tier 2 EEC—larval Humpback Chub habitat;~~  
500 ~~Stressors—habitat fragmentation, turbidity and Tier 2 EEC—Humpback Chub spawning habitat;~~  
501 ~~Stressor—water temperature and Tier 3 EEC—insect production; Stressor—benthic~~  
502 ~~macroinvertebrate habitat quantity and quality and Tier 3 EECs—all; Inter-tier interaction—trophic~~  
503 ~~level interactions; B: Tier 3 EEC—larval Humpback Chub production; Stressor—larval Humpback~~  
504 ~~chub habitat quantity and quality; C: Tier 3 EEC—Humpback Chub egg quality and production;~~  
505 ~~Stressors—Humpback Chub spawning habitat quantity and quality; D: Larval Humpback Chub~~  
506 ~~production; Inter-tier interaction—mortality of Humpback Chub eggs; E: Tier 3 EEC—larval~~  
507 ~~Humpback Chub production; Stressor—predation by invasive species and Tier 3 EEC—Primary~~  
508 ~~production; Stressor—nutrient flux; F: Tier 1 EEC—Biogeochemistry/thermodynamics; Inter-tier~~

509 ~~interaction=sediment adsorption of contaminants and nutrients; G:Tier 3 EEC=Age 0 Humpback~~  
510 ~~Chub recruitment; Inter-tier interaction=mortality of larval Humpback Chub~~

## 511 **Columbia River**

512 White Sturgeon is the largest freshwater fish in North America [63]. Like other sturgeon  
513 species, anthropogenic stressors have negatively affected White Sturgeon productivity. Our  
514 knowledge of factors affecting White Sturgeon productivity remain poorly understood [40].  
515 Therefore, we used the CM to identify knowledge gaps associated with the hypotheses that dam  
516 construction and operation, land-use practices, and invasive species, in some combination, affect  
517 the recruitment of age-0 White Sturgeon (Fig 7). Within the basin, development of hydroelectric  
518 and water-storage dams have changed the magnitude and seasonality of the natural river  
519 discharge (Fig S4) and thermal regimes [64], reduced the quantity and quality of spawning  
520 habitats [65, 66], and disrupted historical migration patterns [67]. Prior to hydropower  
521 development, White Sturgeon experienced a hydrograph that peaked during June-July due to  
522 snowmelt [64]. However, from 1949 to 1993 the average discharge in June decreased from  
523 14,000 m<sup>3</sup>/s to 6,000 m<sup>3</sup>/s and the maximum water temperature has increased by 1.8°C [64].  
524 White Sturgeon likely used the natural hydrograph and thermal regime as cues to seek out  
525 optimal spawning habitats and initiate spawning [65, 68].

526 Fig 7. Conceptual model describing the relationship of anthropogenic drivers to essential  
527 ecosystem characteristics (EECs) affecting the recruitment of White Sturgeon in the Columbia  
528 River, U.S. Essential ecosystem characteristics (EECs) are groupings of ecosystem components.  
529 Tier 1 EECs represent physical and chemical effects; fundamental measures of process that are

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530 directly affected by anthropogenic and natural drivers. Tier 2 EECs represent a broad habitat  
531 category that is intended to encompass the physical, chemical, and biological components of the  
532 riverine habitats that influence reproduction, growth, and survival of biotic communities. The  
533 Tier 3 EECs represent components of the biological systems that respond to changes in the  
534 hierarchical components of the conceptual model. The strength of our understanding of how  
535 natural and anthropogenic drivers interact with habitats, biological systems, and fish in large  
536 ivers is represented by the different types of lines in the figure. Solid blue lines depict a strong  
537 understanding of the relationship, the dotted-dashed blue line represents a moderate  
538 understanding of the relationship, and the black dashed line represents a weak understanding of  
539 the relationship. The different types of lines also represent the strength of our understanding of  
540 within EEC-tier relationships.

541 Factors other than river discharge and water temperature may also be affecting age-0  
542 White Sturgeon recruitment [40]. In areas of the Columbia and Snake Rivers with hydropower  
543 development, White Sturgeon populations are functionally isolated by dams. Consequently,  
544 White Sturgeon depend on conditions within restricted reaches to sustain production. In some  
545 reaches, suitable rearing habitat exists, and individual growth rates are high, but spawning habitat  
546 is limited and recruitment of fish is poor [65]. In other reaches, favorable spawning conditions  
547 exist but growth of young fish may be density limited [69]. How the availability of food  
548 resources for larval and juvenile White Sturgeon varies among reservoirs may affect age-0 White  
549 Sturgeon recruitment. Research has also suggested that contaminants may affect White Sturgeon  
550 reproductive biology. The Columbia River is the fourth largest river by volume in the United  
551 States [68] and drains a basin of 671,000 km<sup>2</sup> that includes parts of seven states, land ceded to 14

552 groups of affiliated tribes in the U.S. portion of the Columbia River Basin, land ceded to three  
553 tribal groups, known as First Nations, in the Canadian portion of the basin, and one Canadian  
554 province ([69]; Fig 1). The Columbia River supports anadromous fish species such as Chinook  
555 (*Oncorhynchus tshawytscha*), Coho (*O. kisutch*), Chum (*O. keta*), and Sockeye Salmon (*O.*  
556 *nerka*), including 12 populations of four species of salmon and steelhead (*O. mykiss*) listed as  
557 threatened or endangered under the ESA. The Columbia River also contains a complement of  
558 resident native and non-native fishes. Among the resident native fish species are White Sturgeon,  
559 the largest freshwater fish in North America [70]. Like other sturgeon species, anthropogenic  
560 stressors have negatively affected White Sturgeon productivity.

561 Our knowledge of factors affecting White Sturgeon productivity remain poorly  
562 understood [38]. Therefore, we used the CM to identify knowledge gaps associated with the  
563 hypotheses that dam construction and operation, land use practices, and invasive species, in  
564 some combination, affect the recruitment of age-0 White Sturgeon. Within the basin,  
565 development of hydroelectric and water storage dams have changed the magnitude and  
566 seasonality of the natural river discharge (Fig S3) and thermal regimes [71], reduced the quantity  
567 and quality of spawning habitats [72, 73], and disrupted historical migration patterns [74]. Prior  
568 to hydropower development, White Sturgeon experienced a hydrograph that peaked during June-  
569 July due to snowmelt [71]. However, from 1949 to 1993 the average discharge in June decreased  
570 from 14,000 m<sup>3</sup>/s to 6,000 m<sup>3</sup>/s and the maximum water temperature has increased by 1.8°C  
571 [71]. White Sturgeon likely used the natural hydrograph and thermal regime as cues to seek out  
572 optimal spawning habitats and initiate spawning [72, 75].

573 Factors other than river discharge and water temperature may also be affecting age-0  
574 White Sturgeon recruitment [38]. In areas of the Columbia and Snake Rivers with hydropower

575 ~~development, White Sturgeon populations are functionally isolated by dams. Consequently,~~  
576 ~~White Sturgeon depend on conditions within restricted reaches to sustain production. In some~~  
577 ~~reaches, suitable rearing habitat exists, and individual growth rates are high, but spawning habitat~~  
578 ~~is limited and recruitment of fish is poor [72]. In other reaches, favorable spawning conditions~~  
579 ~~exist but growth of young fish may be density limited [76]. How the availability of food~~  
580 ~~resources for larval and juvenile White Sturgeon varies among reservoirs may affect age-0 White~~  
581 ~~Sturgeon recruitment. Research has also suggested that contaminants may affect White Sturgeon~~  
582 ~~reproductive biology [77,70].~~ The introduction of non-native fishes has clearly affected the native  
583 fish assemblage in the Columbia River [32, 78,71]. Channel Catfish, Smallmouth Bass  
584 *Micropterus dolomieu*, and Walleye (*Sander vitreus*) that have been introduced into the  
585 Columbia River have all been shown to prey upon or compete with native fish species [78, 79,71,  
586 72] and may also affect White Sturgeon.

587 The CM (Fig 8) provides structure to the multiple competing hypotheses and indicates  
588 how anthropogenic drivers may be affecting Tier 1, 2, and 3 EEC's. ~~We hypothesized pathways~~  
589 ~~of stress arising from anthropogenic drivers that affect age-0 White Sturgeon recruitment (Fig 8).~~  
590 Not surprisingly, the strength of our understanding of the effects of stressors on White Sturgeon  
591 was greater for relationships between life stages that are more easily sampled (e.g., adults) and  
592 that rely on data that are readily accessible as part of monitoring associated with hydropower  
593 development (e.g., discharge and water temperature) or metrics that are from combinations of  
594 these variables (e.g., estimates of White Sturgeon spawning habitat; Table S3). However, for  
595 relationships between harder to sample White Sturgeon life stages (e.g., larvae), biota that  
596 require expertise and equipment atypical of traditional fisheries assessments in large rivers (e.g.,  
597 benthic macroinvertebrates), or stressors that are described by metrics that require specialized



598 modeling expertise (e.g., sediment transport dynamics), the existing information was insufficient  
599 or not available. For example, we identified the need to better understand the effects of channel  
600 morphology and hydraulics on benthic macroinvertebrate habitat, invertebrate production, and  
601 subsequent larval White Sturgeon production. The most certain pathways connected changes in  
602 hydrology, hydraulics, and temperature regimes to reduced spawning habitat in Tier 2, then to  
603 decreased egg quality and production at Tier 3.

604 ~~Fig 8. Conceptual model describing the relationship of anthropogenic drivers to essential~~  
605 ~~ecosystem characteristics (EECs) affecting the recruitment of White Sturgeon in the Columbia~~  
606 ~~River, U.S. Essential ecosystem characteristics (EECs) are groupings of ecosystem components.~~  
607 ~~Tier 1 EECs represent physical and chemical effects, fundamental measures of process that are~~  
608 ~~directly affected by anthropogenic and natural drivers. Tier 2 EECs represent a broad habitat~~  
609 ~~category that is intended to encompass the physical, chemical, and biological components of the~~  
610 ~~riverine habitats that influence reproduction, growth and survival of biotic communities. The~~  
611 ~~Tier 3 EECs represent components of the biological systems that respond to changes in the~~  
612 ~~hierarchical components of the conceptual model. The strength of our understanding of how~~  
613 ~~natural and anthropogenic drivers interact with habitats, biological systems, and fish in large~~  
614 ~~river is represented by the different types of lines in the figure. Solid blue lines depict a strong~~  
615 ~~understanding of the relationship, the dotted-dashed blue line represents a moderate~~  
616 ~~understanding of the relationship, and the black dashed line represents a weak understanding of~~  
617 ~~the relationship. The different types of lines also represent the strength of our understanding of~~  
618 ~~within EEC tier relationships.~~

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619 Our results suggest there are stressors that can affect the management goal of increasing  
620 age-0 White Sturgeon recruitment that are poorly understood and that could confound efforts to  
621 manage White Sturgeon in the Columbia River. Our characterization of the spatial and temporal  
622 scales that data should be collected at could help guide future efforts to fill data gaps to support  
623 the inferences needed to address the goal of improving recruitment of age-0 White Sturgeon (Fig  
624 ~~9S5~~).

625 ~~Fig 9. The spatial and temporal scales of the management goal, the scientific inferences needed~~  
626 ~~to inform the management goal, and that data collection needs to occur to support the inferences~~  
627 ~~for monitoring information needs identified as requiring additional data in the case study~~  
628 ~~addressing White Sturgeon recruitment in the Columbia River (see Table S3 for additional~~  
629 ~~detail). A: Tier 1 EEC= Biogeochemistry/thermodynamic; Stressor= altered biogeochemical~~  
630 ~~regime and Tier 2 EEC= benthic macroinvertebrate habitat; Stressors=channel stability, sediment~~  
631 ~~deposition, fragmentation and Tier 2 EEC=Larval White Sturgeon habitat; Stressors=habitat~~  
632 ~~fragmentation sediment deposition, water temperature and Tier 2 EEC=White Sturgeon~~  
633 ~~spawning habitat; Stressors=contaminants, sediment deposition and Tier 3 EEC=White Sturgeon~~  
634 ~~egg quality and production; Stressor=predation by invasive species and Tier 3 EEC=larval White~~  
635 ~~Sturgeon production; Stressor=predation by invasive species and Tier 3 EEC=benthic~~  
636 ~~macroinvertebrate production; Stressor=benthic macroinvertebrate habitat quantity and quality;~~  
637 ~~B: Tier 1 EEC=sediment transport; Stressors=altered sediment regime, altered hydraulic regime~~  
638 ~~and Tier 1 EECs=channel morphology/hydraulics, sediment transport; Stressor=altered hydraulic~~  
639 ~~regime and Tier 3 EEC=primary production; Stressor=nutrient fluxes; C: Tier 1 EEC=Channel~~  
640 ~~morphology/Hydraulics, Sediment transport; Stressor=altered hydraulic regime and Tier 1 EEC~~

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641 =channel morphology/hydraulics, sediment transport; Inter-tier interaction=sediment transport  
642 dynamics; D: Tier 1 EEC=Channel morphology/Hydraulics, Sediment transport; Stressor=altered  
643 hydraulic regime and Tier 1 EEC=Channel morphology/Hydraulics, Sediment transport; Inter-  
644 tier interaction=sediment transport dynamics; E: Tier 1 EEC=Biogeochemistry/Thermodynamics;  
645 Inter-tier interaction=sediment adsorption of contaminants and nutrients; F: Tier 3 EEC=larval  
646 White Sturgeon production; Stressors=larval White Sturgeon habitat quantity and quality and  
647 Tier 3 EEC=larval White Sturgeon production, age-0 White Sturgeon recruitment; Inter-tier  
648 interaction=mortality and White Sturgeon egg quality and production; Inter-tier  
649 interaction=predation of White Sturgeon eggs by native fish and Tier 3 EECs=larval White  
650 Sturgeon production; Inter-tier interaction=predation of White Sturgeon larvae by native fish and  
651 Tier 3 EECs=all; Inter-tier interactions=trophic level interactions.

## 652 Upper Mississippi and Illinois Rivers

653 In the agricultural Midwest, basin-wide land uses affect the delivery of sediments,  
654 nutrients, and runoff to the Upper Mississippi and Illinois rivers [80-83,73-76]. Within the  
655 floodplain of these two large rivers, agriculture and residential land uses often rely upon the use  
656 of levees to isolate productive or developed lands during seasonal high-flow events. Within the  
657 channel, these rivers support commercial navigation with locks and dams and river-training  
658 structures, which have dramatically altered channel morphology and hydraulics throughout the  
659 system. Together, the cumulative effects of these modifications to the basin, floodplain, and river  
660 have implications for habitat diversity and native fish biodiversity [84],[77]. Additionally, recent  
661 invasion and expansion of non-native species, namely Silver Carp (*Hypophthalmichthys*

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662 *molitrix*) and Bighead Carp (*H. nobilis*), have direct and indirect effects on native fishes that  
663 likely compound or confound stress pathways on native fish biodiversity [85, 86, 78, 79].  
664 Therefore, we used the CM to explore how these primary anthropogenic drivers have likely  
665 influenced fish habitats and associated life stages (Fig 408).

666 Fig 408. Conceptual model of how anthropogenic drivers in the upper Mississippi and Illinois  
667 Rivers influence native fish habitats and recruitment. Essential ecosystem characteristics (EECs)  
668 are groupings of ecosystem components. Tier 1 EECs represent physical and chemical effects;  
669 fundamental measures of process that are directly affected by anthropogenic and natural drivers.  
670 Tier 2 EECs represent a broad habitat category that is intended to encompass the physical,  
671 chemical, and biological components of the riverine habitats that influence reproduction, growth,  
672 and survival of biotic communities. The Tier 3 EECs represent components of the biological  
673 systems that respond to changes in the hierarchical components of the conceptual model. The  
674 strength of our understanding of the relationships of how natural and anthropogenic drivers  
675 interact with habitats, biological systems, and fish in large rivers is represented by the different  
676 types of lines in the figure. Solid blue lines depict a strong understanding of the relationship, the  
677 dotted-dashed blue line represents a moderate understanding of the relationship, and the black  
678 dashed line represents a weak understanding of the relationship. The different types of lines also  
679 represent the strength of our understanding of within EEC-tier relationships.

680 Increased sediment loads in combination with altered hydraulics and morphology have  
681 resulted in high rates of sedimentation, homogeneity of depth, and loss of low-velocity, off-  
682 channel areas [87, 88] [80, 81]. A diversity of off-channel habitat conditions (i.e., increased

683 residence time, low velocity, warm temperatures, availability of food resources) support growth  
684 and development of larval and juvenile fishes [~~89, 90~~82, 83] and often provide important food  
685 resources for adult fishes [~~91-95~~84-88]. Further, deep, low-velocity off-channel habitats are  
686 recognized as important refugia for a wide range of fishes during high-flow events and seasonal  
687 periods of low temperatures [~~96-99~~89-92]. Loss of floodplain connectivity has eliminated the  
688 seasonal exchange of nutrients, organisms and organic matter between river and floodplain  
689 environments that support biological diversity and productivity [~~100, 101~~93, 94]. Reduced  
690 availability of spawning, nursery, foraging, or overwintering habitat conditions can serve as  
691 bottlenecks to fish populations through limited larval production, reduced growth, and increased  
692 overwinter mortality. For example, high sedimentation rates have been filling backwaters in the  
693 Illinois River for decades, thus limiting the availability of overwintering conditions for fishes  
694 that bioenergetically need a deep refuge with slow water velocities. Missing year-classes in this  
695 reach, represented by truncated size structure in the Largemouth Bass (*Micropterus salmoides*)  
696 population are hypothesized to be a result of periodic winter mortality (Fig ~~S4S~~6).

697         The application of our CM makes clear that while the general effects of anthropogenic  
698 drivers on hydrology, sediment transport, biogeochemistry and hydraulics and morphology are  
699 well understood, there is much less known about how those effects influence the quality and  
700 availability of required habitat conditions (Tier 2, Fig ~~408~~). Although there is likely overlap of  
701 habitat requirements among species with similar life histories, the diversity of habitat conditions  
702 necessary to support a native and diverse fish community has not been explored. Consequently,  
703 the existing information needed to assess the relationship between habitat quality and quantity,  
704 and egg production, juvenile recruitment, and adult survival of fish populations within the Upper  
705 Mississippi and Illinois rivers was categorized as insufficient to not available (Tier 3 Inter-tier

706 interaction, Fig 108; Table S4). Addressing these knowledge gaps could improve the  
707 effectiveness of habitat restoration efforts focused on maintaining a diverse native fish  
708 community. The spatial and temporal scales of data collection that would support needed  
709 inferences to address restoring and maintaining native fish biodiversity and habitat quantity and  
710 quality are characterized in Fig 117.

711 ~~Fig 11. The spatial and temporal scales of the management goal, the scientific inferences needed~~  
712 ~~to inform the management goal, and that data collection needs to occur to support the inferences~~  
713 ~~for monitoring information needs identified as requiring additional data in the case study~~  
714 ~~addressing native fish biodiversity and habitat diversity in the Mississippi and Illinois rivers (see~~  
715 ~~Table S4 for additional detail). A: Tier 1 EEC=Sediment transport; Stressor=altered hydraulic~~  
716 ~~regime and Tier 1 EEC=Biogeochemistry/Thermodynamics; Stressor=altered biogeochemical~~  
717 ~~regime and Tier 1 EEC=Biogeochemistry/Thermodynamics; Inter tier interaction=sediment~~  
718 ~~adsorption of contaminants and nutrients; B: Tier 2 EEC=adult native fish overwintering habitat;~~  
719 ~~Stressors=water velocity, water temperature, dissolved oxygen, sediment deposition and Tier 2~~  
720 ~~EEC=Juvenile native fish habitat; Stressors=water depth, water velocity, water temperature,~~  
721 ~~dissolved oxygen, contaminants, sediment deposition and Tier 2 EEC=Native fish spawning~~  
722 ~~habitat; Stressors=water depth, water velocity, habitat fragmentation, sediment deposition, water~~  
723 ~~temperature, dissolved oxygen, contaminants and Tier 3 EEC=Adult and juvenile native fish~~  
724 ~~recruitment; Inter tier interaction=mortality and Tier 3 EEC=all; Stressors=invasive species and~~  
725 ~~Tier 3 EEC=all; Inter tier interaction=trophic level interactions; C: Tier 1 EEC=Channel~~  
726 ~~morphology/Hydraulics; Inter tier interaction=channel forming processes; D: Tier 1~~  
727 ~~EEC=Channel morphology/Hydraulics, Sediment transport; Inter tier interaction=sediment~~

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728 ~~transport dynamics; E:Tier 3 EEC=Adult native fish recruitment; Stressor=adult native fish~~  
729 ~~overwintering habitat quantity and quality and Tier 3 EEC=Juvenile native fish recruitment;~~  
730 ~~Stressor=juvenile native fish habitat quantity and quality and Tier 3 EEC=Native fish egg quality~~  
731 ~~and production; Stressor=spawning habitat quantity and quality.~~

### 732 **Similarities across case studies**

733 We observed similarities in the stressors and interactions within EEC tiers across the four  
734 case studies. For Tier 1, an altered hydrologic regime was identified as a stressor to the  
735 ~~Hydrology~~hydrology EEC in all four rivers (Table 1). Presumably this is due to the ubiquitous  
736 effects of dams on the systems examined. However, in some rivers the altered hydrologic regime  
737 originated from other anthropogenic (e.g., water use, land use, biological community alteration)  
738 and natural (e.g., ~~Climate~~climate) drivers. Similarly, all four case studies listed an altered water  
739 temperature regime as a stressor to the  
740 ~~Biogeochemistry/Thermodynamics~~biogeochemistry/thermodynamics EEC with linkages to  
741 several anthropogenic drivers (Fig 4, 6-8; Tables S1-S4). There were also similarities across case  
742 studies with respect to the identification of interactions between Tier 1 EECs with all four case  
743 studies noting interactions between Tier 1 EEC components.

744 Table 1. Stressors or inter-tier interactions affecting Tier 1 Essential Ecosystem Characteristics (EEC) identified as an information  
 745 need in the application of the conceptual model to case studies in the Canadian River [54], Colorado River [54], Columbia River (3),  
 746 ~~and Upper Mississippi and Illinois rivers (4)-(1), Colorado River (2), Columbia River (3), and Upper Mississippi and Illinois rivers~~  
 747 ~~(4)~~. Tier 1 EECs are measurable characteristics that describe processes that can significantly alter the morphological or chemical  
 748 characteristics within a river channel.

| Stressor or inter-tier interaction                   | Tier 1 EEC |                               |                    | Biogeochemistry/<br>Thermodynamics |
|--|------------|-------------------------------|--------------------|------------------------------------|
|  | Hydrology  | Channel Morphology/Hydraulics | Sediment Transport |                                    |
| Altered Hydrologic Regime                            | 1, 2, 3, 4 | 1                             | 1, 2               |                                    |
| Altered Hydraulic Regime                             |            | 1, 3, 4                       | 3                  |                                    |
| Altered Sediment Regime                              |            |                               | 3, 4               |                                    |
| Altered Water Temperature Regime                     |            |                               |                    | 1, 2, 3, 4                         |
| Altered Biogeochemical Regime                        |            |                               |                    | 1, 3, 4                            |
| Channel forming processes                            |            | 1, 2, 3, 4                    |                    |                                    |
| Sediment transport dynamics                          |            | 1, 2, 3, 4                    | 1, 2, 3, 4         |                                    |
| Sediment adsorption of<br>contaminants and nutrients |            |                               |                    | 1, 2, 3, 4                         |

749

750



751 For Tier 2, there were similarities across case studies; however, the adaptation and  
752 elaboration of the components to the management goal in the case studies was apparent (Table  
753 2). The management goal associated with the case study for the Upper Mississippi and Illinois  
754 Rivers resulted in Tier 2 EEC components (e.g., overwintering habitat) and stressors (e.g.,  
755 dissolved oxygen) that were unique. Spawning habitat was identified as a Tier 2 EEC component  
756 in all the case studies and multiple stressors were identified as affecting this component in two or  
757 more of the case studies. Larval fish and invertebrate habitat were noted as Tier 2 EEC  
758 components with some similarities in stressors across case studies. Habitat fragmentation,  
759 sediment deposition, and water temperature were listed as stressors to Tier 2 EECs in all four  
760 case studies. No interactions between Tier 2 EEC components were listed for the case studies.

761 Table 2. Stressors affecting Tier 2 Essential Ecosystem Characteristics (EEC) identified in the application of the conceptual model to  
 762 case studies in the Canadian River ~~[54], Colorado River [54],(1), Colorado River (2)~~, Columbia River (3), and Upper Mississippi and  
 763 Illinois rivers (4). Tier 2 EECs are broadly described as physical, chemical, or biological components of “habitat” that are  
 764 hypothesized to have overall fitness consequences.

| Stressor                   | Tier 2 EEC (habitat) |               |               |             |              |
|----------------------------|----------------------|---------------|---------------|-------------|--------------|
|                            | Spawning             | Overwintering | Juvenile fish | Larval fish | Invertebrate |
| Altered riparian community |                      |               |               |             | 1            |
| Channel stability          |                      |               |               |             | 2, 3         |
| Contaminants               | 1, 3, 4              |               | 4             |             |              |
| Discharge                  |                      |               |               |             | 1            |
| Dissolved oxygen           | 4                    | 4             | 4             |             |              |
| Habitat fragmentation      | 1, 3, 4              |               |               | 1, 2, 3     | 2, 3         |
| Sediment deposition        | 3, 4                 | 4             | 4             | 3           | 1, 2, 3      |
| Turbidity                  |                      |               |               | 2           |              |
| Water Depth                | 4                    |               | 4             |             |              |
| Water temperature          | 1, 2, 3, 4           | 4             | 4             | 1, 3        |              |
| Water velocity             | 3, 4                 | 4             | 4             |             |              |

765

766  
767 The ~~adaption~~adaptation of Tier 3 EECs and elaboration of the biological system related to  
768 the management goal addressed by the case studies resulted in EECs that were comprised of fish  
769 life stages ranging from eggs to adult fish, primary and invertebrate production, ~~invertebrates~~ and  
770 biodiversity (Table 3). All Tier 3 EEC components, except biodiversity, were present in the four  
771 case studies. Not surprisingly, habitat quantity and quality were listed as stressors to all the EECs  
772 related to fish and invertebrates. Six of eight stressors or inter-tier interactions were listed as  
773 affecting fish larvae and five of eight were noted as affecting egg quantity and quality. In  
774 contrast to Tier 2, interactions were extensively noted between Tier 3 EECs and trophic level  
775 interspecific interactions were listed in all four case studies.

776 Table 3. Stressors or inter-tier interactions affecting Tier 3 Essential Ecosystem Characteristics (EEC) identified in the application of  
 777 the conceptual model to case studies in the Canadian River [54], Colorado River [54], (1), Colorado River (2), Columbia River (3), and  
 778 Upper Mississippi and Illinois rivers (4). Tier 3 EECs represent components of the hypothesized biological system upon which the  
 779 cascading effects of anthropogenic and natural drivers act, and interactions occur.

| Stressor or inter-tier interaction        | Tier 3 EEC             |                           |                        |                             |                         |                    |              |
|---|------------------------|---------------------------|------------------------|-----------------------------|-------------------------|--------------------|--------------|
|   | Adult fish recruitment | Juvenile fish recruitment | Larval fish production | Fish egg quality/production | Invertebrate production | Primary production | Biodiversity |
| Direct mortality                          |                        |                           | 1                      |                             |                         |                    |              |
| Predation/competition by invasive species |                        |                           | 1, 2, 3                | 3                           |                         |                    | 4            |
| Habitat quantity/quality                  | 4                      | 4                         | 1, 2, 3                | 1, 2, 3, 4                  | 1, 2, 3                 |                    |              |
| Nutrient flux                             |                        |                           |                        |                             |                         | 1, 2, 3            |              |
| Trophic level interspecific interactions  | 1, 2, 3, 4             | 1, 2, 3, 4                | 1, 2, 3, 4             | 1, 2, 3, 4                  | 1, 2, 3, 4              | 1, 2, 3, 4         | 4            |
| Predation                                 |                        |                           | 3                      | 3                           |                         |                    |              |
| Mortality                                 | 1, 3, 4                | 1, 2, 3, 4                | 1, 2, 3                |                             |                         |                    |              |
| Fish condition                            |                        |                           |                        | 1, 3, 4                     |                         |                    |              |

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781

782 **Discussion**

783           The main objective of our exploration of CMs was to impose some structure on the  
784 complex ecosystems found in large rivers and from that structure, identify gaps in monitoring  
785 information that could inform the management of fish. Comparison across our four case studies  
786 provides some insights into large rivers and the utility of the CM to identify gaps in our  
787 understanding of factors affecting fish in large rivers.

788           Despite large differences in the physical and ecological contexts of the river systems, the  
789 case studies ~~also~~ demonstrated substantial commonalities in the data needed to better understand  
790 how human activities affect these systems and in the application of the CM. The general tiered  
791 structure of drivers and cascading responses through EECs worked well with the four examples.  
792 Each of the four rivers could be placed in the tiered CM to illustrate current perceptions about  
793 drivers and responses. The hierarchical CM generally increased in complexity from top to  
794 bottom. Among all rivers, there tended to be greater understanding of links from drivers to Tier 1  
795 and Tier 2 EECs, and less understanding about linkages to Tier 3.

796           The strength of understanding of interactions between anthropogenic and natural drivers  
797 and EECs, and between and within EECs, varied considerably among river systems, however,  
798 resulting from both variable complexity and existing knowledge. For example, linkages from  
799 drivers to Tier 1 EECs were considered strong in the case of the Humpback Chub in the Grand  
800 Canyon, but between Tier 1 and Tier 2 only moderate. This is probably indicative of the  
801 substantial research investments in examination of physical processes in this river system

802 ~~[10295]. A logical next step in the process of identifying and prioritizing data collection needs,~~  
803 ~~once major hypothesized stressor response pathways have been described based on expert~~  
804 ~~elicitation, is to conduct an extensive literature review to support or refute those pathways and~~  
805 ~~the strength and understanding of the pathways.~~

806 Although we did not prescribe a specific approach to the CM process, the case studies  
807 employed similar strategies. Our modelling exercises started with the definition of a management  
808 goal. In all our case studies, the management goals pertained to a desired biological endpoint  
809 represented in Tier 3. After the definition of the management goal, we conceptualized  
810 interactions between drivers and EECs and between EECs with a combination of top-down and  
811 bottom-up approaches. A top-to-bottom approach to working with these models is generally  
812 consistent with a management perspective wherein anthropogenic drivers that are most directly  
813 managed in a large-river system (e.g., land and water use, etc.) cascade from top to bottom  
814 through fluxes to physical and chemical habitats, and then to biological responses. While this is  
815 generally true for anthropogenic drivers, a notable exception to the top-to-bottom management  
816 approach would be that in the U.S., there are few actions currently directed at reducing emissions  
817 affecting climate ~~[103][96]~~ which is a natural driver in our CM. Climate was hypothesized to be  
818 a stressor in the case study application of the CM to Arkansas River Shiner management in the  
819 South Canadian River and is hypothesized to be affecting hydrologic regimes elsewhere ~~[104,~~  
820 ~~105][97, 98], but was not specifically mentioned in other case studies. The CMs can readily be~~  
821 ~~modified to incorporate other factors or pathways (e.g., climate effects) as new information or~~  
822 ~~perspectives become available.~~ A bottom to top approach is equally or more valuable as it starts  
823 with the foundation of understanding about the species or community, and then seeks to identify  
824 which stressors affect population or community responses. A bottom-up approach can readily

825 identify information gaps in linkages from ecological processes to demographic parameters

826 ~~106~~[99].

827 The top-to-bottom and bottom-up approaches meet in the middle in Tier 2 in the concept

828 of habitat: the resources and conditions present in an area that produce occupancy ~~107~~[100].

829 Tier 2 is critical as it has little value if it is not defined based on biological requirements or if

830 managers lack understanding on how habitat is formed. Among our examples, the Upper

831 Mississippi River is notable for asserting strong understanding of the linkages from land-use

832 stressors to sediment regime to diminished overwintering habitat for native adult fishes. After

833 that, interactions with other processes and life stages combine to increase uncertainty about

834 whether overwintering habitat is a limiting factor in biodiversity. In contrast, the high confidence

835 in understanding how White Sturgeon egg quality and production are linked to spawning habitat

836 in the Columbia River Basin, provides a strong linkage upward through Tier 1 EECs and

837 potential management actions (Fig 87). Although at times elusive, the concept of habitat is

838 critical for linking management to biotic endpoints ~~108~~[101].

839 Large rivers are typically managed for multiple objectives, including fisheries, multi-

840 species, or ecosystem objectives. Management decisions typically require an understanding of

841 how management actions propagate through a river ecosystem. Although the emphasis may be

842 on a biological endpoint (among other objectives), understanding the intermediate steps and the

843 processes linking them, and potential interactions between processes or EEC components, can

844 help formulate effective management strategies; especially as multiple objectives compete. In a

845 multi-species context, the conceptual models can help identify commonalities and differences in

846 in how stressors propagate to biota and therefore provide a basis for prioritizing monitoring

847 efforts. In the case where species or guilds have similar habitat affinities and life histories, a

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848 dominant anthropogenic stress pathway may be hypothesized and focus on a single or few  
849 monitoring components may be justified. An example may be multiple large-river species that  
850 are known to be cued to spawn by spring flow pulses. In such a case, the characteristics of the  
851 annual hydrograph would be a dominant physical monitoring variable and biological monitoring  
852 could focus on reproductive success of one or more of the species. In the case where multiple  
853 species of concern have different reproductive strategies – for example, rheophilic species like  
854 sturgeon that may require in-channel dispersion of young to flowing habitats compared to  
855 invasive carp whose young thrive when they can disperse to lentic floodplain pools – pathways  
856 and monitoring strategies will diverge. In the latter case, it would probably not be sufficient to  
857 monitor and assess the characteristics of the annual hydrograph; instead, hydrologic metrics  
858 would need to be integrated with hydraulic and geomorphic metrics to assess where and when  
859 the different habitats would be available and could be targeted for young-of-the-year sampling.  
860 Effectively addressing multiple species would rely on detailed knowledge of life histories and  
861 how they play out on the landscape – such information is missing for many species and may  
862 need to be developed for effective design of monitoring and management actions.

863 Management actions intended to benefit fish in large rivers can directly or indirectly  
864 affect multiple ecosystem components. Without consideration of the effects of management on  
865 non-target ecosystem components, unintended consequences may limit management efficacy.  
866 Hypothesizing inter-tier interactions in the Tier 3 EEC (e.g., see Fig 7), can provide insight on  
867 the potential interactions among fish species and other biological components in the context of  
868 the hierarchical CM. In all our case studies, the lumping of multiple biological interactions in  
869 Tier 3 resulted in a simplification of complex trophic interactions. For example, as Tier 3  
870 encompasses all biological responses, it includes multiple life stages of many interacting species



871 at varying trophic levels. Because of this, the four CMs diverged significantly at Tier 3 as  
872 components were expanded to accommodate existing understanding. Even as the Tier 3  
873 components were expanded in complexity, they remained highly simplified views of the  
874 ecosystem. Simplification was based, in part, on the importance of key species in management  
875 goals and the experts' existing knowledge. Even though the hypothesized Tier 3 interactions in  
876 our case studies conveyed a simplification of the trophic interactions, the hypothesized  
877 interactions do suggest the need for information that clarifies the trophic interactions and effects  
878 of Tier 3 EEC components on the biological endpoint. If desired or warranted, the Tier 3 EEC  
879 could be elaborated to capture more complexity. For example, in Fig 7, the Tier 3 inter-tier  
880 interaction between anadromous and resident fishes and white sturgeon larvae could expanded to  
881 include interactions with specific fish species. Monitoring can help clarify the effects of  
882 management actions, including on non-target ecosystem components, but only if data are  
883 collected to characterize key ecosystem processes that could affect the outcome. The process of  
884 considering and elucidating Tier 3 EEC interactions can help identify the non-target ecosystem  
885 components that could be affected when managing for a specific biological endpoint.

886 ~~The CMs explored here also provide a framework for considering return on science~~  
887 ~~investments. The CMs explored here also provide a framework for considering return on science~~  
888 ~~investments. Large rivers are typically managed for multiple objectives, including fisheries,~~  
889 ~~multi species, or ecosystem objectives. Management decisions typically require an~~  
890 ~~understanding of how management actions propagate through a river ecosystem. Although the~~  
891 ~~emphasis may be on a biological endpoint (among other objectives), understanding the~~  
892 ~~intermediate steps and the processes linking them, and potential interactions between processes~~  
893 ~~or EEC components, can help formulate effective management strategies; especially as multiple~~

894 ~~objectives compete. For example, to increase recruitment of a fish species, it is not enough to~~  
895 ~~know that increased reservoir flow releases are associated with increased spawning unless we~~  
896 ~~understand how much flow, when, for how long, and at what temperature, are needed to optimize~~  
897 ~~other EECs to increase survival and recruitment.~~

898 The knowledge needed for effective management of large rivers can be gained by  
899 monitoring intermediate endpoints along the cascade, but the type of information and costs vary  
900 widely. Costs for monitoring Tier 1 EECs can be high but some programs are already in place.  
901 For example, large rivers are likely to have monitoring infrastructure installed for Tier 1  
902 monitoring of discharge and temperature regimes, with varying potential for monitoring  
903 sediment transport and water quality. Investment at Tier 2 may emphasize physical processes and  
904 habitats that can be measured at relatively low cost, assuming that habitats are adequately  
905 defined based on biological criteria. In larger rivers, Tier 2 habitat assessments can be more cost  
906 effective compared to smaller rivers because they can rely on automated data collection through  
907 hydroacoustics and remote sensing ~~[408]~~[101]. As discussed above, habitat assessments have  
908 value only to the extent that they are based on well-defined biological requirements; it is notable  
909 that some large-river management efforts have found that relatively simple habitat models are  
910 useful to predict biological responses ~~[409]~~[102]. At Tier 3, costs can increase substantially  
911 because of structural uncertainties (i.e., which life stages, which species are most important to  
912 monitor) and because of the inherent uncertainties of monitoring fish in large river systems  
913 where detection probability can be low and highly variable [36, ~~410]~~[103]. ~~The CMs presented~~  
914 ~~here can be used to assess which pathways are thought to be most important, and which~~  
915 ~~components of EECs would yield the best return on investment for decision making. Generally,~~  
916 ~~the cost of monitoring increases from Tier 1 to Tier 3 in the CM hierarchy; at the same time, the~~

917 relevance of information to decision making is typically greater for biological responses depicted  
918 in Tier 3 [104].

919 Because both costs and information benefits increase from Tier 1 to Tier 3 in the CM  
920 hierarchy, it is difficult to generalize about where the benefit:cost ratio would be optimized.  
921 Indeed, as discussed by Jacobson and Berkley [30], the decision about where in the hierarchy  
922 monitoring resources would get the highest return on investment may depend more directly on  
923 managers' and stakeholders' perceptions about risks of acting with incomplete information. For  
924 example, the details of how a fish's reproductive strategy depends on the nuances of a seasonal  
925 hydrograph may not be known, but stakeholders may believe strongly that the natural  
926 hydrograph was functional for the species and therefore monitoring of the flow regime will have  
927 the highest return on investment and, by extension, restoration of the flow regime is likely to  
928 have the most positive effects. On the other hand, in systems where stakeholders opinions are  
929 divided or socio-economic values would be compromised by a return to a natural flow regime,  
930 managers may be required to demonstrate more precisely how elements of the flow regime  
931 propagate to species' benefits [105]. Thus, once information needs are identified and there is an  
932 assessment of the availability of data identified as information needs, there needs to be a process  
933 whereby the costs of collecting the information need to be placed in a socioeconomic context  
934 (e.g., see [30]).

935 The development of the CMs described in this manuscript can be a first step in  
936 application of structured decision-making (SDM) and its iterative form-adaptive management  
937 (AM) processes [106, 107]. Structured decision-making is a stakeholder driven process by which  
938 a problem can be defined with conceptual models and decomposed into decision components  
939 that include the problem context, stakeholder objectives, potential management actions,

940 consequences of those actions on the objectives, and trade-offs related to different decisions  
941 (actions) [107-109]. One primary focus of SDM is the identification of uncertainties such as  
942 those identified in the CMs for the case studies in this paper [110]. Quantification of the  
943 influence of decision relevant uncertainties can be modeled using sensitivity analysis and other  
944 techniques and ranked [107, 109, 111]. In addition, the quantitative techniques available to assist  
945 in solving complex ecological problems are robust and range in complexity from consequences  
946 tables to Bayesian models to dynamic optimization models [107-109, 112, 113]. The SDM  
947 process is often used as the set-up phase for adaptive management which includes monitoring  
948 over time to reduce uncertainty related to how management will influence important outcomes  
949 (e.g. fish population status; [109, 112].

950         The CM may also help to identify which processes or components are amenable to a field  
951 monitoring effort and which are more aptly addressed through laboratory or mesocosm  
952 experiments. For example, if it is hypothesized that the condition of age 1+ Arkansas Shiners is a  
953 critical determining factor in egg quality or production (Fig 54), it could be determined that the  
954 best approach to developing a quantitative relation between condition and eggs is through a  
955 controlled laboratory experiment rather than field-based monitoring. The CM helps to visualize  
956 where different types of information may be applied within a decision-making framework.

957         A large-river CM may also serve as a precursor to computational ecological or population  
958 models [30][30]. Similar questions about how monitoring and other science efforts should be  
959 distributed among EECs and processes can be addressed iteratively by carrying out sensitivity  
960 analyses in a modeling framework. -Indeed, given substantial uncertainties associated with  
961 monitoring data, computation modeling can be considered a necessary component of large-river  
962 monitoring and evaluation systems [106, 11499, 114].

963 **Conclusions**

964 We found the process of conceptualizing the relationships between and within EECs  
965 fostered a critical assessment of what we know about factors affecting the management endpoint  
966 ~~being considered.~~ By visualizing how EEC drivers directly and indirectly affect management  
967 endpoints, our CM identified critical information gaps and uncertainties that, if resolved, could  
968 improve our understanding of how to best meet management objectives. The process of  
969 conceptualizing the EEC relationships affecting fish in large rivers could help to structure, or  
970 restructure, monitoring programs around scientifically sound monitoring questions, promote the  
971 selection of relevant ecological indicators that characterize resource condition or management  
972 outcomes, and facilitate communication and information sharing within and between  
973 organizations managing or researching management endpoints. Ultimately, understanding the  
974 mechanisms by which EECs influence large-river fishes will improve the effectiveness of  
975 restoration and management actions.

976 As shown with our case studies, our CM is flexible and applicable to a wide range of  
977 river systems with different anthropogenic drivers and management objectives. We feel our CM  
978 provides a generic structure that scientists can adapt to their management goals and needs. By  
979 not being overly prescriptive, for example, with respect to the components of the Tier 2 and 3  
980 EEC components, scientists can adapt the CM to different biological communities and  
981 management endpoints. By doing so, we feel that users have the flexibility to place their  
982 management questions in the context of EECs that are specific to their large-river system.

983 Although the case studies addressed management issues that were river or basin specific,  
984 there were similarities relative to information needs and data availability. For example, in most

985 systems information on river discharge and water temperature were needed and available.  
986 Conversely, information regarding trophic relationships and the habitat requirements of larval  
987 fishes were generally lacking. This result suggests that there may be a common need for a better  
988 understanding of certain factors across large-river systems.

### 989 **Acknowledgements**

990 We thank Megan Dethloff of the Pacific Northwest Aquatic Monitoring Partnership for her role  
991 in organizing the logistics associated with the workshop and conference calls needed to develop  
992 this manuscript. David Ward from the U.S. Geological Survey's Grand Canyon Monitoring and  
993 Research Center provided many valuable comments and suggestions that improved the  
994 manuscript. This work was funded in part by U.S. Geological ~~Survey's Core~~ Survey, Science  
995 ~~Systems Mission Area~~ Synthesis, Analysis, and Research Program. This research is a contribution  
996 of the Ball State University, Illinois Natural History Survey, Oregon Department of Fish and  
997 Wildlife, Pacific Northwest Aquatic Monitoring Partnership, the ~~Oklahoma and~~ Alabama  
998 Cooperative Fish and Wildlife Research ~~Units~~ Unit, and the U.S. Geological Survey Columbia  
999 Environmental Research Center, Grand Canyon Monitoring and Research Center, Oregon Water  
1000 Science Center, Upper Midwest Environmental Sciences Center, and Western Fisheries Research  
1001 Center. Any use of trade, firm, or product names is for descriptive purposes only and does not  
1002 imply endorsement by the U.S. Government. An animal care and use protocol was not required  
1003 for this research.

1004

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1379 **Supporting Information Captions**

1380 Fig S1. Discharge (m<sup>3</sup>/s) patterns over time in the Canadian River, Oklahoma near Canadian, TX  
1381 (USGS 2019; USGS Gage 07228000).

1382 Fig S2. Hydrograph showing pre- and post-Glen Canyon Dam closure in 1964 (dashed line)  
1383 mean monthly discharge (m<sup>3</sup>/s), which transitions from seasonally stochastic to a more  
1384 homogeneous regime focusing on anthropogenic interests.

1385 Fig S3. The spatial and temporal scales of the management goal, the scientific inferences needed  
1386 to inform the management goal, and that data collection needs to occur to support the inferences  
1387 for monitoring information needs identified as requiring additional data in the case study  
1388 addressing Humpback Chub recruitment in the Colorado River between Glen Canyon Dam and  
1389 Lake Mead, Arizona (see Table S2 for additional detail). A: Tier 2 EEC= larval Humpback Chub  
1390 habitat; Stressors=habitat fragmentation, turbidity and Tier 2 EEC= Humpback Chub spawning  
1391 habitat; Stressor= water temperature and Tier 3 EEC=insect production; Stressor=benthic  
1392 macroinvertebrate habitat quantity and quality and Tier 3 EECs=all; Inter-tier interaction=trophic  
1393 level interactions; B: Tier 3 EEC=larval Humpback Chub production; Stressor= larval Humpback  
1394 chub habitat quantity and quality; C: Tier 3 EEC=Humpback Chub egg quality and production;  
1395 Stressors= Humpback Chub spawning habitat quantity and quality; D:Larval Humpback Chub  
1396 production; Inter-tier interaction=mortality of Humpback Chub eggs; E: Tier 3 EEC= larval  
1397 Humpback Chub production; Stressor=predation by invasive species and Tier 3 EEC=Primary  
1398 production; Stressor=nutrient flux; F: Tier 1 EEC= **biogeochemistry/thermodynamics; Inter-tier**  
1399 **interaction=sediment adsorption of contaminants and nutrients; G: Tier 3 EEC=Humpback Chub**  
1400 **age-0 recruitment; Inter-tier interaction=mortality of larval Humpback Chub.**



1401 Fig S4. Proportion of total annual Columbia River discharge at The Dalles, OR occurring in the  
1402 month of June from 1879 to 2015.

1403 Fig S5. The spatial and temporal scales of the management goal, the scientific inferences needed  
1404 to inform the management goal, and that data collection needs to occur to support the inferences  
1405 for monitoring information needs identified as requiring additional data in the case study  
1406 addressing White Sturgeon recruitment in the Columbia River (see Table S3 for additional  
1407 detail). S4A: Tier 1 EEC= biogeochemistry/thermodynamic; Stressor= altered biogeochemical  
1408 regime and Tier 2 EEC= benthic macroinvertebrate habitat; Stressors=channel stability, sediment  
1409 deposition, fragmentation and Tier 2 EEC=Larval White Sturgeon habitat; Stressors=habitat  
1410 fragmentation sediment deposition, water temperature and Tier 2 EEC=White Sturgeon  
1411 spawning habitat; Stressors=contaminants, sediment deposition and Tier 3 EEC=White Sturgeon  
1412 egg quality and production; Stressor=predation by invasive species and Tier 3 EEC=White  
1413 Sturgeon larvae production; Stressor=predation by invasive species and Tier 3 EEC=benthic  
1414 macroinvertebrate production; Stressor=benthic macroinvertebrate habitat quantity and quality;  
1415 B: Tier 1 EEC=sediment transport; Stressors=altered sediment regime, altered hydraulic regime  
1416 and Tier 1 EECs=channel morphology/hydraulics, sediment transport; Stressor=altered hydraulic  
1417 regime and Tier 3 EEC=primary production; Stressor=nutrient fluxes; C: Tier 1 EEC=channel  
1418 morphology/hydraulics, sediment transport; Stressor=altered hydraulic regime and Tier 1 EEC =  
1419 channel morphology/hydraulics, sediment transport; Inter-tier interaction=sediment transport  
1420 dynamics; D: Tier 1 EEC=channel morphology/hydraulics, sediment transport; Stressor=altered  
1421 hydraulic regime and Tier 1 EEC=channel morphology/hydraulics, sediment transport; Inter-tier  
1422 interaction=sediment transport dynamics; E: Tier 1 EEC=biogeochemistry/thermodynamics;  
1423 Inter-tier interaction=sediment adsorption of contaminants and nutrients; F: Tier 3 EEC=White

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1424 Sturgeon larvae production; Stressors=larval White Sturgeon habitat quantity and quality and  
1425 Tier 3 EEC=White Sturgeon larvae production, age-0 White Sturgeon recruitment; Inter-tier  
1426 interaction=mortality and White Sturgeon egg quality and production; Inter-tier  
1427 interaction=predation of White Sturgeon eggs by native fish and Tier 3 EECs=White Sturgeon  
1428 larvae production; Inter-tier interaction=predation of White Sturgeon larvae by native fish and  
1429 Tier 3 EECs=all; Inter-tier interactions=trophic level interactions.

1430 Fig S6. Largemouth bass (*Micropterus salmoides*) data from the Pool 13 of the Upper  
1431 Mississippi River (A, B) and the La Grange Pool of the Illinois River (C, D). The two river  
1432 reaches are roughly the same latitude, but the La Grange Pool is more limited in overwintering  
1433 habitat. Population abundance is presented in panels A and C where each point is an individual  
1434 fish cumulatively caught with standardized day time electrofishing (Ratcliff et al. 2014) in a  
1435 specific year. The dashed triangle highlights ‘missing’ >400 mm size classes since 2000 in the  
1436 La Grange Pool. Population size structure is indexed by proportional stock density (PSD) is  
1437 presented in panels B and D with the dashed line showing trends in the largest size classes over  
1438 time. Data and methodology were downloaded from the publicly available databases via the  
1439 Upper Mississippi River Restoration’s Long Term Resource Monitoring Graphical Fish Browser  
1440 [~~112~~115].

1441 Fig S7. The spatial and temporal scales of the management goal, the scientific inferences needed  
1442 to inform the management goal, and that data collection needs to occur to support the inferences  
1443 for monitoring information needs identified as requiring additional data in the case study  
1444 addressing native fish biodiversity and habitat diversity in the Mississippi and Illinois rivers (see  
1445 Table S4 for additional detail). A: Tier 1 EEC=sediment transport; Stressor=altered hydraulic  
1446 regime and Tier 1 EEC=biogeochemistry/thermodynamics; Stressor=altered biogeochemical

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1447 regime and Tier 1 EEC=biogeochemistry/thermodynamics; Inter-tier interaction=sediment  
1448 adsorption of contaminants and nutrients; B: Tier 2 EEC=adult native fish overwintering habitat;  
1449 Stressors=water velocity, water temperature, dissolved oxygen, sediment deposition and Tier 2  
1450 EEC=juvenile native fish habitat; Stressors=water depth, water velocity, water temperature,  
1451 dissolved oxygen, contaminants, sediment deposition and Tier 2 EEC=native fish spawning  
1452 habitat; Stressors=water depth, water velocity, habitat fragmentation, sediment deposition, water  
1453 temperature, dissolved oxygen, contaminants and Tier 3 EEC=adult and juvenile native fish  
1454 recruitment; Inter-tier interaction=mortality and Tier 3 EEC=all; Stressors=invasive species and  
1455 Tier 3 EEC=all; Inter-tier interaction=trophic level interactions; C: Tier 1 EEC=channel  
1456 morphology/hydraulics; Inter-tier interaction=channel forming processes; D: Tier 1 EEC=channel  
1457 morphology/hydraulics, sediment transport; Inter-tier interaction=sediment transport dynamics;  
1458 E: Tier 3 EEC=adult native fish recruitment; Stressor=adult native fish overwintering habitat  
1459 quantity and quality and Tier 3 EEC=juvenile native fish recruitment; Stressor=juvenile native  
1460 fish habitat quantity and quality and Tier 3 EEC=native fish egg quality and production;  
1461 Stressor=spawning habitat quantity and quality.

1462 Table S1. Summary of information needs identified in the Conceptual Model describing factors  
1463 affecting the recruitment of the Arkansas River Shiner in the South Canadian River, OK (Fig 4;  
1464 this publication) by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or within  
1465 Tier interactions and an assessment of the status of existing information that could be used to  
1466 address the information needs.

1467 Table S2. Summary of information needs identified in the Conceptual Model describing factors  
1468 affecting the recruitment of the Humpback Chub in the Colorado River, Arizona (Fig 6; this  
1469 publication) by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier

1470 interactions and an assessment of the status of existing information that could be used to address  
1471 the information needs.

1472 Table S3. Summary of information needs identified in the Conceptual Model describing factors  
1473 affecting the recruitment of age-0 White Sturgeon in the Columbia River (Fig [87](#); this  
1474 publication), by Essential Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier  
1475 interactions and an assessment of the status of existing information that could be used to address  
1476 the information needs.

1477 Table S4. Summary of information needs identified in the Conceptual Model describing factors  
1478 affecting the restoration and maintenance of native fish biodiversity and habitat quantity and  
1479 quality in the Upper Mississippi and Illinois rivers (Fig [98](#); this publication), by Essential  
1480 Ecosystem Characteristic (EEC) Tier, EEC, and stressor or inter-tier interactions and an  
1481 assessment of the status of existing information that could be used to address the information  
1482 needs.

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PONE-D-21-12444

Identifying monitoring information needs that support the management of fish in large rivers

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Reviewer 1 wonders about the utility of such conceptual models in the more realistic case of multiple species contexts. How could the model be expanded in this regard, besides the case of simple richness measures? In addition, how could the model help in actually prioritising or ranking the variables or interactions identified? Finally, reviewer 1 also noticed that an important stressor related to fragmentation and connectivity is only marginally discussed and included in the model. This is critical for meta-population dynamics and should be given more emphasis.

Reviewer 2, similarly raises the critical issue of the multi-species context, and how the needs of different species could be simultaneously identified. Therefore, I advice to expand the Discussion in this regard, eventually acknowledging limitations and suggesting future research needs. Reviewer 2 also wonders how such models could effectively guide restoration and decision-making beyond monitoring needs; if the relative importance of data gaps and interactions is not quantified (e.g. via a cost-benefit analysis), how could it help prioritise the focus of monitoring and action?

Besides carefully responding to each reviewers' comments and modify the manuscript accordingly, I also suggest to simplify the manuscript, which feels rather long. Perhaps some of the background information from each case study could be included as supplementary or shortened. Also, caption from Fig.5 (and sister-figures) is rather hard to digest for the reader. I wonder if this could be simplified as well.

Response: Thank you for the opportunity to revise our manuscript. We have tried to address comments of Reviewer 1 and 2 below and in the revised manuscript. To shorten and simplify the manuscript, we relocated some of the contextual information from the case studies and moved it to an Appendix in Supplemental Information. With respect to Fig 5 and sister figures, we have discussed trying to simplify the figure captions but have not come up with a good solution. There is a lot of information contained within the figures and feel that further generalizations would not be clarifying. We do, however, acknowledge that the figure caption format is awkwardly long. What we propose is

that we retain Fig 5 in the main body of the text as an example, and then move subsequent sister figures to Supplemental Materials. Please let us know if this satisfies you and the reviewer's comments to reduce the length of the manuscript.

## **Comments to the Author**

### 5. Review Comments to the Author

Reviewer #1: In this study a conceptual model is used to aid the development of best practices of large river monitoring programs. The model was developed based on former scientific works and during scientist's workshop negotiations. Case study applications prove that the application of this complex conceptual model can be useful to identify critical information gaps, which can then be used to develop management and monitoring objectives.

I like the approach of developing such conceptual models, which can reveal information gaps, and think that the model in general can be useful to adopt across large river systems with some refinements and local adaptations. Consequently, I believe showing such an approach can provide useful information for the readers.

- 1) What I lack is to show more convincingly how such complex models can be used for multispecies systems, where not only the requirements of a single species is evaluated, which in fact the more realistic situation. How can individual species level models be put together to provide meaningful information for management? It would be useful to discuss this in more detail in the Discussion section.

Response: Thank you for this comment. We have added text in the discussion that describes how the CM could contribute to our understanding of the need for a multi-species context in management activities. Please see: L645-691

- 2) Also a critical issue which should be briefly discussed is how the identified critical target variables should be prioritized, especially in a multispecies systems, where several variables will appear. Development of this section could convince the reader and could clearly show the applicability of such conceptual models by management.

Response: Thank you for this insight. We have provided language in the discussion that describes how the CM could be used to identify critical target variables in a multispecies context. Please see: L650-668

- 3) Although channel morphology/hydraulics may contain fragmentation/connectivity issues this should be made more clear in the material, because this is one of the most critical issue, which determine fish (meta)population or metacommunity dynamics. In fact fragmentation is often used as one of the most critical variable of anthropogenic drivers and as such is a critically important target to mitigate by management. However, it does not appear either in Fig 2 or Fig 3, but only on the case study figures belonging to morphology/hydraulics TIER1 components.

Response: Thank you. We agree with your assessment. We have further emphasized the importance of fragmentation by specifically mentioning it in the manuscript section describing the CM form. Please see: L223-234. Also, in Table 2, habitat fragmentation is emphasized as affecting multiple facets of the CM in multiple river systems and is mentioned in the text describing Table 2. This result indicates the need to better study the effects of habitat fragmentation on multiple biotic components.

Reviewer #2: Dear Editor,

This study demonstrates how a conceptual model can be used to identifying knowledge gaps in the mechanisms by which Essential Ecosystem Characteristics influence large-river fish species in the USA. These gaps should then be filled to improve the effectiveness of restoration and management.

I agree on the value of these conceptual models to identify knowledge gaps and inform decisions on what to monitor to fill them and allow a better understanding of the system and, therefore, enhance our capacity to manage them adequately. However, I disagree with some of the arguments:

- 1) The conceptual model represents potential interactions across different structural element of the river system but does not allow quantitative evaluations of strength of those interaction. As such, the value of is conceptual model is limited to identifying knowledge gaps and cannot be used to evaluate the relative importance of each interaction. Therefore, this conceptual model should only be used for identifying knowledge gaps and not for decision-making, as argued (see L771-773), beyond monitoring.

Response: This is an excellent point and we have removed the statement in L771-773 and elaborated on the considerations that need to be accounted for, and the difficulties with, assessing benefit:cost ratios. Please see: L692-726. Also, you are correct that the CM does not provide quantitative evaluations of the strength of the relations. We do acknowledge this and suggest that the CM could provide a basis for developing quantitative assessments in L749-754 and have added language that describes how the CMs could be the basis for Structural Decision Making and Adaptive Management processes (see L727-741).

- 2) The conceptual model lacks a cost analysis to evaluate the most efficient way of filling knowledge gaps. Some of the gaps might be more difficult/ costly or even feasible to fill. Without such analysis we can only identify the gaps but cannot prioritise where to focus monitoring on a cost-effective way and just confirm where gaps exist.

Response: Thank you for this comment. In addition to addressing the benefit:cost issue above, we have provided language in the discussion that describes how the CM could be used to identify critical target variables in a multispecies context but that there are critical uncertainties that need to be considered. See: L650-668. We agree with you about prioritizing based on cost effectiveness but respectfully suggest that the CM could provide information that would suggest where to focus monitoring effort.

- 3) Three of the case studies present conceptual models for individual species. While I see the value of developing these conceptual models for charismatic endangered species, I wonder how feasible/ useful it would be this method when facing management needs for many species simultaneously. One of the case studies does present a conceptual model for the full fish community, but focused on diversity, rather than individual species, so no information of particular species issues are addressed. Would it be feasible to elaborate a conceptual model that addressed all individual species needs/ issues simultaneously? This would allow identifying knowledge gaps common to multiple species simultaneously.

Response: Thank you for this comment. We have added text in the discussion that describes how the CM could contribute to our understanding of the need for a multi-species context in management activities. Please see: Please see: L645-691



4) Minor comments:

- L304 & 369. What does ATV stand for?

Response: Thank you for bringing this to our attention. ATV stands for all-terrain vehicle. We have removed the acronym from the revision.

- The manuscript is quite long, especially because of the description of each case study. It would be good to present the information of these case studies in a more synthetic way (maybe on a table?).

Response: Thank you for the comment. Per your and the Associate Editor's recommendation we have pulled out some of the contextual information from the case studies and moved the information to an Appendix in Supplemental Information. We have also moved three figures and associated captions to the supplemental information section.

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