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Listed as endangered in 1988, the Lost River sucker (*Deltistes luxatus*) and Shortnose sucker (*Chasmistes brevirostris*) were once abundant and widely distributed in the Klamath Basin in Southern Oregon and Northern California. Populations of both species have been declining since the late 1960's. Factors thought responsible for declines include naturally occurring disturbances (e.g., periodic drought), water resource and land development activities, degradation of habitat and water quality, and interactions with introduced exotic species. Detection of any substantial adult recruitment for the last few decades has been minimal. We used a quantitative decision modeling approach to explore potential outcomes of alternative conservation strategies that include captive propagation and catch, grow, and release. Uncertainty about the factors responsible for the apparent lack of recruitment was represented using alternative models of system dynamics. Sensitivity analysis indicated that the model predictions were highly sensitive to population dynamics during early life stages and the alternative ideas of system dynamics. To address these uncertainties, I propose an adaptive approach to sucker recovery that integrates monitoring, research, and management.

Development of a Structured Adaptive Approach to Klamath Basin Sucker Recovery Planning

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Miguel F. Barajas, Author

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1 Introduction

Within the family Catostomidae, there are approximately 75 fish species distributed throughout North America (Cooke et al. 2005). From the Late Pleistocene to present day, suckers of the genus *Chasmistes* inhabit many of the lakes found in North America (Belk et al. 2011). Lake suckers historically served as a subsistence fishery for native tribes and as a recreational fishery (NRC 2004; Cooke et al. 2005). Currently all Chasmistes species are either extinct or listed as endangered due to the human-induced changes that have rapidly occurred over the last century (Scoppettone and Vinyard 1991).

The isolated nature of lakes found in the semi-arid environments has led to high rates of endemism in lake suckers (Belk et al. 2011). A series of separate shallow lakes, remnants of the ancient Lake Modoc, located in the Upper Klamath Basin in southern Oregon and northern California (Figure 1) contain two of these species, the Lost River Sucker (*Deltistes luxatus*) and Shortnose Sucker (*Chasmistes brevirostris*; Dicken and Dicken 1985). The Upper Klamath Basin is characterized as dry, high elevation desert due to the rain shadow effect from the Cascade Range. Hydrologic conditions in the Klamath Basin are largely dependent upon seasonal melt of winter snowpack (Bortleson and Fretwell 1993). During the dry summer months, lake water quality can become severely degraded resulting in recruitment failure of juvenile suckers and at times large scale fish kills (Saiki et al. 1999; Janney et al 2008). Lake suckers in the Klamath Basin have presumably, adapted to these cycles of poor environmental conditions by being long-lived and resilient to degraded habitat conditions, albeit only to a certain extent (Martin and Saiki 1999; Saiki et al. 1999).

The Lost River Sucker and Shortnose Sucker were once abundant and widely distributed in the Klamath Basin (Andreasen 1975). With the arrival of European settlers and the expansion of agriculture and cattle production in the basin, lake sucker habitats were significantly changed (NRC 2004). The draining and conversion of Lower Klamath Lake and Tule Lake as well as lake-adjacent wetlands into agricultural land severely restricted historical sucker habitat and degraded the water quality conditions of Upper Klamath Lake forcing the lake into a hypereutrophic state (Kann 1997; Eilers et al. 2004). Populations of both sucker species noticeably began to decline during the late 1960's and were listed as endangered in 1988 (NMFS & USFWS 2013). Factors thought responsible for their declines include naturally occurring periodic drought, water resource and land development activities, degradation of habitat and water quality, and interactions with introduced exotic species (i.e., Fathead Minnows) (Bortleson and Fretwell 1993; USFWS 2013; Perkins et al. 2000a).

The full extent of the underlying processes responsible for population declines and reproductive failure are poorly understood (Rasmussen 2011). With so many potentially interacting factors in the Klamath Basin, it is difficult to disentangle their effects on sucker population dynamics making management difficult. Effective recovery of Klamath sucker populations requires an integrated approach in assessing future population response to conservation strategies and natural variability over time and space. The recovery approach should allow for quantifying the level of uncertainty associated with each potential conservation strategy outcome. One such approach is quantitative decision analysis. By modeling hypothesized effects of conservation decisions on sucker population dynamics, quantitative decision analysis provides a means for evaluating the relative utility of alternative management strategies. Decision analysis also can identify the assumptions and hypotheses regarding underlying mechanisms that substantially influence management decision-making that can then be targeted for future research.

The goal of my research was to develop an adaptive, decision support tool for assisting biologists in understanding the ecology of the Klamath Basin and managing Klamath suckers and their habitats. Towards this end, I have worked with managers and scientists in the Klamath basin to accomplish the following objectives: (1) to identify Klamath Basin sucker conservation objectives, decision alternatives, and relevant consequences of management actions; (2) to develop a model relating decision alternatives and ecological mechanisms underlying population dynamics to the predicted responses of Klamath Basin suckers to management actions; (3) to identify the optimal management action and key uncertainties and assumptions in the decision model; (4) and lastly to develop a means to integrate new and existing monitoring data to reduce key uncertainties and improve future decision-making.

2 Problem Background

Located in southern Oregon and northern California, the Klamath Basin is generally divided into an upper and lower basin. The spatial extent of this is the upper basin, the only area in the world where endangered Lost River and Shortnose Suckers currently exist (NMFS & USFWS 2013). The upper basin is defined as the area north and east of Iron Gate Dam on the Klamath River (NRC 2004). The climate in the Upper Klamath Basin is characterized as dry, high elevation desert due to the rain shadow from the Cascade Range (Eilers et al. 2004). Most of the precipitation in the basin comes in the form of snow and most water entering the basin comes from snowmelt in the spring (Eilers et al. 2004). Water levels in the basin are highest in the spring and then decrease to minimum levels by August-September (NRC 2004). Light precipitation in the summer and groundwater inputs through springs also serve as water sources (Gannett et al. 2007).

Historically, the major natural water bodies in the upper basin included Upper Klamath Lake, Lower Klamath Lake, and Tule Lake. Major modifications in land use due to the U.S. Bureau of Reclamation's irrigation project, the Klamath Project, Lower Klamath Lake and Tule Lake were drained along with many of the wetlands and were converted to agricultural land in the early 1900's (NMFS & USFWS 2013). A series of irrigation reservoirs were also constructed, most notably Clear Lake and Gerber Reservoirs. Presently, only Upper Klamath Lake remains somewhat intact out of the three historical lakes in the upper basin. The major rivers occurring in the upper basin include the Williamson and Wood Rivers, which feed into Upper Klamath Lake and the Klamath and Lost Rivers which drains Upper Klamath Lake (NRC 2004). Several National Wildlife Refuges, including the first waterfowl refuge in the US

Fish and Wildlife Service refuge system, Lower Klamath National Wildlife Refuge, as well as public and private preserves are in the upper basin (NRC 2004).

Aquatic Systems in the Upper Klamath Basin

The largest aquatic system in the upper basin is Upper Klamath Lake, spanning 27,114 ha (NRC 2004). Upper Klamath Lake is a relatively shallow lake with average mean depths ranging from 2.4 to 3 m and a maximum depth of 6 m located in the southwestern side of the lake (Banish et al. 2009). Lake level historically varied as little as 1 m within a year but now range about 1.8 m due to irrigation for the Klamath Project (NMFS & USFWS 2013). The lake is located on volcanic deposits from the eruption of Mount Mazama 7,000 years ago (present day Crater Lake), and thus, high levels of phosphorus from the volcanic soils infiltrate the lake resulting in naturally eutrophic conditions (Dicken and Dicken 1985; Walker 2001). Conversion of wetlands into land used for agriculture around the lake has altered wetland-lake water quality dynamics and contributed to increased nutrient inputs and the lake is now classified as hypereutrophic (Wood et al. 1996; ASR 2005). The increased nutrient loads have led to blooms of nitrogen-fixing bluegreen algae (*Aphanizomenon flos-aquae)* that regularly occur in the summer and increase pH and ammonia levels (ASR 2005). When the algae blooms crash, dissolved oxygen decreases and fish kills can occur (Wood et al. 2008).

Before the Klamath Project, Lower Klamath Lake and Tule Lake were similar in size to Upper Klamath Lake spanning 38,040 and 44,515 ha respectively (NRC 2004). After being drained and converted to agriculture as part of the Klamath Project, Lower Klamath Lake and Tule Lake were reduced to 1,902 and 3,824 to 5,261 ha (NRC 2004).

Clear Lake is like Upper Klamath Lake in that it is a shallow lake relative to its surface area with a mean depth of 2.4 m and a surface area of 10,117 ha (USBR 2000). Suckers in Clear Lake utilize Willow Creek, one of the tributaries to Clear Lake for spawning (Burdick and Rasmussen 2013). Both endangered sucker species occupy Clear Lake and multiple age classes have been observed (Barry et al. 2009). Due to a smaller surface area and a deeper water column, water quality conditions in

Clear Lake are better than in Upper Klamath Lake and Clear Lake is much more turbid and does not have algal blooms (NRC 2004).

Gerber Reservoir has a surface area of about 1,538 ha and is much deeper than Clear Lake and Upper Klamath Lake with most of the reservoir having waters deeper than 4.6 m (NRC 2004). Water quality in Gerber Reservoir is considered eutrophic and it has moderate algae blooms but not as severe as Upper Klamath Lake (NMFS & USFWS 2013). Small populations of suckers have been observed in Gerber Reservoir (NMFS & USFWS 2013).

The Williamson River fed in part by the Sprague River feeds into the northern side of Upper Klamath Lake along with the Wood River. The Williamson and Sprague River system provides more than half the water entering Upper Klamath Lake with the rest provided by Wood River (Kann and Walker 2001).

The Klamath Project

Initiated by the U.S. Bureau of Reclamation in 1905, the Klamath Project is a vast series of canals and reservoirs intended to provide irrigators in the Klamath Basin with a steady supply of water (NRC 2004). Many changes to aquatic systems have occurred in Upper Klamath Basin because of the Klamath Project (Doremus and Tarlock 2003). Before the Klamath Project, Lower Klamath Lake and Tule Lake were larger than present day Upper Klamath Lake (NRC 2004). The lake complexes contained open water, wetlands, and marshes that likely served as habitat for suckers at all life stages. By 1924, the Klamath Project converted 90% of the open water and wetlands into agriculture and disconnected Lower Klamath Lake and Tule Lake from the Klamath River (NRC 2004). In times of high runoff, the Klamath River overflowed into the Lost River and then eventually drained into Tule Lake (NRC 2004). To prevent flooding, settlers built dikes across the Lost River in the late 1800's (Dicken and Dicken 1985). After the Lost River was disconnected from the Klamath River by settlers in the late 1800s, the U.S. Bureau of Reclamation's Klamath Project drained what remained of Tule Lake and converted it to irrigated pasture (NRC 2004).

Before 1910, the Lost River historically drained the marsh system that is now Clear Lake into the Klamath River (USBR 2000). A dam was constructed in 1910 that impounded Clear Lake with water from the Lost River to store agricultural runoff for irrigation (NMFS & USFWS 2013). Presently the Lost River and Klamath River are only connected by a series of canals managed through the Klamath Project (NMFS & USFWS 2013). The Lost River, once a major spawning site for suckers, is now a channelized canal with regulated flows (NRC 2004). Similarly, to Clear Lake, current day Gerber Reservoir was a 3,500-acre wetland that was converted to a reservoir in 1926 for irrigation in the Klamath Project (NRC 2004).

Life History of Endangered Suckers in the Klamath Basin

The Lost River and Shortnose Suckers are relatively large (0.3 to 0.6 meters in length) with Lost River Suckers growing larger than Shortnose Suckers (Buettner and Scoppettone 1990; Hewett et al. 2012). Both suckers are relatively long-lived with reported maximum ages of 57 and 33 years for Lost River Suckers and Shortnose Suckers, respectively (Scoppettone 1988; Terwilliger et al. 2010). Lost River Suckers become sexually mature at 7 to 9 years of age, while Shortnose Suckers mature at 5 to 7 years of age with males maturing before females (NRC 2004). Lost River Sucker fecundity ranges from 44,000 to 236,000 eggs/fish/season and Shortnose Sucker fecundity ranges from 18,000 to 72,000 eggs/fish/season (NRC 2004). Both sucker species reside in lakes and spawn in tributaries (Buettner and Scoppettone 1990). A proportion of the Lost River Sucker population is known to spawn near springs on the margins of Upper Klamath Lake (Buettner and Scoppettone 1990). Juvenile sucker habitat consists of shallow lakeshore environments but as they mature they occupy deeper water (Markle and Cooperman 2002).

Sucker populations in Upper Klamath Lake experience periodic mass mortality events due to naturally degraded water quality conditions (Morace 2007). In addition to periodic fish kills, populations declined due to many other factors including reduction of habitat and further degradation of water quality from agricultural runoff, overfishing, predation by birds and introduced non-native fish, parasites, blockage to historical spawning areas, and entrainment into irrigation systems (NMFS & USFWS 2013). Recreational and commercial fishing for Lost River and Shortnose Suckers in Upper Klamath Lake was banned in 1987 and sucker were listed as endangered under the Endangered Species Act in 1988 (53 Fed. Reg. 27130, 18 July 1988). Since their listing, there has been no significant recruitment of juvenile suckers into the adult population in Upper Klamath Lake (Scoppettone and Vinyard 1991; Hewett et al. 2012).

Regulatory Context: The Endangered Species Act

The Endangered Species Act is the primary regulatory mechanism for managing lake suckers and their habitats in the upper basin. The principal listing agency is the U.S. Fish and Wildlife Service. They are responsible for identifying sucker critical habitat and producing a sucker recovery plan (NMFS & USFWS 2013). All other agencies and organizations must consult with the U.S. Fish and Wildlife Service before carrying out conservation actions (NMFS & USFWS 2013). The U.S. Fish and Wildlife Service's duty is to ensure that no actions in the basin jeopardize the existence of endangered species and/or modify critical habitat (NMFS & USFWS 2013). This duty also pertains to assessing operation of the U.S. Bureau of Reclamation's Klamath Project, specifically the maintenance of water levels in Upper Klamath Lake (NMFS & USFWS 2013).

Enforcement of the U.S. Fish and Wildlife Service's authority occurred in the spring of 2001 when it was decided that the U.S. Bureau of Reclamation could not follow through with contractual obligations to deliver water to irrigators (Doremus and Tarlock 2003). Their reasoning was that low lake levels due to water drawdowns would jeopardize the persistence of endangered sucker in Upper Klamath Lake (UFWS 2002). The decision to prohibit water delivery to irrigators resulted in protests and contributed to building tension and conflict in the Klamath Basin as well as a sense of distrust and skepticism in the scientific conclusions put forth in the decision-making process (Doremus and Tarlock 2003).

History of Land Use in the Upper Klamath Basin

The Upper Klamath Basin has endured a series of events over the past 200 years that has significantly altered the region (NRC 2004). The Upper Klamath Basin was occupied by native tribes for 11,000 years prior to the arrival of fur trappers from the Hudson Bay Company of Canada in the early 1800's, (Cressman 1956; Dicken and Dicken 1985). The Gold Rush of the 1850's brought miners and ranchers, leading to the first European settlers in the area (Dicken and Dicken 1985). The Klamath Reservation was established in 1864 but tensions grew between settlers and native tribes culminating in the Modoc Indian War of 1872-1873 (NRC 2004). In the late 1800's cattle ranching and commercial logging increased in the region and altered land usage (NRC 2004). To improve ranching and increase farming in the Klamath Basin, irrigators needed more land and secure access to water (Dicken and Dicken 1985). Subsequently, the Klamath Project was initiated in 1905 and Lower Klamath Lake and Tule Lake were drained and converted to agricultural land (NRC 2004). A series of National Wildlife Refuges were created in the region in the 1910's and 1920's to try to retain the Klamath Basin's historical ecological importance, particularly for waterfowl habitat (NRC 2004). During World War II, an internment camp for Japanese-American citizens was stationed at Tule Lake (NRC 2004). After the war, land for ranching and agriculture in the basin was parceled out to veterans through a lottery process (NRC 2004).

In the 1960's, observations of sucker population decline in Upper Klamath Lake were first observed (Markle and Cooperman 2002). Klamath suckers were finally listed as endangered under the Endangered Species Act in 1988 (NMFS & USFWS 2013). A series of fish kills occurred in Upper Klamath Lake in the 1990's (NMFS & USFWS 2013). With the release of the U.S. Fish and Wildlife Service's Biological Opinion on Klamath Project operations in 2001, water delivery to irrigators was cut-off to retain habitat for endangered suckers (Doremus and Tarlock 2003). After the water crisis of 2001, conservation efforts have been initiated, notably the restoration of the Williamson River Delta, removal of Chiloquin Dam, and the installation of fish screens of some of the irrigation systems of the Klamath Project (NMFS & USFWS 2013). Most recently, the adjudication process to determine claims in water rights in the Upper Klamath Basin have been initiated (KBRA 2010).

Causes of Decline of Klamath Basin Suckers

The decline of Klamath Basin sucker populations is believed to be due to multiple factors that affect each of the major life stages: egg, larvae, juvenile, and adult. Historical spawning habitat in the Sprague River was blocked by the Chiloquin Dam, which was constructed in the early 1900s and was removed in 2008 to allow access to the historic spawning habitat (NMFS & USFWS 2013). Suckers that spawn along lakeshores in Upper Klamath Lake require depths of 0.6 m to access the spawning locations (Buettner and Scoppettone 1990; Markle and Cooperman 2002). Spawning habitat depth is optimal when lake levels are at or above 1,263 m elevation but quickly diminish as levels approach 1,262 m. Thus, lake spawning suckers are unable to spawn during periods of low lake levels due to drought or human water use (NMFS & USFWS 2013). Suckers require gravel substrates for spawning, so channelization of streams has reduced gravel substrates and spawning success (Perkins and Scoppettone 1996; Markle and Cooperman 2002). Diking, ponding, and rerouting water over time have resulted in suckers abandoning some of the historical spawning sites near springs on Upper Klamath Lake including Ouxy, Sucker, Harriman, and Barkley Springs (Andreason 1975; Perkins et al. 2000b; Cooperman and Markle 2003; Rasmussen 2011).

Factors affecting the larval and juvenile stages are not well understood due to the difficulties in observing the dynamics of these early life stages. From the observations that do exist, there appears to be a high level of morphological anomalies that could indicate physiological stresses during development (Plunkett and Snyder-Conn 2000; Carlson et al. 2002; Bottcher and Burdick 2010; Markle et al. 2014). Deformities can impair swimming ability that can then impair escapement ability and result in lower survival (Plunkett and Snyder-Conn 2000). Predation by non-native fish species, specifically fathead minnow, has been observed to occur on larval and juvenile suckers (Markle and Dunsmoor 2007; Markle et al. 2014). Entrainment through irrigation systems and dams is another factor believed to affect larval and juvenile sucker survival (Bennetts et al. 2004; USFWS 2008; Hewitt et al. 2011; NMFS & USFWS 2013). Wind-driven currents in Upper Klamath Lake rotate in a clockwise pattern sweeping larval and juvenile suckers towards the southern part of Upper Klamath Lake, then become trapped in irrigation systems (Wood et al. 1996, 2008; USFWS 2008; Banish et al. 2009). Efforts to place fish screens on the intakes of the irrigation systems have helped to decrease entrainment rates but these have been successful primarily in reducing mortality in adult fish (USFWS 2013). Larval and juvenile suckers require emergent vegetation along shallow shores for habitat (Buettner and Scoppettone 1990; Markle and Cooperman 2002). Much of the historical vegetation around Upper Klamath Lake has been greatly reduced and the emergent vegetation that does exist becomes dewatered as lake levels fall over the course of the summer (USFWS 2008).

Since the beginning of recorded observations in the 1800s, adult sucker populations have experienced periodic mass mortality events in Upper Klamath Lake. Due to the combination of natural geologic conditions and anthropogenic influences, water quality in Upper Klamath Lake has become degraded (Kann and Walker 1999). During the summer, conditions in the lake can deteriorate quickly with the culminating effects of algae blooms, high temperatures, high pH, high ammonia, and low dissolved oxygen resulting in fish kills (Wood et al. 1996; Kann 1997; Eilers et al. 2004; Morace 2007). Poor water quality conditions are known to affect adult suckers and can be assumed to affect all other life stages although to what extent is unknown. In addition, parasite loads and infections on adult and juvenile suckers have been shown to occur at high rates (Carlson et al. 2002). Entrainment through irrigation systems also poses a threat to adult suckers (Gutermuth et al. 2000). Although some of the main intakes pipes have been screened, entrainment via Link River Dam still occurs (NMFS & USFWS 2013). Avian predation by American white pelican and double-crested cormorant is known to occur in the Upper Klamath Basin through the recovery of sucker PIT tags on nesting sites (Roby and Collis 2011; Burdick 2013). It has been hypothesized that during dry years when lake levels are lower, avian predation efficiency is higher, resulting in lower survival (Evans et al. 2015).

Recovery Strategies for Klamath Basin Suckers

The U.S. Fisheries and Wildlife Service's 2012 Recovery Plan for Lost River and Shortnose Suckers states that the recovery goal is to, "arrest the decline and enhance Lost River Sucker and Shortnose Sucker populations so that Endangered Species Act protection is no longer necessary." Recovery units are split up into two units that are then split up into management units: the Upper Klamath Lake Unit (river and shoreline spring spawners, Keno Reservoir, and populations below Keno) and the Lost River Basin Unit (Clear Lake, Tule Lake, Gerber Reservoir, and Lost River). Proposed strategies include: 1) restore/enhance spawning/nursery habitat, 2) reduce negative effects of poor water quality, 3) reduce the effects of introduced species, 4) reduce entrainment losses, 5) establish redundancy/resiliency enhancement programs, 6) increase juvenile recruitment, 7) maintain and/or increase spawning populations, and 8) establish sucker recovery implementation program. Within each of the main 8 recovery strategies outlined in the 2012 U.S. Fisheries and Wildlife Service's Recovery Plan for Lost River and Shortnose Suckers are a variety of actions that served as the basis for the Klamath Basin sucker decision model that was developed in my thesis.

3 Methods

An initial stakeholder workshop was conducted in November 2012 to evaluate the suitability of structured decision making (SDM) for assisting in the implementation of the Klamath sucker recovery plan. The workshop was facilitated by Oregon Cooperative Fish and Wildlife Research Unit personnel and attended by members or representatives of Klamath Tribes and various state and federal agencies (henceforth, stakeholders; Table 1). Following the workshop, the stakeholders decided that structured decision making would benefit the implementation of the sucker recovery plan and should be used to facilitate recovery management decision making.

3.1 Structured Decision Making Process

Structured decision making is a process that is used to inform and guide decision making. The process breaks down the decision into three parts: 1) management objectives, 2) candidate management actions, and 3) a model that predicts the effects of management actions on objectives (Conroy and Peterson 2013). Information about the effects of management actions and other factors on the management objectives is required to build a decision model. Because this information is typically incomplete or poorly understood, uncertainty must be incorporated into the model. These uncertainties can be categorized as three basic types: statistical uncertainty that arises due to the use of sample data to estimate parameters; environmental uncertainty that is due to uncontrollable environmental factors, such as the weather; and structural uncertainty that is due to the incomplete understanding of system dynamics. The first two of these are generally incorporated into decision models using statistical distributions. Uncertainty regarding underlying dynamics within the system can be incorporated into a decision model using alternative models, with each model representing alternative ideas about how the system works. The alternative models are constructed based on known or hypothesized relationships and levels of information and uncertainty. The effects of management actions are predicted with each alternative model, weighted, and combined to provide a composite estimate. This composite estimate is then used to identify the management action or series of actions that best satisfies the objectives. This action is defined as the optimal decision. As the system is monitored over time, predictions under alternative models can be compared to actual outcomes and the relative belief (i.e., the weights) in the hypotheses can be updated in the model. Within this updateable process, decision makers can iteratively use models to express an ever-evolving conceptualization of the system dynamics and explore action-reaction decision scenarios as the system being modeled changes. This is often defined as adaptive resource management (Walters and Holling 1990; Williams et al 2009).

In addition to determining what actions are optimal or have the greatest likelihood of achieving management objectives, decision models can be used to identify factors or model components that are highly influential and prioritize areas for additional research. Identification of these highly sensitive components also can help decision makers in determining where to direct monitoring effort.

The following sections outline the structured decision making (SDM) process used to identify the Klamath sucker stakeholder objectives and alternative management actions. It also documents the process of building the decision model to connect the actions to the objectives. Development of the model is broken down into three sections: the first describes the framework of the model and how it was parameterized; the second describes the differences between the two models that were built; and the third documents the evaluation of actions by the decision model.

During the SDM process, it is essential that all participants agree on the fundamental aspects of the decision-making process, namely defining the specifics of the decision situation. Clearly defining the situation allows for participants to collectively form a path towards identifying fundamental management objectives and developing alternative actions that satisfy the objectives. During the November 2012 meeting, it was agreed upon that the decision situation is as follows:

> *"To obtain wild, genetically diverse, self-sustaining populations of Shortnose and Lost River Suckers above Keno Dam that provides harvest and other cultural uses' and minimizes disruptions to existing human uses and native species."*

Along with the decision situation, spatial and temporal dimensions for the decision model were also identified. The extent of the decision included the upper Klamath Basin (Figure 1) that includes Upper Klamath Lake, Agency Lake, Clear Lake, Keno Reservoir, Sprague River, Lost River, Wood River, and the Williamson River. The spatial grain or smallest level of resolution to be modeled was individual lake systems. The desired temporal extent or planning horizon for the decision was long term and specified as 100 years. Participants indicated that sucker management decisions could potentially be made on an annual basis but that some decisions, such as propagation would be carried out over multiple years. Therefore, the temporal grain or time step was defined as annual to coincide with the potential frequency of decision making and to facilitate the updating of information gathered through monitoring. In the context of the Klamath decision model, a time-step began at the end of summer when most reliable young-of-year sucker monitoring data is collected (S. Burdick, personal communication).

The next step of the process was identifying the management objectives. There are two types of objectives, means objectives and fundamental objectives (Conroy and Peterson 2013). Means objectives, oftentimes confused as fundamental objectives, are actions that are taken to help achieve fundamental objectives. Fundamental objectives are the outcomes that are important to stakeholders for their own right. To illustrate, consider the objective of having or making more money. For most people, it is not the physical money that is desired but what having the money provides. Money, therefore, is a means towards satisfying the fundamental objective of financial freedom or being able to purchase desirable goods and services.

The stakeholders originally identified three fundamental objectives for the Klamath sucker conservation as: 1) maximize self-sustaining populations of Klamath suckers, 2) maintain genetic diversity of sucker populations, and 3) remain within budgetary constraints of the management agencies. After discussions on the feasibility of modeling and measuring (monitoring) genetic diversity, the stakeholders decided to remove that objective from consideration. The remaining objectives needed to be quantified to provide the basis for evaluating the relative benefits of alternative decisions and determine whether the objectives are being met after implementing a management action. The stakeholders identified adult sucker abundance as the measurable attribute representing the fundamental objective maximizing self-sustaining populations of Klamath suckers. To incorporate the quantifiable objective- remain within budgetary constraints, the stakeholders decided to use the estimated costs of each management alternative. To put both objectives on a common scale for comparison, a method called proportional scoring was used

(Clemen and Reilly 2001; Conroy and Peterson 2013). To calculate scores, the best, worst, and estimated outcomes for each objective were determined quantitatively as:

$$score = \frac{estimated\ outcome - worst\ outcome}{best\ outcome - worst\ outcome},$$

where each objective had a total score ranging from 0 to 1. The scores for each objective were combined into a total score using a weighted sum. The weights when added together had to equal to 1. The objectives were weighted based on the importance placed on each of them by the decision makers.

The next step in the SDM process was identifying the decision alternatives. The decision alternatives were the actions that could be taken towards satisfying the objectives (Conroy and Peterson 2013). The alternatives were initially identified by the stakeholders in the November 2012 workshop and later refined in a series of stakeholder meetings. The decision alternatives identified were categorized as: 1) translocating adult suckers, 2) controlling avian predators, 3) increasing juvenile sucker habitat, 4) improving water quality, and 5) propagating juvenile suckers in captivity then releasing into wild population, 6) reduce entrainment, and 7) no action (status quo).

3.2 Baseline Population Dynamics Model

The foundation of the Klamath Lost River Sucker (LRS) decision model is a stage-based population model, defined as a Lefkovitch matrix model. A Lefkovitch matrix model incorporates separate life stages rather than age classes (Caswell 2001). I decided to use a stage-based model due to the long-lived nature of the Klamath sucker populations rather than an age-based model because there are upwards of 50+ age classes for Lost River Suckers. The model consisted of total of 5 stages for each species and included both males and females. All statistical computations related to the Klamath sucker decision model were performed using *R 3.1.1* (R Core Team 2014).

3.3 Life Stages

The sucker population model consists of 5 life stages: young-of-year, age-1 juveniles, subadults, small adults, and large adults (Figure 2). The young-of-year stage were fishes spawned during the most recent spawning season. Within the young-of-year stage are survival estimates for eggs, larvae, and age-0 stages. Age-1 juveniles are suckers spawned in the previous year's spawning season. Subadults are suckers that are 2+ years old but are not yet reproductively active. Small adults are suckers within the first few years of reproductive maturity. Large adults are suckers that have been spawning for many years. The population operates on an annual time step that runs from late summer to late summer. This coincides with the sampling period that provides the most reliable estimates of young-of-year abundance to facilitate the evaluation of competing ideas of population dynamics in an adaptive management framework.

3.4 Population Model Overview

The model begins with a specified number of individuals in each of the 5 stages. Using river discharge and lake levels during the spawning season and the abundance of small and large adults along with estimated sex ratios and fecundity values, the number of eggs spawned is predicted. The eggs hatch and transition to larvae using egg-to-larvae survival rates. These larvae are added to the population as age-0 fish as a function of larval survival, which was modeled as a function of habitat availability, entrainment, and predation rates. Age-0 fish transition to age-1 juveniles using age-0 survival. Age-1 survival is estimated as a function of body condition, entrainment, aquatic predation rates, parasites, streamflow, and water quality. Age-1 juveniles become subadults through a survival function that relates avian predation, body condition, entrainment, aquatic predation, parasites, and water quality. These are separate models for estimating juvenile and subadult survival. Subadults become small adults as a function of survival and stage transition probability, with the latter calculated using the geometric stage duration technique (Caswell 2001). Small adult and large adult survival is a function of avian predation, entrainment, water quality, and water quality refuge availability with the effects on survival decreasing from small adults to large adults. Stage duration in the Lost River Sucker small adult stage was determined using the fixed stage duration method (Caswell 2001; Table 2).

Reproduction.- The model includes both males and females, so a sex ratio constant was multiplied to fecundity values to account for the presence of males in the population. Sex ratio data was used from Hewett et al. (2014) and fecundity values were calculated from estimates of age at maturity (Buettner and Scoppettone 1990), growth (Terwilliger et al. 2010); and length-fecundity relationship (Perkins et al. 2000; Table 2). Duration of the larval stage in Klamath suckers ranges from 40 to 50 days (NRC 2004). After the larval stage but before the next spawning season, they are considered age-0 juveniles.

Survival.- Each of the stage-specific survival parameters described below are functions of alternative models that represent alternative hypotheses of system dynamics. These alternative hypotheses are described in the *Demographic submodels* section below. Because the submodels are based on hypothesized effects, it was important that they produce similar estimated survival values under current conditions (i.e., the observed monitoring data). Therefore, the submodels were parameterized using the expected demographic rates described below.

Egg-to-larvae survival was not available for Klamath suckers. Therefore, I used reported values for a similar western Catostomid, the Cui-ui Sucker (Scoppettone et al. 2000). The larvae to young-of-year survival parameter was obtained from Houde (1994), which stated that in patterns of freshwater fish, 95% of larvae typically do not reach the young-of-year stage, also known as age-0 juveniles. Egg to young-of-year survival was estimated as the product of egg-to-larvae and larvae to young-of-year survival. There are no reported estimates of juvenile sucker survival in the Klamath Basin, so I used juvenile and subadult survival estimates for a similar species the June sucker (Billman and Crowl 2007; Table 2). Average survival for male and female Lost River Suckers were obtained from published reports based on capture-recapture (Hewett et al. 2014; Table 2). Given the resolution of detail in published reports, survival was assumed to be the same for both small adults and large adults.

One of the greatest sources of uncertainty for Klamath suckers is the fate of age-0 fishes. Very few age-1 Klamath suckers have been collected during monitoring over the years. To obtain young of year survival rates, I used the demographic estimates described above (Table 2) to create a stage transition matrix. I then created a model that estimated the difference between estimated population growth rate (lambda) and observed values (Hewitt et al. 2015). Using this model, I estimated young-of-year survival, or survival to 1-year old, by finding the values that minimized the squared difference between the observed and estimated lambda using the bounded Broyden–Fletcher–Goldfarb–Shanno algorithm implemented in the *R optim* function. The process resulted in relatively good fits (Figure 3).

3.5 Demographic Submodels

Klamath sucker demographic rates described above were modeled using submodels that represented nine alternative hypotheses of the effect of environmental and ecological factors on Klamath sucker population dynamics (Figure 4). The alternative hypotheses were developed by the stakeholders based on their knowledge of the system and included:

1) *Spawning* - low lake levels at lake spawning areas in Upper Klamath Lake reduce spawning duration and spawning success of lake-spawning Lost River Suckers,
2) *Streamflow* - high Williamson River streamflow during the spring results in more larval suckers distributed in open water rather than nearshore areas increasing entrainment and reducing larval survival,
3) *Habitat availability* - low lake levels in Upper Klamath Lake during the juvenile rearing period in early summer reduce nearshore larval habitat availability thereby reducing larval survival,

4) *Fathead minnow and parasite induced predation* - Fathead Minnow, and parasite-induced predator prevalence reduces juvenile abundance and juvenile body condition,
5) *Condition* - lack of nearshore habitat results in inadequate food availability reducing food quality and sucker body condition,
6) *Larval water quality* - poor water quality in the Williamson River Delta contributes to chronically harmful environmental conditions such as low pH and dissolved oxygen thereby reducing larval survival,
7) *Juvenile, subadult, and adult water quality* - periodic poor water quality events lake-wide contributes to chronically harmful environmental conditions reducing juvenile, subadult, and adult sucker survival,
8) *Avian predation* - avian predator prevalence results in increased avian predation reducing juvenile and adult abundance, and
9) *Entrainment* - high streamflow over the Upper Klamath Lake outlet, Link River Dam, during late summer increases entrainment losses and reduces abundance.

Spawning.- The abundance of Lost River Suckers that attempt to spawn in Upper Klamath Lake is hypothesized to be related to lake levels prior to and during spawning. When the level of Upper Klamath Lake is low during the spawning season, the proportion of Lost River Suckers that attempt to spawn in the lake can be reduced, although at least some individuals do manage to successfully spawn (Burdick et al 2015a). Burdick et al. (2015a) observed that 14% fewer female Lost River Suckers spawned in 2010 and median spawning duration was 36% lower. Reductions were believed to result from decreased spawning habitat due to low lake levels during the spawning season. Burdick et al. (2015a) also suggested that it was unlikely that the proportion of the population that attempted spawning would not be reduced when lake levels were above 1,262.4 meters. To incorporate the effect of lake levels on Lost River Sucker reproduction in Klamath Lake, I calculated the proportion of decreased spawners when lake levels were partially below threshold during spawning season from February to June using USGS lake level data (Table 3-4).

Streamflow.- When streamflow is higher in the Williamson River, it is hypothesized that larvae originating from the river move through the river too quickly (Burdick and Brown 2010). My assumption in the model was that if larvae were pushed out into the lake prematurely rather than staying in the nearshore in the spring, survival would be reduced. To model to effect of the Williamson River streamflow on larval survival, a centered logistic function was made using Williamson River mean spring (March to August) streamflow (USGS 11502500) by year 1917 to 2015. The centered logistic curve was fit to the minimum and maximum spring mean streamflow by year. I restricted the upper and lower bounds on the function to get mean survival around the baseline survival estimate at mean spring streamflow (Table 2-3).

Habitat availability.- Reiser (2001) stated that larval suckers are usually found in nearshore emergent macrophyte habitat. Numerous studies state the importance of habitat for larval suckers (Burdick et al. 2008; Cooperman and Markle 2004; NRC 2004; Reiser 2001). I developed a habitat availability function that relates larval survival to nearshore habitat availability for larvae. In Reiser (2001) taken from Dunsmoor et al. (2000) report, a relationship between lake level and nearshore habitat, as defined by presence of emergent macrophyte around lakeshore of Klamath, was modeled using logistic regression and the coefficients are used in the function. Mean May-July lake levels in Upper Klamath Lake come from USGS data for each year. Minimum and maximum survival values were incorporated into the function to restrict output to a realistic biological baseline. When lake levels are high during May-July, there is more available nearshore habitat thereby increasing survival (Table 3-4).

Fathead minnow and parasite predation.- It is known that fish predators in Upper Klamath Lake, such as Fathead Minnows (*Pimephales promelas*), prey upon larval and juvenile sucker stages (Markle et al. 2014b). A logistic function was made to relate Fathead minnow catch per unit effort (CPUE) in nearshore areas in Upper Klamath Lake from Markle et al. (2014b) to sucker survival. The function was centered using the minimum and maximum CPUE for Fathead Minnows from 2009-

2013 (Table 3-4). Survival ranges were restricted for each individual stage from larvae to subadults so that mean survival was close to expected values from other sucker species at similar stages.

Parasites have been found to infect both Fathead Minnow and Klamath sucker species (Markle et al. 2014a; ML Kent, personal communication). The effect of parasites was incorporated into this function using a model associated with Red Queen dynamics (Rabajante et al. 2015). The model describes that a system with multiple host populations cycling up and down in abundance. Under these conditions a parasite population can sustain high levels as it switches hosts (Rabajante et al. 2015). Borrowing a concept in Red Queen dynamics, I hypothesized that those parasite populations that were killing suckers were supported by Fathead Minnows. If Fathead Minnow abundance were above average in year_{t-1}, higher mortality due to parasites would be expected in suckers in year_{t}. For each sucker stage, a "parasite penalty" was applied that would reduce survival up to a certain percentage related to maximum Fathead Minnow abundance. The "parasite penalty" decreased in older sucker stages because they are less susceptible to parasites. Logistic regression was used to estimate coefficients and relate the penalty to survival (Table 4).

Condition.- Studies have related differences in sucker survival to body condition (Burdick et al 2015b). Stakeholders hypothesized that if juvenile sucker condition is higher than average, survival would increase. Using data from Burdick et al. (2015b), I calculated a mean Fulton's condition factor (1.47) and standard deviation (0.14) for LRS in UKL and a mean (1.73) and standard deviation (0.17) for Shortnose Suckers in UKL to simulate condition (K) from a gamma distribution. I then subtracted the mean condition from the simulated condition, added 1 and then separately multiplied by the estimated survival for age-0, age-1, and subadults. For age-1 and subadults values were restricted between realistic survival bounds of 0.2 to 0.9 for age-1 juveniles and 0.4 to 0.9 for subadults. For model diagnostics, deterministic values of condition were held at the calculated mean values (Table 4).

Larval Water Quality.- Poor water quality is believed to be a major factor in the recovery of Klamath suckers (NRC 2004). Unfavorable conditions may be linked to occasional larval and juvenile sucker fish kills (Saiki et al. 1999). To incorporate the hypothesis that poor water quality affects survival, I created a water quality LC50 function relating poor water quality and larval sucker abundance (Table 4). Daily mean values for dissolved oxygen (DO), pH, and water temperature from 2003 to 2015 were compiled from the USGS gage in larval habitat area in the Williamson River Delta (USGS 422719121571400, Table 3). I used the 96-hour confidence limit estimates for DO, pH, and temperature from Saiki et al. (1999) for larval suckers (LRS and Shortnose Suckers combined) to define water quality thresholds. An LC50 "event" was defined when at least one water quality threshold was exceeded for three consecutive days (96-hours). The total number of "events" were added for each year and then used to estimate larval survival.

Juvenile, Subadult, and Adult Water Quality.- Occasional severe sucker mortality events have occurred in Upper Klamath Lake reportedly because of poor water quality (NRC 2004). While many factors contribute to poor water quality, the single most direct factor associated with these events is low dissolved oxygen (Saiki et al. 1999). Klamath suckers older than the larval stage can move throughout much of Upper Klamath Lake (Wood et al. 2013). Using a single water quality gage as proxy to water quality in the whole lake would ignore a sucker's mobile ability. To represent a general characteristic of water quality throughout the lake, data from all available USGS gages in Upper Klamath Lake recording dissolved oxygen (DO) were used for the water quality function for juvenile stages and above, excluding larvae (Table 3). DO was used because it was the most common water quality metric consistently recorded and low DO is the result of many factors contributing to poor water quality in the lake and is the direct cause of sucker mortality during fish kills (NMFS & USFWS 2013). Mean daily DO was calculated for all gages with data from 2003 to 2015. It is important to note that not all gages were recording data the entire time. Some years had more gages running than other years. Low levels of DO were defined as less than 4 mg/L because at that level, it was observed that suckers begin seeking out water quality refuge habitat (Banish et al. 2009). If mean daily DO at a gage was below 4 mg/L for at least 3 consecutive days, a low DO "event" was determined to have occurred at that gage. To account for differences in the number of gages each year, lakewide low DO "events" were decided to have occurred if at least 20% of the gages recording data that year each had low DO "events" occur on the same 3 consecutive days. Lakewide low DO "events" were added up for each year. The number of events was then converted into a percentage (number of events/100) and survival was arbitrarily reduced by that amount. I hypothesized that the overall effect of poor water quality was decreased from 100% effect on age-0 juveniles, 90% effect on age-1 juveniles and subadults, 60% effect on small adults, and 30% on large adults. Survival values used as inputs to the water quality functions were adjusted so that mean survival was equal to baseline survival values under average environmental conditions. The input survival values were adjusted as follows: age-0 juvenile survival was adjusted from 0.005 to 0.008, age-1 juvenile survival was adjusted from 0.4225 to 0.437, subadult survival was adjusted from 0.63225 to 0.654, and adult survival was adjusted from 0.9 to 0.911. The range of potential survival values was adjusted on a stage-by-stage basis to constrain the output survival estimates within biologically realistic levels no greater than 0.99 (Table 4-5).

Adult suckers have been observed in Pelican Bay, a groundwater influenced bay with relatively constant high levels of dissolved oxygen in Upper Klamath Lake, during times of poor water quality (Banish et al. 2009). Reduced adult survival from poor water quality was adjusted based on a hypothesized water quality refuge availability function. When lake elevations in Pelican Bay (USGS 11505800 Rocky Point) during July-September were above average, adult survival was slightly increased (Tables 3 and 5).

Avian predation.- There is evidence that juvenile and adult suckers are preyed upon by avian predators (Evans et al 2015). Avian predation may be a factor limiting recovery of Klamath suckers (Evans et al 2015). Linear regression was used to model the relationship between abundance of American White Pelican and Double Crested Cormorants that stayed throughout the summer season in Upper Klamath and Clear Lakes with observed maximum predation rates of suckers by year from Evans et al

(2015) (Table 3). Predation rates were estimated to range from 0% to 8% based on observed sucker PIT tags found on nesting sites using meta-analysis. In Evans et al. (2015), it was observed that predation rates were higher for juveniles than for adult suckers. Differing effects of avian predation on different sucker life stages were modeled by multiplying predation rates by hypothetical stage-based constants. Predation rates were multiplied by 4 for age-1 and subadults, 3 for young adults, and 2 for large adults (Table 5).

Entrainment.- In PacifiCorp Report (2013), it was reported that entrainment of Klamath suckers was directly proportional to flow. I interpreted this to mean that higher flows in the Link River, the outlet of Upper Klamath Lake, would lead to higher entrainment out of Upper Klamath Lake and therefore lower survival. For stages age-0 to adult, streamflows from Upper Klamath Lake's outlet, the Link River, were used to model entrainment (Table 3). Larval entrainment also is believed to occur because of pumping and diversion of water out of Klamath Lake (NMFS & USFWS 2013). To model entrainment, I made a centered logistic function that modeled survival as a function of discharge and the number of unscreened diversions around the lake. Entrainment of age-0 to adult suckers is highest during the months of August and September; therefore, I used mean streamflow values during that time for this function. Streamflow data was collected from USGS stream gage 11507500 from 1998 to 2013. For each stage, separate minimum and maximum survival values were adjusted until mean survival varied around a presumably realistic range. Age-1 survival range was between 0.32-0.90, subadult survival range was between 0.61-0.73, and adult survival was between 0.73-0.95 (Table 4-5).

A separate entrainment function was made for larvae because they susceptible to pumping and diversion and they move through the river and lake in a more passive manner than older stages. The function was built using data from simulations of larval retention and dispersal from Wood et al. (2013). Results of the simulations suggested that larval retention decreased at low and high lake elevations and that retention was maximized at an intermediate elevation. I used logistic regression to model the relationship between the retention ratios and spring peak lake elevations (April-May) from Wood et al. 2013. A quadratic term was added to the regression to incorporate the hypothesis that retention was maximized at an intermediate lake elevation. To fit the model to a presumed survival range associated with larvae, the quadratic term was centered on average larvae survival (Table 4).

To account for the effect of diversion, I use the unscreened diversion larval entrainment estimates from Nobriga et al. (2004) and the estimates of larvae abundance in nearby locations that were sampled concurrently (J.T. Peterson unpublished). These estimates, however, only reflected the entrainment relative to the number of fish that were available (i.e., in the area of the diversion). To estimate the proportion of larvae, on average, available for entrainment near a diversion, I used the advection diffusion model similar to the Wood et al. (2013), but without the mortality terms to estimate the distribution of larval along the shoreline in 5 km section for each of 70 days that began with emergence (day zero). I then used the resulting distribution to estimate the average proportion of larvae available in the 5 km sections across the 70 days. This value was then used to adjust the estimated entrainment. I then estimated the parameter for the diversion entrainment effect using average larval survival (0.005) and the estimated diversion entrainment mortality. To fit the model to a presumed survival range associated with larvae, the model was calibrated to produce the average survival under the average spring peak lake elevations and assuming 20 unscreened diversions of 0.005.

3.6 Upper Klamath Lake Decision Model

The baseline population model described above was modified for approximating the dynamics of three separate populations: river-spawning Lost River Suckers, lake-spawning Lost River Suckers, and Shortnose Suckers. Each model is a variation of the baseline model. The function that relates Upper Klamath Lake water levels and a reduction in spawning was not included in the river-spawning Lost River Sucker and Shortnose Sucker models because both of those groups spawn in the river not in the lake. The function that relates Williamson River streamflow and larval survival was not included in the lake-spawning Lost River Suckers model because that group spawns in the lake not in the river.

Modified parameters.- Certain life-history parameters were also modified to reflect species differences. Based on survival estimates in Hewitt et al. 2015, adult survival in lake-spawning Lost River Suckers was higher than river-spawning Lost River Suckers, while Shortnose Suckers was lower than both LRS groups (Table 6). Transition probabilities, sex ratio, and fecundity values for Shortnose Suckers were also different than LRS based on published reports.

Modified functions- The avian predation, entrainment, water quality, and water quality refuge availability submodels were modified to reflect the changes in survival among species/spawning groups. The input survival values of each of the small and large adult functions were increased from the baseline model river-spawning Lost River Sucker input survival value of 0.90 to 0.92 to reflect the increased survival observed in lake-spawning Lost River Suckers. Those same input survival values were also decreased to 0.84 to reflect the lower survival observed in Shortnose Suckers.

The larvae and young-of-year entrainment functions were also modified for the lake-spawning Lost River Sucker group. The original functions used Williamson River flows to relate entrainment and survival rates for larvae and young-of-year river-spawning Lost River Suckers. Lake-spawning Lost River Suckers spawn in the lake not in the Williamson River; therefore, I assumed that Link River (UKL outlet) streamflows would affect entrainment of lake-spawned larvae instead of Williamson River streamflow. In the lake-spawning Lost River Sucker larvae and age-0 entrainment functions, Williamson River streamflow was replaced with Link River streamflow.

Initial Abundance.- Initial adult abundance estimates for each group were calculated using total 2014 PIT tag observation data and recapture percentages from Hewitt et al. (2015) and abundance estimates from the Klamath Sucker Extinction Prevention Action Plan (US Fish and Wildlife Service, unpublished). To estimate abundance, the total number of suckers observed for each group was divided by their respective recapture rates (Table 6). To determine an initial population stage distribution, I multiplied the adult abundances by the baseline population model stable age distribution proportions.

The Upper Klamath Lake decision model runs the 3 separate species/ spawning groups simulations at the same time using the same decision alternative scenario. Each population has a different starting abundance and age distribution. For the captive propagation decision alternative, the proportion of the 44,000 larvae that were captured each year were assigned groups based on expert opinion where 50% were Shortnose Suckers, 40% were river-spawning Lost River Suckers, and 10% were lake-spawning Lost River Suckers (J. Rasmussen, *personal communication*). After the simulations were complete, the abundance of small and large adults from each of the 3 groups at the end of the last year were summed as final adult abundance.

Utility.- The utility function for the Klamath sucker decision model expresses model simulation results as a single utility score for quantitative comparison. The results incorporated into the utility score were adult sucker abundance of the last year and total management costs for all years of the simulation. A single utility score for each of these results was calculated using proportional scoring. To parameterize the proportional scoring equation, the expected minimum and maximum values for each of the results were determined by simulating all possible combinations of decision alternatives (Table 7). The objectives were to maximize abundance and minimize management costs. To minimize management costs, the cost utility score was made negative. The utility scores were then equally weighted and added together as a final utility value.

3.7 Modeling Decision Effects

The decision alternatives were initially identified by the stakeholders in the November 2012 workshop and later refined in a series of stakeholder meetings. The decision alternatives identified were categorized as: 1) entrainment reduction, 2) avian hazing, 3) habitat restoration, 4) water quality improvement, and 5) captive propagation (Figure 5). Cost estimates to implement each alternative are presented below (Table 8).

Entrainment reduction.- Implementing entrainment reduction involves two separate actions (1) screening lake diversions and (2) collecting and relocating entrained suckers to the upper part of the lake (Figure 5a). Under the first decision, the number of unscreened diversions was reduced by one/year at a cost of $21,000/screen based on Nobriga et al. (2004). I assumed that a screened diversion remained screened in subsequent years and that the cost of maintaining the screen was negligible. When the decision was to collect and relocate, survival of stages age 0 to adult increased from 1%-5%, with the percent increase randomly simulated from a uniform distribution. Survival was only increased for the year that entrained suckers were collected and relocated. For decision alternatives related to the Klamath Sucker Near-Term Extinction Prevention Action Plan, annual costs were determined by dividing the total estimated costs of actions 2.3, 4.1, and 5.4 by the number of years remaining of the revised Recovery Plan (2016 through 2023).

Avian hazing.- In the avian hazing decision alternative, non-lethal methods to deter avian predators from nesting along the lake are initiated. The effect of hazing reduces avian abundance, thereby increasing sucker survival (Figure 5b). Each year when the avian hazing decision alternative is implemented, avian abundance in that year is randomly reduced by 25%-50% simulated from a uniform distribution. Avian hazing costs were taken from the total costs per year of Phase 1 of Alternative B described in the Draft Environment Impact Statement for Double-crested Cormorant non-lethal hazing in the Columbia River Estuary.

Nearshore habitat restoration.- Initiating conservation and restoration activities along riparian and wetland areas can help to increase the size and/or quality of juvenile habitat. When enacting the habitat restoration alternative in the model, juvenile condition for age-0, age-1, and subadults will increase (Figure 5e). The effect of habitat restoration is stronger for age-0 and age-1 stages and less strong for the subadult stage. An estimated 3,200 acres adjacent to Upper Klamath Lake are available for rehabilitation as nearshore habitat for juvenile suckers (Stillwater

Sciences 2013). The total cost for restoring 3,200 acres of habitat was estimated at \$30M - \$150M (Stillwater Sciences 2013). In the habitat restoration decision, I divided the total acreage available into four 800 acre parcels. Every year that the habitat restoration decision is enacted, a single 800-acre parcel is converted into habitat over a 3-5-year period according to estimated timelines to effectiveness in Kuwabara et al. (2012). Once all four parcels are converted, restoring additional acres is not possible. If 1 or more parcels of habitat were restored, age-0 condition was increased by 50%, age-1 condition by 25%, and subadult condition by 15%.

The effect on age-0 survival by restored habitat was modeled using logistic regression relating the number of acres restored to a resultant increase in emergent macrophytes. The data is from Reiser (2001) taken from Dunsmoor et al. (2000) relating lake elevation and emergent macrophytes. Under the assumption that habitat restoration increases nearshore habitat (i.e. emergent macrophytes) similarly to higher lake elevation, age-0 survival would also increase, however the effect on age-0 survival was restricted to a maximum value of 0.015 if all 4 parcels were restored. As more and more habitat is available in the decision model, survival for age-0 and condition for age-1 increased at an identical rate.

<u>Controlled propagation program</u>.- To supplement sucker populations, wild-caught larval suckers will be raised in semi-natural ponds up to a size and/or certain amount of time and will then be released into the lake (Figure 5d). In the model, a total of 44,000 larval suckers are collected from the larval population and reared for 1, 2, or 3 years and then stocked into the wild. Based on details in the Klamath Sucker Extinction Prevention Plan, 50% of captured larvae were Shortnose Suckers, 40% of captured larvae were river-spawning Lost River Suckers, and 10% of captured larvae were lake-spawning Lost River Suckers. I hypothesized that while in captivity, suckers will have higher survival than wild suckers. I also hypothesized that stocked suckers will have lower survival than wild suckers for the first year that they are stocked. Captive sucker survivals of all ages were increased 25% compared to wild suckers. Stocked sucker survivals for all ages were decreased by 50%. After the first year, stocked suckers assimilate into the wild sucker population and take on wild

sucker survival parameters. For decision alternatives related to the Klamath Sucker Extinction Prevention Plan, annual costs were determined by dividing the total estimated costs of actions 2.3, 4.1, and 5.4 by the number of years remaining of the revised Recovery Plan (2016 through 2023).

Water quality improvement.- Several techniques have been proposed to improve water quality for all sucker life stages including water storage wetlands, treatment wetlands, and algae filtration. In the decision model, water quality improvement technique decreases mortality in larvae and increase survival in juvenile and adult stages (Figure 5c). When the water quality improvement decision alternative is enacted, the annual number of LC_{50} events for larvae are decreased by the standard deviation of the number of LC_{50} events/year. For juvenile and adult suckers, the annual number of low dissolved oxygen days are reduced by the standard deviation of the number of low dissolved oxygen days/year (Table 3).

Treatment wetlands.-The treatment wetland decision entails the construction of wetlands either adjacent to Upper Klamath Lake or at riparian areas along tributaries to Upper Klamath Lake. Based on conceptual designs illustrated in the Klamath Basin Water Quality Improvement Report by Stillwater Sciences 2013, treatment wetlands could be built on 1,600 acres of land in the Klamath Basin. The wetlands filter out excess nutrients before they reach the lake and could improve water quality (Stillwater Sciences 2013). The total cost for 1,600 acres of treatment wetland was estimated in the water quality report at $17M. Treatment wetlands can range from 10s of acres to 1,000s of acres (Stillwater Sciences 2013). In the context of the decision model, I decided to restrict the size of the treatment wetlands to 400 acres for each wetland. In this way, the decision model can determine whether to build 0 to 4 treatment wetlands over the course of a simulation. Based on research by Kuwabara et al., 2012, a 4-year cumulative effect delay was added to the wetland decision to account for the time it takes a newly restored wetland to fully function as a natural wetland. The construction of treatment wetlands was hypothesized to affect water quality parameters similarly to the linear regressions correlating decreases in DO, pH, and temperature exceedance events in post-restoration monitoring in Hayden and Hendrixson's (2013) post-restoration analysis of the Williamson River Delta. A relationship between the maximum percent decrease in water quality exceedance events (85% for DO, 65% for pH, and 72% for temperature) and the total number of acres available for treatment wetlands (0-1,600 acres) was made using linear regression. The coefficients from the linear regressions were used to simulate the reduction in poor water events based on the numbers of acres used to build treatment wetlands.

<u>Sediment sequestration</u>.- The large amount of phosphorus in Upper Klamath Lake contributes to the severity of algal blooms and poor water quality (Kann and Walker 1999). Treating the lake with alum, a compound that binds to phosphorus, would sequester phosphorus and prevent it from being used by algae (Eldridge et al. 2012; Stillwater Sciences 2013). It was estimated that the bound phosphorus is sequestered in the sediments for up to 15 years and to treat the entire lake would cost approximately $180M (Stillwater Sciences 2013). Cooke et al. (2005) found that alum removed 50% of phosphorus in the water column. Therefore, I hypothesized in the decision model that if the alum treatment was enacted, it would simply reduce the frequency of poor water quality events by 50% ignoring the effect of newly introduced phosphorus. I also hypothesized that the survival rate of age-0 suckers would increase by 50% (i.e., 1.5 times baseline survival) with improved water quality. After the 15 years of treatment is over, the phosphorus would become biologically available again and the frequency of water quality events returned to baseline values.

<u>Algae filtration.</u>-The algae filtration decision is a mobile barge-based design that would traverse the lake and filter algae out of the water column (Stillwater Sciences 2013). It was estimated that the total costs of the barge including operation and maintenance would be $3.7M with the barge having an operation lifetime of 10 years. By removing algae out of the lake, it is expected to reduce algae bloom potential and the resulting detrimental effects algae blooms have on water quality parameters such as dissolved oxygen and pH (Eldridge et al. 2012). I hypothesized that when the algae filtration decision is enacted in the decision model, it would

reduce of the frequency of poor water quality events annually by 25% based on its nutrient removal efficacy rating as "medium" in the Stillwater Sciences (2013).

Dredging.- The action of dredging Upper Klamath Lake would involve the physical removal of accumulated sediments rich in phosphorus from the lake (Stillwater Sciences 2013). Similarly to treating the lake with alum, the removal of sediments rich in phosphorus would reduce the severity of algae blooms and the frequency of poor water quality events in the lake (Eldridge et al. 2012; Stillwater Sciences 2013). It was estimated that dredging the entire lake would take approximately 5 years to complete and cost $460M (Stillwater Sciences). Unlike treating the lake with alum, dredging and removing sediments would have a longer positive effect on water quality, lasting up to ~20 years before phosphorus begins to affect water quality again, depending on external loading of excess nutrients (Ruley and Rusch 2002). In the decision model, I hypothesized that dredging the lake would reduce the frequency of poor water quality events by 50%, while also increasing age-0 survival by 50%, similarly to treating the lake with alum. The effects would increase each year, starting from year 1 of dredging and up to year 5. The effect rate at year 5 would last for another 15 years.

3.8 Stochastic Simulation

The decision model was solved using stochastic simulation. Stochasticity was incorporated for all environmental inputs, life-history parameters, and effects of alternative decisions using statistical distributions (Table 9). The recurrent decisions entrainment reduction, avian hazing, and captive propagation were implemented each of the 30 years in the simulations. Screening water diversions occurred once per year for 20 years. Habitat restorations were implemented over 15 to 20-year periods with effects lasting up to 50 years. Water quality improvement decisions were one time decisions with changes to water quality lasting 10-15 years as described above. For each decision alternative, model was run a total of 10,000 iterations and the utility, number spawning adults, and cost at year 30 were recorded. The optimal decision was that with the greatest mean utility.

3.9 Sensitivity Analysis

Sensitivity analysis was used to identify parts of the model that affected what actions were considered optimal and the expected value of each action. Three types of sensitivity analyses were conducted including: 1) one-way sensitivity, 2) one-way response profiles, and 3) two-way response profiles.

One-way sensitivity analysis is useful for finding parameters in the model that have the most effect on the expected value of a decision. In a one-way sensitivity analysis, one parameter is varied at a time from a minimum value to a maximum value and the decision model is run with the value of the other parameters remaining fixed. Each time the model is run, the estimated utility of the optimal decision is recorded. After each parameter has been varied, the information is displayed as a tornado diagram. A tornado diagram consists of horizontal bars, one for each parameter in the model that displays the value of the utility across the range of values of the parameter that was varied. These are sorted from most to least influential on the y-axis from top to bottom. The x-axis is the percent change in the estimated score resulting from varying the value of the parameters.

Like one-way sensitivity analysis, one-way response profiles varied one parameter at a time. Response profiles are different in that they record the score for each decision not just the optimal decision. Response profiles are graphically displayed as line plots, each line representing a decision and its change in score along the range of values in a parameter. A decision with the highest score is identified as optimal and can be visually determined by being above the other decision lines. If lines cross on a response profile, it is interpreted as a change in what decision is considered optimal. If a response profile of a parameter changes multiple times, it is considered a sensitive parameter in the decision model.

A two-way response profile varies two parameters at a time and identifies the optimal decision. The decision model is run using every combination of values for the two parameters being varied and the optimal decision is recorded. The results of a two-way response profile are displayed as a policy plot. A policy plot has the range of values for each parameter on the x-axis and y-axis. Each decision alternative is assigned a color and the optimal decision for each combination of parameters is displayed in the gridded policy plot. These plots are useful to quickly identify thresholds for parameters or pairs of parameters that result in a change in what is identified as the optimal decision.

System state-dependent policies.- To examine how different system states in the decision model affect the optimal decision outcome, I ran a series of simulations where the system states were varied one-by-one, across a range (described above), and recorded the optimal decision scenario and utility. The inputs and parameters for all simulations were held at mean values. All system states except the state being varied were kept at baseline values during each simulation. The system states included: the initial adult abundance (low, medium, high), and the 12 environmental inputs, each having a low, medium, and high level corresponding to minimum, average, and maximum values in observed field data (Table 10). Each of these simulations were run using the composite model that applied equal weight to each of the alternative model hypotheses.

Information state dependent policies.- Information on the true underlying mechanisms affecting Klamath sucker populations is defined as the information state and it too can affect the optimal decision. To evaluate the sensitivity of optimal decisions across the alternative models, I ran simulations with each of the 13 alternative model hypotheses to see if and how the different model weights affected the optimal decision (Table 11). The effect of the alternative models was examined by individually varying 4 different system states described above and running the simulation with a weight of one (100%) for each of the 13 alternative models. When the model weight of a single juvenile or adult alternative demographic model was set to one (i.e., assumed to be the true model), the other demographic rates were estimated using all alternative models combined with equal weights. The 4 different system states, divided into 5 levels were: initial adult sucker abundance (30,000, 60,000, 120,000, 180,000, and 200,000 adult suckers), the number of years in a simulation with "high predator abundance" (3, 6, 9, 12, and 18 years), the number of years in a simulation with a "high amount of poor water quality events" (3, 6, 9, 12, and 18 years), and the number of "dry years" during a simulation (18, 12, 9, 6, and 3 years). Low and high values were defined as the 1st and 3rd quantiles calculated from the compiled historical environmental data (Table 3). High predator abundance was defined as years when Fathead Minnow abundance (*FHM*) had a mean of 232 CPUE and avian abundance (*AVIAN*) had a mean of 1,862 birds at nesting sites. A high amount of poor water quality events was defined as a mean value of *pH*, *DO*, and *temperature* events/year at 0.1 in the Williamson River Delta and mean low DO events/year at 20% of lake gages at 4.6 (*lowDO20*). Dry years were defined as years when mean Williamson River streamflow (*WR.MAR.AUG*) was at 843 cfs and mean spring Upper Klamath Lake elevation (*UKL.FEB.JUN*) was at 4,142.8 (m). Because the abundance of the two species and lake and river spawning populations differed, each initial abundance state level (50%, 75%, 100%, 125%, 150%) differed between the species (Table 3, 6). Similarly, the abundance of predators differed among predator types, so each predator type had a different value associated with the abundance states. Each combination of system state level, alternative model, and decision was run for 100 iterations with each iteration maintaining the same stochastically realized values across alternative models. The average utility for each decision for every combination was calculated and the highest average utility for each combination was identified as the optimal decision and was then plotted on the policy plots.

4 Results

4.1 Stochastic Simulation

Stochastic simulation with the decision model indicated that 1-year captive propagation was the optimal decision with a utility of 0.316 (Figure 6, Table 12). Mean and standard deviations for end adult sucker abundances for the optimal decision at the end of the 30-year simulation were 38,457 (5,112) for river-spawning Lost River Suckers, 5,046 (633) lake-spawning Lost River Suckers, and 4,759 (320) Shortnose Suckers. Translocation and reducing entrainment was the 2nd best decision with a utility of 0.309. Mean and standard deviations for end adult sucker abundances for the translocation and reducing entrainment decision were 45,220 (6,502) for river-spawning Lost River Suckers, 3,979 (528) lake-spawning Lost River Suckers, and 581 (80) Shortnose Suckers. Filling out the top 5 optimal decisions were screening 20 water diversions (0.305), no action (0.304), and restoring 4 800-acre parcels of habitat (0.303). Estimated adult abundance was greatest when enacting the restoring nearshore juvenile habitat decision with 80,399 (13,990) for river-spawning Lost River Suckers, 5,968 (1,016) lake-spawning Lost River Suckers, and 759 (112) Shortnose Suckers. The Shortnose Sucker young adult population was 10 times greater in the 1-year captive propagation decision than the "no action" decision.

4.2 One-way Sensitivity Analysis

One way sensitivity analysis indicated that the most influential parameter was river-spawning Lost River Sucker subadult survival (Figure 7). In fact, the top five most influential parameters were adult survival parameters. The juvenile alternative hypothesis models and transition parameters for subadults also had considerable influence on utility (Figure 7). Parameters in the model that were least sensitive were Shortnose Sucker juvenile parameters and small adult fecundity. A separate tornado diagram was made to evaluate the sensitivity of the decision model environmental inputs (Figure 8). In this diagram, the Fathead Minnow and parasite abundance inputs had the greatest influence. The second most influential input was the avian abundance index that affected predation rates on juvenile and adult suckers. Inputs that were least influential were the availability of poor water quality refuge habitat for adult suckers and the frequency of LC_{50} temperature events for juvenile suckers.

One-way response profiles were made for each parameter to observe when the optimal decision changed across a range of single parameter perturbations. Out of the 150 parameters tested, the optimal decision did not change over the range of 138 parameter values (e.g., Figure 9). For river-spawning Lost River Sucker subadult survival, the optimal decision changed as survival increased (Figure 10). For most of the perturbed range, the optimal decision scenario was 1-year captive propagation. When subadult survival was increased to 0.75, the optimal decision scenario changed to restoring nearshore juvenile habitat with utility increasing from 0.3 to 0.5. For river-spawning Lost River Sucker subadult transition, the trend was almost an inverted version of the survival response profile (Figure 10). Overall, utility decreased with an increase in the transition value, which determines how quickly subadults become young adults. The lower the transition value, the sooner they mature. When the transition parameter was reduced to 0.6, the optimal decision scenario was restoring nearshore juvenile habitat with utility between 0.3-0.4. Anything greater than 0.6, the optimal decision was the decision to initiate 1-year captive propagation.

4.3 Two-way Response Profile Sensitivity Analysis

Life history parameters found to be influential in the tornado diagram were included in the two-way sensitivity analysis. These included survivals of age-0 and juvenile lake-spawning Lost River Suckers, survival of age-1 and subadult river-spawning Lost River Sucker, survival of captive age-0 and stocked age-1 Shortnose Suckers, and the transition probability of subadult Shortnose Suckers and river-spawning Lost River Sucker.

Two-way response profile plot of lake-spawning Lost River Sucker age-1 survival and age-0 survival, indicated that most of the decision space was dominated by the 1-year captive propagation decision (Figure 10). When both age-0 and age-1 survivals were high, the decision scenario changed to restoring nearshore juvenile habitat. If age-1 survival was below 0.3, the decision changed to translocation and reducing entrainment regardless of the value of age-0 survival. This suggests that for lake-spawning Lost River Suckers, captive propagation is not worth enacting if age-1 survival is low. The two-way response profile plot of Shortnose Sucker stocked age-1 survival and Shortnose Sucker captive age-0 survival was similar to the previous plot but did not include the restoring habitat decision (Figure 10). When either survival was at least at its mean value, the decision was 1-year captive propagation. The decision was likely to change to translocation and reducing entrainment if either one of the survivals was less than their mean value, even if the other had high survival.

These results suggest that both captive age-0 and stocked age-1 survival must be at least at the mean values used in the decision model, 0.35 and 0.21 respectively, for captive propagation to be the optimal decision.

The response profile sensitivity analysis plot of river-spawning Lost River Sucker subadult survival and age-1 survival indicated that only two decisions were considered optimal across the range of survival values (Figure 11). One-year captive propagation was the optimal decision across most of the combinations of subadult and age-1 survival, particularly when subadult survival was low. When subadult survival was less than 0.7, the optimal decision did not depend on the values of age-1 survival regardless of how high its value. If both parameters were at their highest values, the optimal decision was to restore nearshore juvenile habitat. If subadult survival was high, but age-1 survival was low, then the decision remained to initiate 1-year captive propagation. Two-way response profile plots of the adult transition probabilities of the two sucker species indicated a more complicated relationship (Figure 12). When transition durations were low, subadults would become adults quicker, whereas it took longer for subadults to become adults at higher values. When Shortnose Suckers mature quicker, the 1-year captive propagation decision was the optimal decision. When river-spawning Lost River Sucker matured quicker, the decision changed to restoring nearshore juvenile habitat. As long as Lost River Suckers matured quickly, the decision wouldn't change. However, if Shortnose Suckers and Lost River Suckers both matured slowly, then translocation and reducing entrainment was identified as the optimal decision.

4.4 System State Dependent Policies

Out of the 12 possible decision scenarios, 1-year captive propagation was the optimal decision in most system-state conditions (Figure 13). Only 2 of 36 instances were other decisions optimal. The decision to restore juvenile habitat was optimal when Fathead minnow abundance was low. When avian abundance was high, screening water diversions was the optimal decision. The highest utility and end population abundance was when restoring juvenile habitat was the optimal decision.

The lowest utility and end population abundance was when screening diversions was the optimal decision.

4.5 Information State Dependent Policies

The results of the system and information state simulations are visually summarized into 4 separate policy plots. The policy plots correspond to the 4 selected system states: initial sucker abundance, predator abundance, the frequency of poor water quality events during a simulation, and the frequency of "wet" years during a simulation. Together the policy plots suggested that the decision that was optimal the most was 1-year captive propagation regardless of system state and alternative model (Figures 13 and 14). Other decisions that were also optimal included restoring nearshore juvenile habitat and translocation and entrainment reduction. Out of the remaining 9 decision alternatives, other decisions that appeared as optimal in at least one of the system state and alternative model combinations included filtering algae, and avian hazing.

The optimal decision in the composite model was somewhat sensitive to initial sucker abundance. When initial sucker abundance was low to medium, the optimal decision was 1-year captive propagation, whereas when abundance was high, it became restoring nearshore juvenile habitat (Figure 14). The second most frequent decision across initial abundance and information states was juvenile habitat restoration. The greatest variation in optimal decisions across alternative models was when initial sucker abundance was very high. When abundance was very low, the decision alternative 1-year captive propagation was optimal across all alternative models.

In contrast to the initial abundance policy plots, the optimal decision under the composite model did not vary across predator abundances and was always 1-year captive propagation. Similar to the abundance state-dependent policies, 1-year captive propagation was the most frequent optimal decision across system state and model combinations. Overall, predator abundance did not influence the optimal decision (Figure 13). Restoring nearshore juvenile habitat also was commonly found to be optimal among the predator abundance state results, but only if the habitat models were true.

The evaluation of changes in optimal decisions for combinations of the frequency of poor water quality events and frequency of wet years in combination with alternative models indicated similar patterns (Figure 15). Regardless of water quality frequency or wet year frequency system state, the optimal decision was 1-year captive propagation under the composite model. Similarly, the optimal decision under the alternative models coincided with the assumptions of the alternative models. For instance, restoring habitat was the optimal decision under the alternative habitat models and translocation and reducing entrainment were the optimal decisions under the entrainment models. Interestingly, entrainment reduction was only selected as the optimal decision under the juvenile entrainment model when the frequency of water quality events was low. Overall the results suggest that water quality state and the wet year frequency were not very influential on changing the optimal decision.

5 Discussion

My goal was to build a decision model for evaluating alternative conservation strategies for Lost River Suckers and Shortnose Suckers in Upper Klamath Lake in Oregon. To do so, I participated in a structured decision making process where stakeholder objectives and management alternatives were identified and a decision model was developed. The model that I developed with the assistance of stakeholders was based on the best information that has been collected to date. Like all models, the Klamath sucker decision model is imperfect. However, I believe that this model could serve as the beginning of an ongoing process. Using decision models as a support tool to aid decision making and conservation planning should be an iterative process that includes updating and refining the model over time as new information is made available. I developed the Klamath sucker model such that that it can continually integrate new data and hypotheses in a transparent way. For example, predictions under the alternative models can be compared to monitoring data and information states (model weights) can be updated (Conroy and Peterson 2013). The underlying

Klamath sucker model also facilitates exploration of alternative hypotheses of sucker population dynamics. Sensitivity analyses of the decision model provided insight into how assumptions about the dynamics of Klamath suckers can affect management. It is these insights that also provided a strong case for implementing one decision alternative, 1-year captive propagation. In the following, I discuss the influence of model assumptions and uncertainties on the estimated outcomes and provide recommendations for improvements. Finally, I provide my rationale for the optimal decision being 1-year captive propagation.

The simulation results for the composite model with alternative hypotheses equally weighted indicated that the optimal decision for Klamath suckers was 1-year captive propagation. The other management decisions that were most frequently identified as optimal in sensitivity analyses were translocation and reducing entrainment, restoring juvenile habitat, and screening diversions. All four decisions focused on management strategies aimed at improving juvenile sucker recruitment. However, sensitivity analyses indicated that the identity of the optimal decision differed with system state (e.g., initial abundance) and population dynamics assumptions (e.g., survival hypotheses). Before adopting a management strategy based on a decision model, it is important that decision makers understand the behavior of the model and relative robustness of optimal decisions to assumptions.

The basis for determining the optimal decision was the utility score that was calculated using two objectives: 1) to maximize adult abundance of each of the three sucker groups and 2) to minimize management costs at the end of each simulation. A factor that may have affected utility scores was the objective weights. In the Klamath sucker utility function, equal weight (i.e., 25% of the total weight) was allocated to each of the three separate sucker groups (river-spawning Lost River Suckers, lake-spawning Lost River Suckers, and Shortnose Suckers) as well as management costs. Any decision that largely affected one of the four main objectives be it positively or negatively, affected that decision's utility score. In looking at the 1-year captive propagation decision (i.e., the optimal decision) a couple insights were gained. The model assumed that half of the suckers intended for captive propagation were

Shortnose Suckers based on expert opinion. This group of suckers are the least abundant of the three groups. They are distinct in that they mature quicker than both Lost River Sucker groups and they have much lower fecundity estimates (Buettner and Scoppettone 1990; Perkins et al. 2000). The estimated abundance of Shortnose Suckers did not increase as dramatically from the translocation and reduce entrainment and restore juvenile habitat decisions as the Lost River Suckers. Their weaker response to these two decisions is perhaps due to their much lower fecundity estimates. Additionally, the habitat restoration decision was much more expensive than the 1-year captive propagation decision. With both of those factors combined and the allocation of objective weights in the utility function, it becomes clear as to perhaps why the 1-year captive propagation decision was found to be the optimal decision.

The one-way sensitivity analyses of the population model parameters were surprising. I had expected juvenile survival to be more influential, but it turned out that the most influential parameters affecting utility was adult survival and age at reproductive maturity. Utility values were highest when either juvenile suckers became adults quickly or when adult suckers had very high survival. These results become less of a surprise when keeping in mind the fact that these suckers are long-lived and highly fecund species (Buettner and Scoppettone 1990; Perkins et al. 2000; Terwilliger et al. 2010). The adult stage should be the most influential component of their life cycle considering that they are adults for much of their lifespan. In contrast, I found that alternative model hypotheses also were very influential in the outcome of utility. Between the adult models and the juvenile models, the juvenile models were far more influential, indicating that the ability to discern influence between the competing model hypotheses in the juvenile life stage is an important next step in further refining the decision model.

Interestingly, most of the response profile sensitivity analysis showed no change in the optimal decision when parameters were adjusted +/-50% of their mean value. This result suggests that most of the decisions were robust to the parameter estimates used in the model and therefore, additional effort spent on improving the estimates would have little effect on changing the optimal decision outcome. For the parameters that did influence the optimal decision, the decisions that repeatedly alternated as being optimal were the 1-year captive propagation and the juvenile habitat restoration. In all cases, it was a single change, meaning that a change in optimal decision only occurred one time over the range of values. The most dramatic changes in decision occurred in the maturation duration parameter for subadults becoming adults, where the decision changed three time across the range of values. In the model, Lost River Suckers were estimated to mature between 7-9 years and Shortnose Suckers were estimated to mature earlier between 5-7 years (Buettner and Scoppettone 1990; NRC 2004; NMFS & USFWS 2013). If Lost River Suckers matured at least 30% faster than the mean value used in the decision model, the optimal decision was to restore juvenile habitat regardless of Shortnose Sucker maturity rates. If however Lost River Suckers matured slower than 30%, Shortnose Sucker maturity rate had much greater influence on optimal decisions. When Shortnose Suckers matured slower than assumed in the model, the translocation decision was optimal but when they matured quicker than estimated, 1-year captive propagation was the optimal decision. These results highlight that importance of observing age-at-maturity trends for Klamath suckers. It is reported that age-at-maturity can decrease as an evolutionary strategy to reproduce quicker and compensate for low abundance (Stearns and Koella 1986). Determining whether this trend is occurring in sucker populations in Upper Klamath Lake would be crucial in implementing successful recovery strategies.

Altering pairs of related parameters in the two-way sensitivity analyses provided further insights into how model assumptions affected decisions. In the response profile analysis of survival of age-0 and age-1 lake-spawning Lost River Suckers, I found that 1-year captive propagation was optimal if age-1 survival was no less than 40% of the mean value of 0.42 used during the simulations. I also found that if both age-0 and age-1 survival were greater than 0.0065 and 0.55 respectively, the optimal decision changed to restoring juvenile habitat. My interpretation of the change in optimal decision is that it represents a shift in focus on management strategy. Although both decisions focus on juveniles, they differ in that if juvenile survival is too low, the management strategy should be to propagate fish beyond this fragile stage. If juvenile survival is sufficiently high, the strategy should then shift towards improving rearing conditions because their survival rate is high enough to justify managing wild populations. For example, Cui-ui Suckers (*Chasmistes cujus)*, a similar sucker species, has been propagated in Pyramid Lake since 1973 (Day and Rasmussen 2014). Currently, approximately 1 million larvae are produced/year and about 200,000 are held in rearing ponds and released each year at ca. 10 cm in length (Day and Rasmussen 2014). The Cui-ui propagation program has been considered successful at avoiding population declines (Schooley and Marsh 2007; Scoppettone et al. 1986). Another similar sucker species, the June Sucker (*Chasmistes liorus***)**, located in Utah Lake, also has a propagation program (Day and Rasmussen 2014). The June Sucker program's goal is to stock 350,000 200 mm TL fish/year while also pursuing habitat restoration (Utah Division of Wildlife Resources 2004).

The optimal decision also was substantially influenced by subadult survival. Unfortunately, there is little to no knowledge about the subadult stage of Klamath suckers due to the fact there very few subadult suckers have been captured (Burdick 2013). It is believed that this is because few juvenile suckers manage to survive long enough to ever get to the subadult stage (Hewitt et al 2014). To obtain juvenile and subadult survival estimates, juvenile suckers must survive and be detected (captured) by biologists. Given the lack of success in past monitoring efforts to detect subadults and the dominance of the captive propagation decision at low to very low adult and age-1 survival, I believe that best way to improve our understanding of juvenile and subadult survival while simultaneously improving the sucker populations is likely through the 1-year captive propagation decision.

The survival of captive age-0 and stocked age-1 suckers had a significant influence on the optimal decision. If survival of these fishes was at or above the mean values used in the simulation, captive propagation was optimal. However, when the values were below the mean values used, captive propagation was not the optimal decision. I assumed that the survival of age-0 suckers in captivity was 0.35 based on rearing survival estimates in the Klamath Sucker Near-Term Extinction Prevention Action Plan (unpublished). I also assumed that the survival of stocked captivity raised fish was half of wild fish, which is similar to reported differences between hatchery and wild salmonids (Melnychuk et al. 2014). The mean survival values I assumed were within the range observed for released propagated June Suckers at 300-375 mm TL in Utah Lake with survival probabilities between 0.1-0.4 (Billman et al. 2011). However, the mean survival I used was greater than reported for Razorback Suckers (*Xyrauchen texanus)* that were released into Lake Mohave after 1-year in captivity with survival rates of 0.1 - 0.2 (Day and Rasmussen 2014). The uncertainty in survival of captive and stocked juveniles is a major knowledge gap and should be a priority for further study moving forward in Klamath sucker recovery. Getting these estimates, however, requires actual implementation of captive propagation, which further supports my conclusion based on data and a transparent modeling approach that 1-year captive propagation is the optimal decision.

The initial sucker population abundance state (i.e., abundance at t=0) had the greatest influence on the optimal decision compared to the three other states evaluated. When abundance was very low, the 1-year captive propagation decision was optimal across competing model hypotheses. This indicates that 1-year captive propagation was a stochastically dominant decision, or a decision that was consistently the best decision under various conditions, when the populations of the three sucker groups were very low. As initial sucker abundance was increased, other management alternatives were optimal. Interestingly, when I assumed that juvenile predation model was true, the 1-year captive propagation decision was only optimal when initial abundance was very high (200,000). These results suggest that once the population increases, identifying the best recovery strategy to employ becomes an issue of determining which alternative model best reflects the dynamics of the system. This suggests that the best adaptive management strategy for Klamath suckers is to build up populations via captive propagation. When the population is sufficiently large, the response to alternative management actions (other than propagation) would help resolve the uncertainty regarding sucker population dynamics. There also needs to be enough individuals in multiple stages to resolve these uncertainties. Thus, I argue that captive propagation is the superior decision because it would quickly build up the juvenile population. From there, monitoring of juveniles will be provide crucial information about system dynamics needed to improve vital rate estimates and alternative model weights in the decision model.

Surprisingly, predator abundance and the frequency of poor water quality events and wet and dry years had minor influences on the optimal decision. When predator abundance was high, I would have expected avian hazing, a predator control decision, to be the optimal decision, but it was not. I also expected water quality related decisions to be optimal when the frequency of poor water quality events was high, but that was not the case. I interpreted these results to be more of an artifact of model structure, meaning that the design of these information state scenarios could be refined, rather than an important result due to the recurring dominance of the captive propagation decision. The avian hazing decision was ineffective because predator abundances included both avian predators and aquatic predators yet the management decision only addressed avian predators because controlling the aquatic predators (e.g., Fathead Minnows) was considered not feasible. Even if avian predators could be reduced greatly, aquatic predators were still highly abundant and therefore continued to reduce sucker populations. Similarly, the decisions relating to improving water quality were only optimal for the filtering algae decision under the assumption that water quality was the true (and only) factor affecting juvenile and adult survival. This was most likely because many of the water quality decisions were very expensive and the least expensive of them was to filter algae.

Lost River Suckers and Shortnose Suckers have life history strategies adapted to tolerating periods of poor water quality by being long-lived and highly fecund (Buettner and Scoppettone 1990). With these strategies under historical conditions, the population was able to remain stable despite intermittent recruitment (Terwilliger et al. 2010; Rasmussen 2011). However, there have been increasingly difficult and complex issues that suckers in Upper Klamath Lake are not fully equipped to deal with and populations cannot persist if recruitment rates do not increase. The remaining adults are approaching the end of their natural lifespan and there is no detectable subadult cohort to take their place (Hewitt et al. 2014). With drastic reductions in quantity and quality of juvenile rearing habitat coupled with the introduction of aquatic predators, I hypothesize that juvenile survival is the survival bottleneck. The issues facing suckers in Upper Klamath Lake are complex but their effects can be observed by comparing the sucker age structure in Upper Klamath Lake to that of suckers residing in nearby Clear Lake. Clear Lake suckers have at least seen some recruitment into the adult population (Burdick and Rasmussen 2013). The issues facing suckers in Clear Lake are less complicated in that entrainment and water quality are not believed to be major problems as they are in Upper Klamath Lake (NMFS & USFWS 2013). It is possible that through initiating management actions that include 1-year captive propagation in both systems, more knowledge about sucker population dynamics could be gained. Lost River Suckers and Shortnose Suckers are not alone in the problems they face. Related sucker species such as June suckers in Utah Lake, Utah and Cui-ui suckers in Pyramid Lake, Nevada have also dealt with similar issues (Belk et al. 2011). Management strategies like the captive propagation decision detailed in the Klamath sucker decision model have been enacted in attempts at recovering these other sucker populations (Andersen et al. 2007).

Briefly I provide a few monitoring-focus recommendations based on the decision model analyses that may provide for the disentangling of the four alternative system dynamics hypotheses moving forward in the Klamath sucker recovery planning process. I assume here that the optimal decision, the stocking of tagged juveniles from the optimal 1-year captive propagation, has been implemented.

1) *Water Quality Model* - monitoring patterns of juvenile distribution in the lake during poor water quality events and water quality related mortality,
2) *Predation Model* - tracking avian predation through collection of juvenile PIT tags on avian nesting sites,

3) *Habitat Model* - estimation of juvenile densities in nearshore habitats and/or occupancy estimates related to lake elevations,

4) *Entrainment Model* - quantify entrainment rates through private diversions and over the Link River Dam using PIT tag data from stocked juveniles and streamflow.

All models are approximations of reality, so I would like to provide some caveats to the Klamath sucker decision model and to models in general. It is impossible to include everything in a model and even if it was possible, it is impractical and unnecessary. Models are purposeful simplifications of reality. Constructing a model is an attempt to interpret the world around us in a way that is comprehendible and communicable rather than dealing with the reality that it is very complex and often includes many unknowns. By diagnosing model behavior, we can tease out the major drivers that are responsible for the patterns we observe in the natural world. In the Klamath sucker decision model, the sensitivity analyses found only a few model components out of more than 150 parameters that largely influenced the management decision. These model components included: initial sucker population abundance, the competing juvenile dynamics models, age-at-maturity, and adult survival. There are many areas of uncertainty in the model, particularly in the juvenile stages, largely due to a lack of data on survival rates because only limited numbers of suckers appear to survive to this stage. Thus, the model identified that initiating 1-year captive propagation could build up the juvenile population past the survival bottleneck thereby creating the quickest opportunity to learn more about juvenile sucker dynamics through monitoring. However, the success of that strategy depends on the survival of captive raised individuals and should be considered a key uncertainty.

Decision models are tools for thinking and gaining insight into complex systems such as the sucker dynamics in Upper Klamath Lake. Models can be used to explore how alternative management strategies may be employed to learn about a system. In the Klamath sucker decision model, I discovered that employing management strategies that focus on juvenile suckers, such as 1-year captive propagation, could be the fastest way to gain knowledge about the system thereby reducing uncertainty in the model because it would increase the ability to observe (capture) age-1 and presumably, subadults. It is in this ability, to identify key drivers and uncertainty in a system that decision models excel in increasing our understanding of the underlying principles of a subjectively perceived system under specific conditions.

Decision models are also excellent tools for communicating ideas about system dynamics and testing hypotheses related to those ideas. Whether we are aware of it or not, we all have conceptual models of how systems function. These models already exist. However, it is through the framework of quantification in decision models that we can make these models communicable, transparent, testable, and updateable. Decision models have the capacity to accommodate differing beliefs concerning how a system functions in the form of competing alternative models. These alternative models can then be tested through time by comparing model performance to monitoring data all the while management decisions are being made in real time and working with uncertainty. The end goal of my thesis was not to model every detail of sucker dynamics in Upper Klamath Lake to perfection. My goal was to build a framework for integrating previously collected data and to allow for the integration of future data to test hypotheses about system dynamics. It was my intent to build a decision support tool for gaining insight into an ever-changing complex system and to aid in the management of natural resources in Oregon's Klamath Basin.

6 Figures

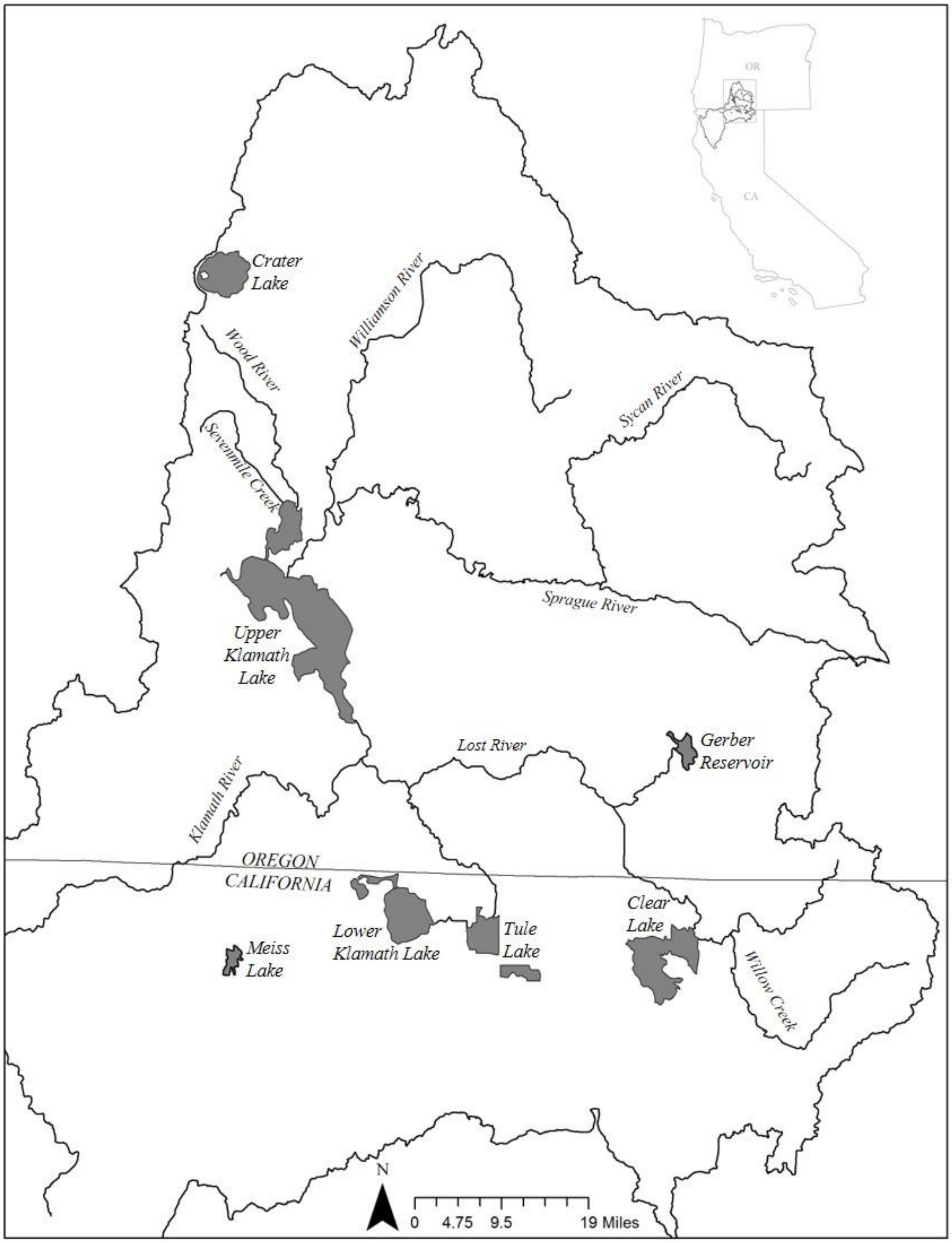

Figure 1. Map of Upper Klamath Basin in Southern Oregon and Northern California. The Klamath sucker decision model focused on sucker populations in Upper Klamath Lake.

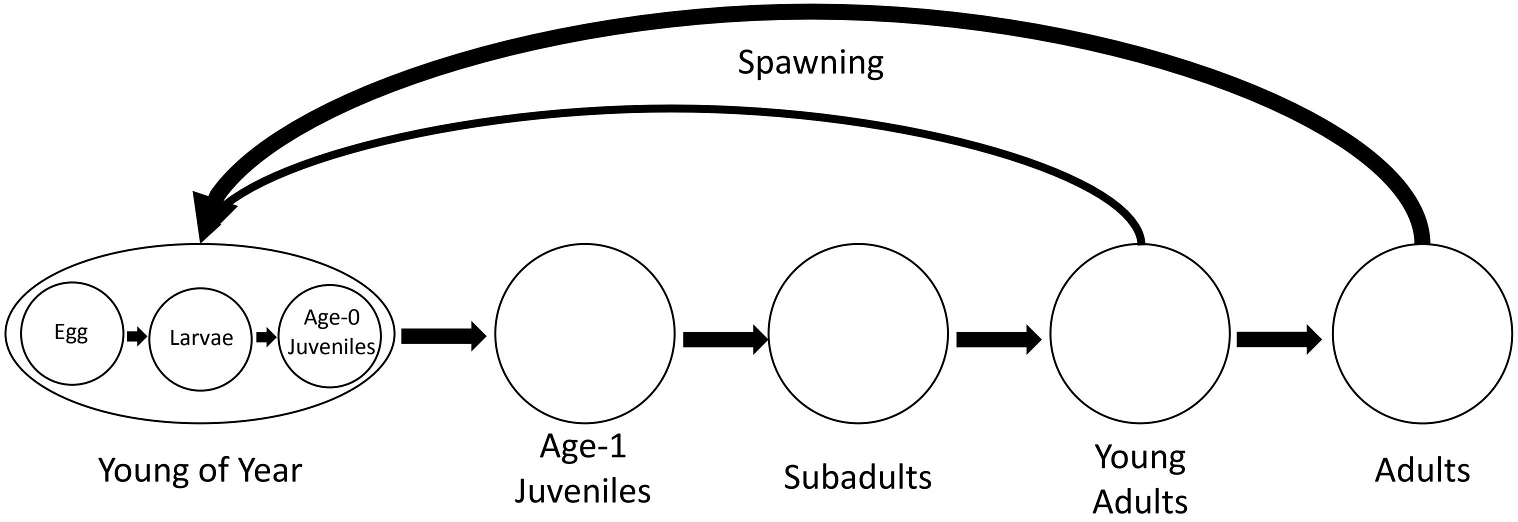

Figure 2. Graphical depiction of the 5-stage Klamath sucker baseline population model. The young-of-year stage is a composite stage that represents 3 distinct substages (egg, larvae, and age-0 juvenile) during the first year of life. The subadults stage is juveniles that are at least age-2 but have not reached reproductive maturity (5 to 9 years of age). Young adults (age-5 to age-9) are reproductively mature but have lower fecundity (75,000) than older adults (140,000).

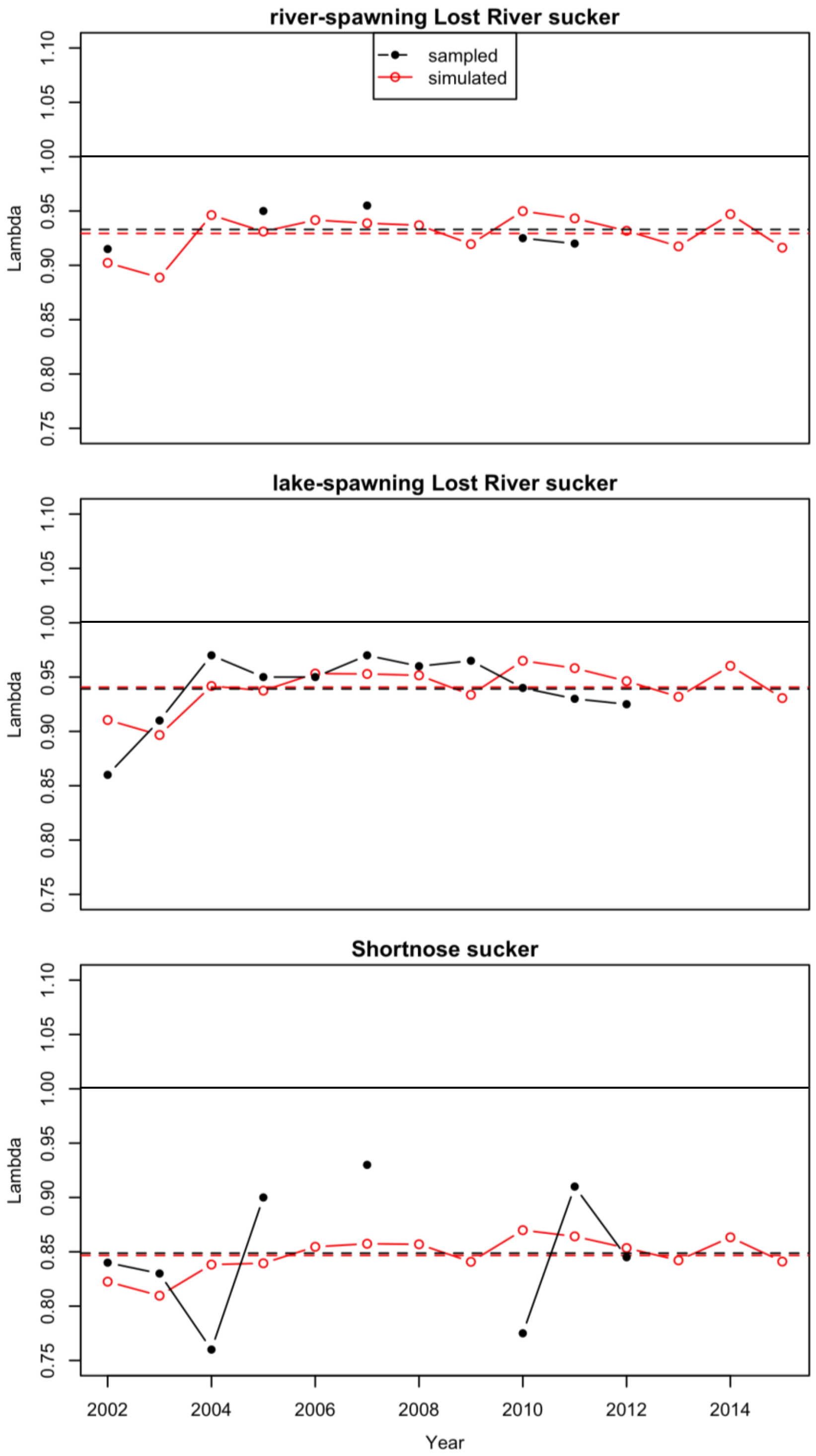

Figure 3. Matching simulated lambda to lambda estimates from Hewitt et al. (2015). Age-0 survival estimates in the population model were adjusted to fit lambda data using optimization. Dotted lines represent mean lambda. Values >1 suggest population growth and values <1 suggest population decline.

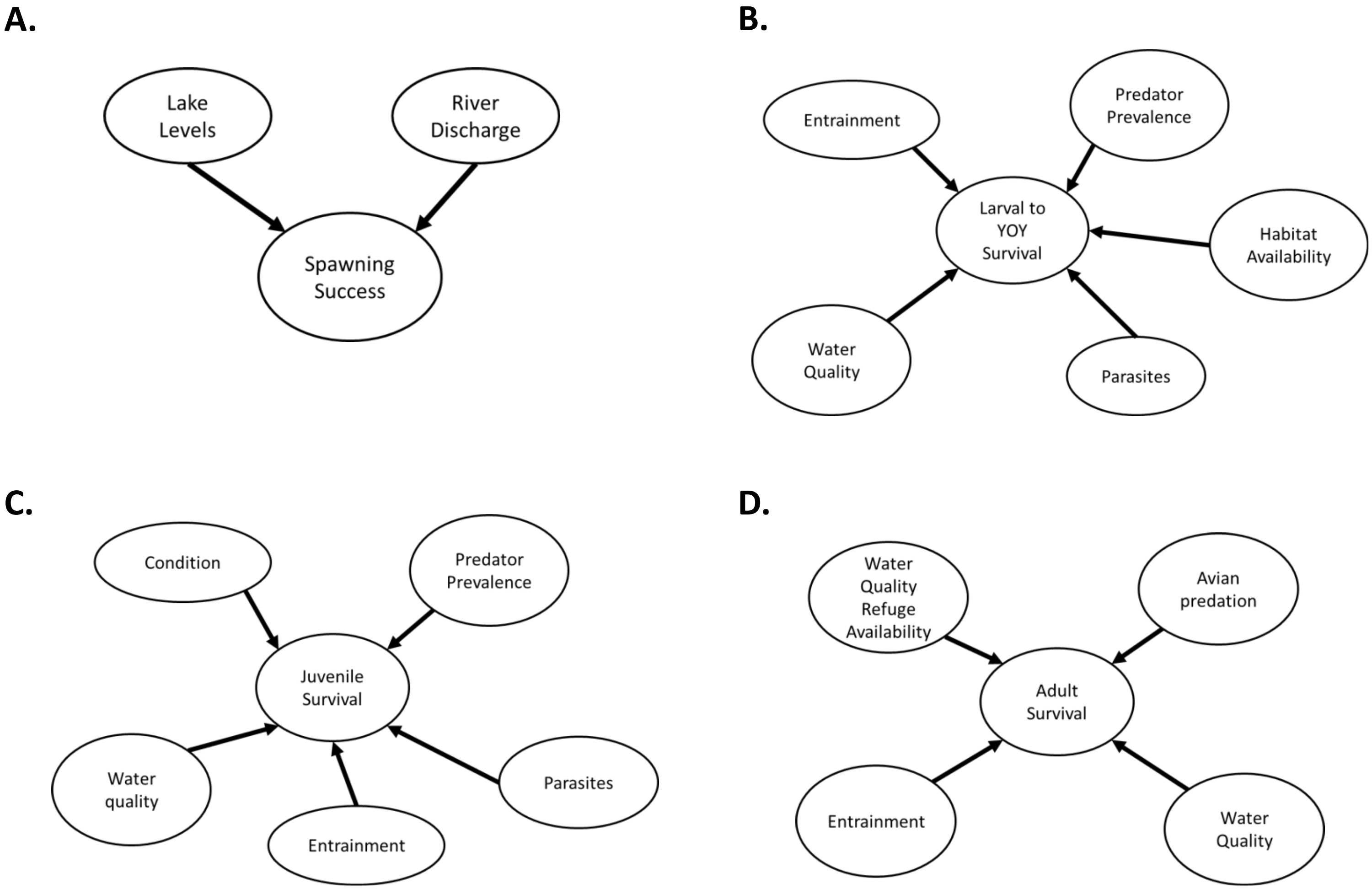

Figure 4. Graphical depiction of (A) spawning success, (B) larval to young-of-year survival, (C) juvenile survival and (D) adult survival conceptual models represent all of the hypotheses.

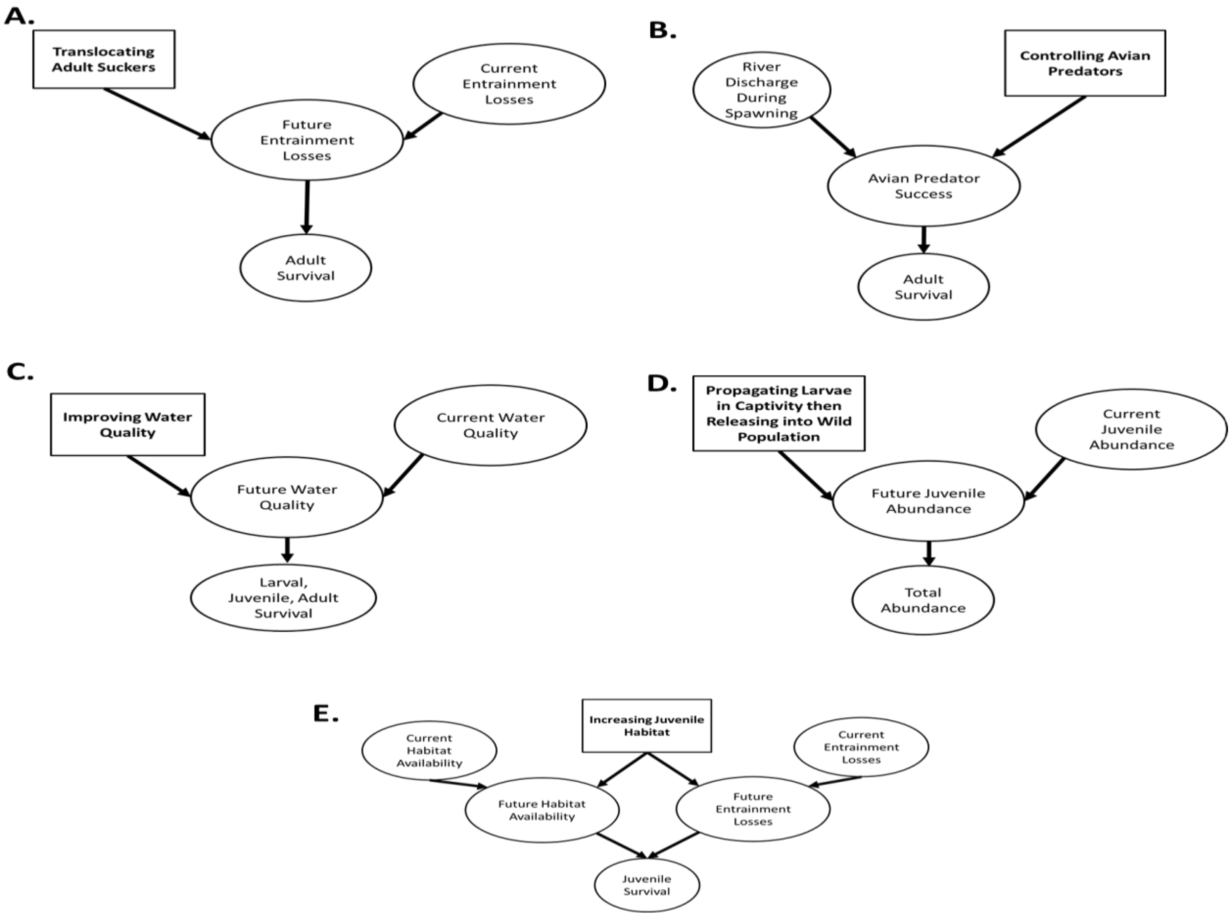

Figure 5. Graphical depiction of the decision alternatives: (A) translocate adult suckers, (B) control avian predators (C) improve water quality, (D) propagate larvae suckers and then release into wild populations and (E) increase juvenile habitat and the factors that they influence.

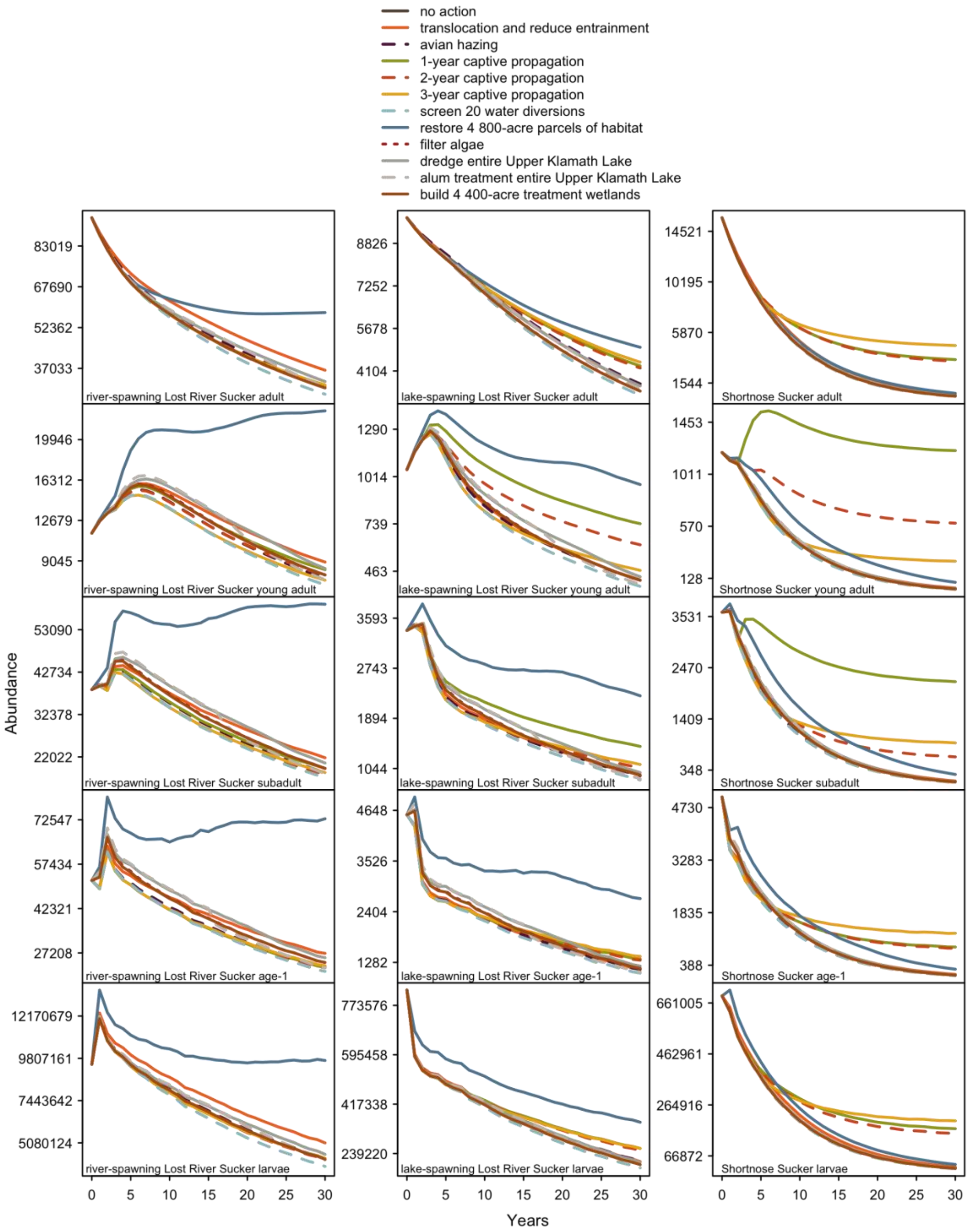

Figure 6. 30-year population trajectories from stochastic simulations for river-spawning Lost River Suckers (left column), lake-spawning Lost River Suckers (middle column), and Shortnose Suckers (right column). Each row corresponds to life stages. Within each figure are the average decision alternative specific population trajectories from 10,000 iterations per decision alternative.

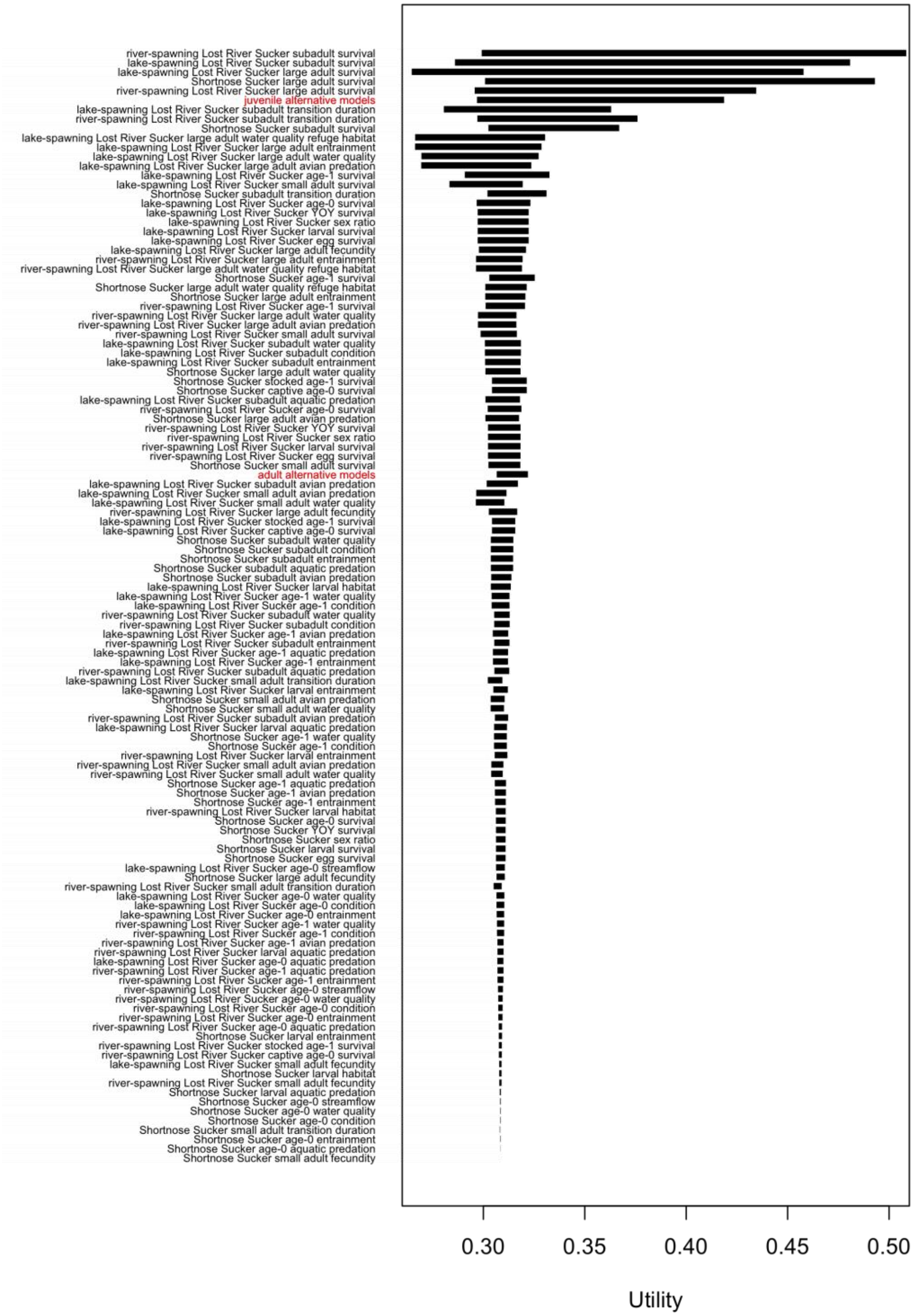

Figure 7. Tornado diagram of decision model population parameters. A tornado diagram consists of horizontal bars, one for each parameter in the model that displays the value of the utility across the range of values of the parameter that was varied. These are sorted from most to least influential on the y-axis from top to bottom. The x-axis is the percent change in the estimated score resulting from varying the value of the parameters.

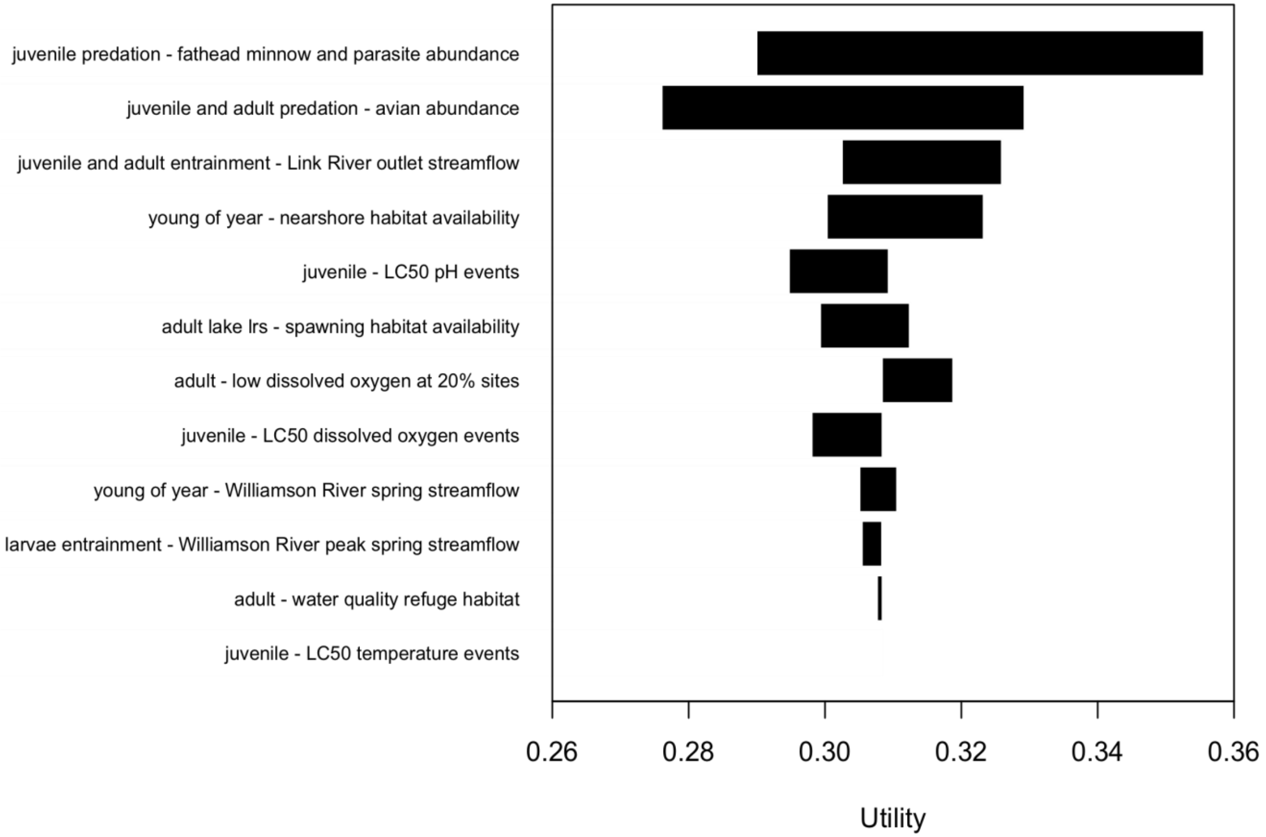

Figure 8. Tornado diagram of decision model environmental inputs. The top 3 most sensitive inputs include elements that affect juvenile survival. A tornado diagram consists of horizontal bars, one for each parameter in the model that displays the value of the utility across the range of values of the parameter that was varied. These are sorted from most to least influential on the y-axis from top to bottom. The x-axis is the percent change in the estimated score resulting from varying the value of the parameters.

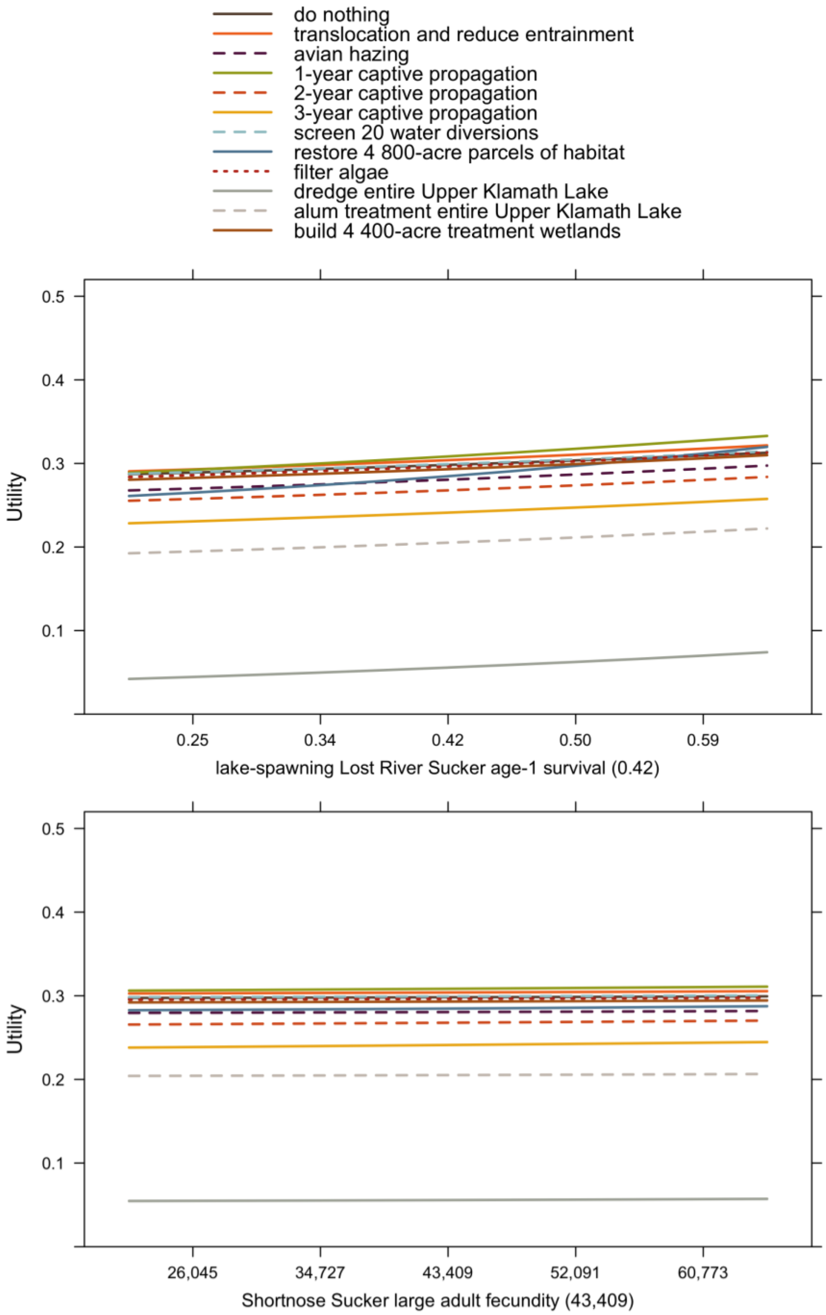

Figure 9. Examples of response profiles that indicated no change in the optimal decision (greatest utility) for lake-spawning Lost River sucker age-1 survival (top) and Shortnose sucker large adult fecundity (bottom). Utility scores are calculated for each decision alternative using proportional scoring of the model simulation objectives 1) management costs and 2) end adult sucker abundances, combined using a weighted sum ranging from 0 to 1 with the highest utility being the optimal decision.

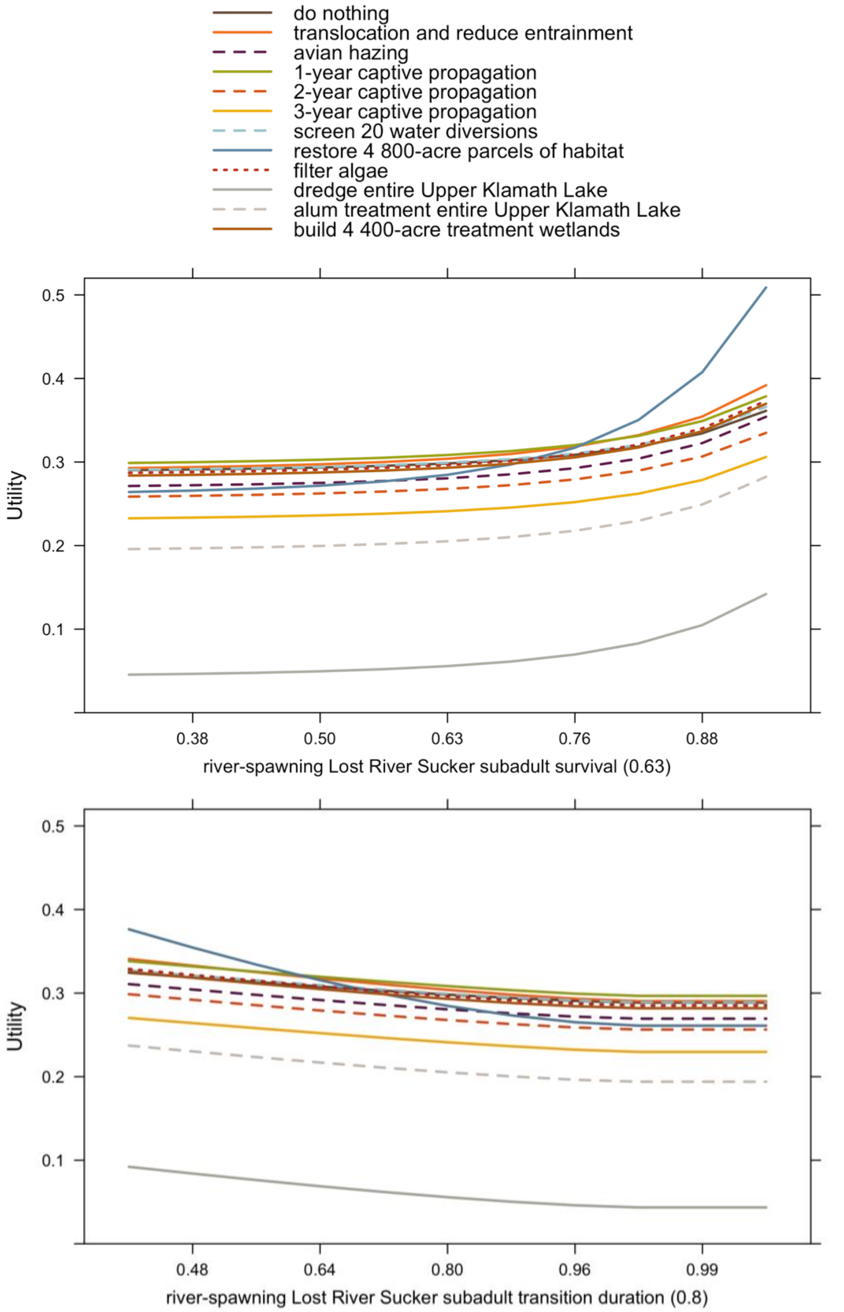

Figure 10. Response profile of river-spawning Lost River Sucker subadult adult survival (top) and transition duration (bottom). Top line in each plot is the greatest utility and the optimal decision. Utility scores are calculated for each decision alternative using proportional scoring of the model simulation objectives 1) management costs and 2) end adult sucker abundances, combined using a weighted sum ranging from 0 to 1 with the highest utility being the optimal decision.

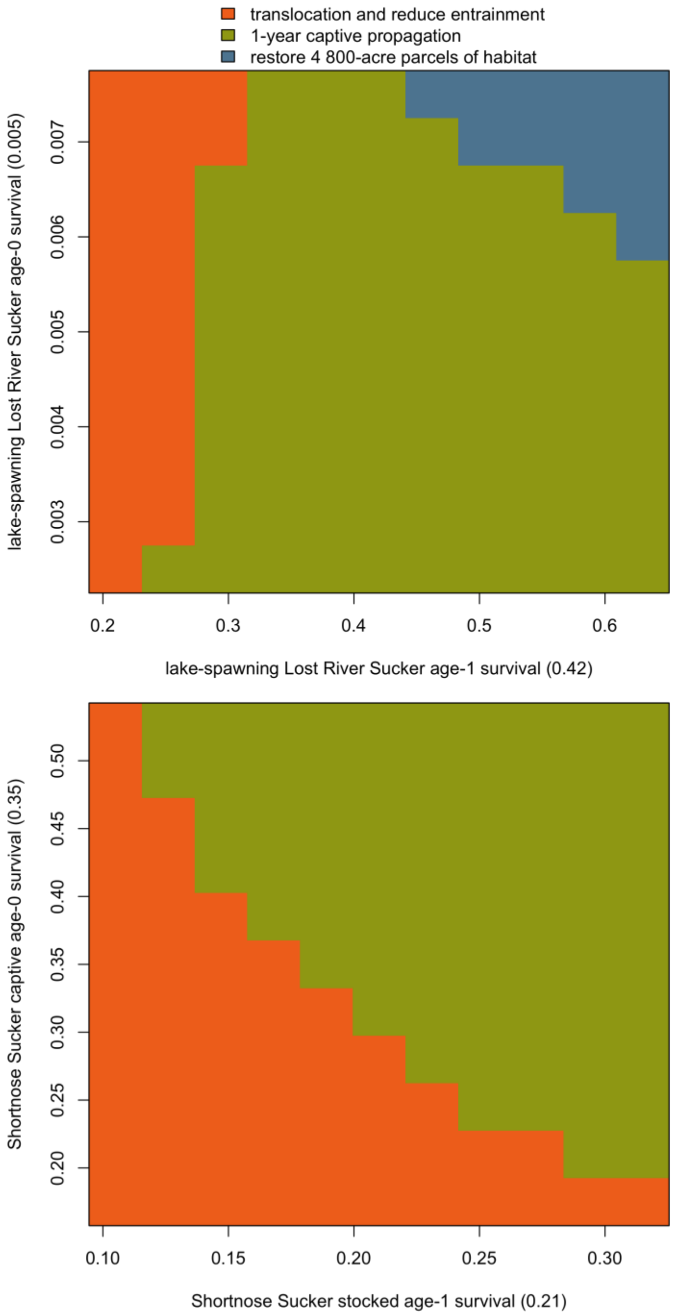

Figure 11. Two-way response profile plot of (top) lake-spawning Lost River Sucker juvenile survival and lake-spawning Lost River Sucker age-0 survival and (bottom) Shortnose Sucker stocked juvenile survival and Shortnose Sucker captive age-0 survival.

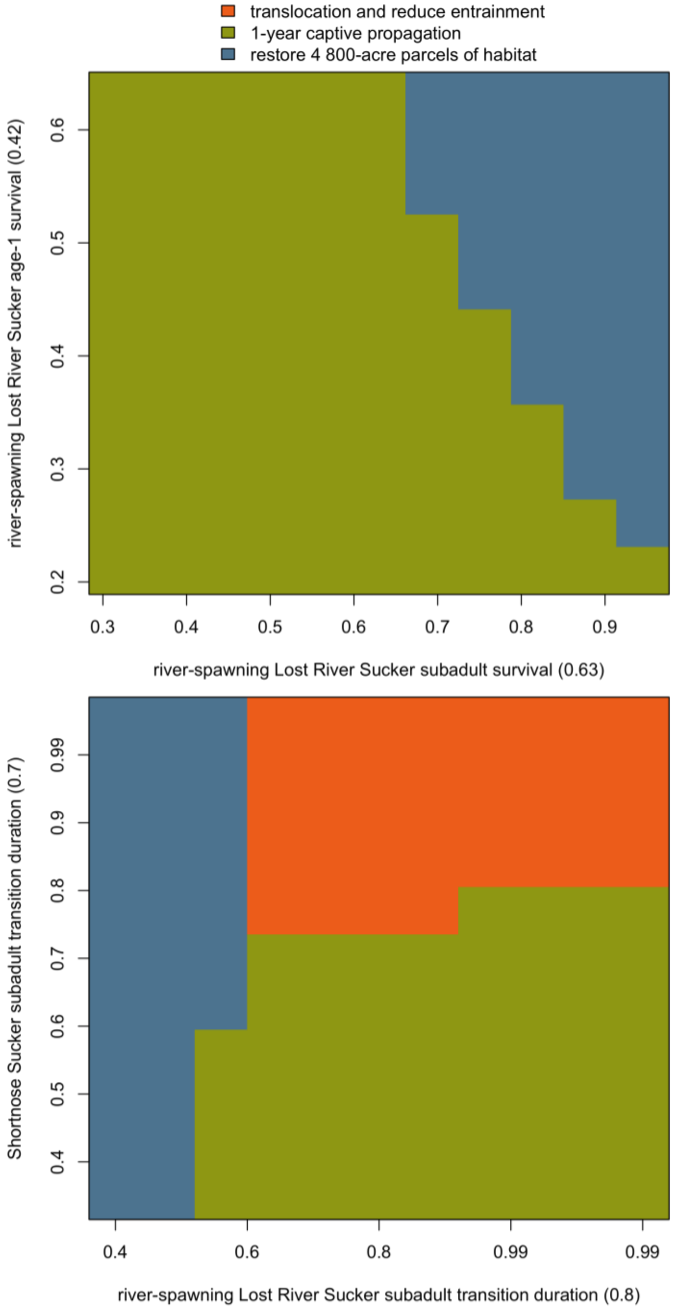

Figure 12. Two-way response profile plot of (top) river-spawning Lost River Sucker subadult survival and river-spawning Lost River Sucker juvenile survival and (bottom) river-spawning Lost River Sucker subadult transition duration and Shortnose Sucker subadult transition duration.

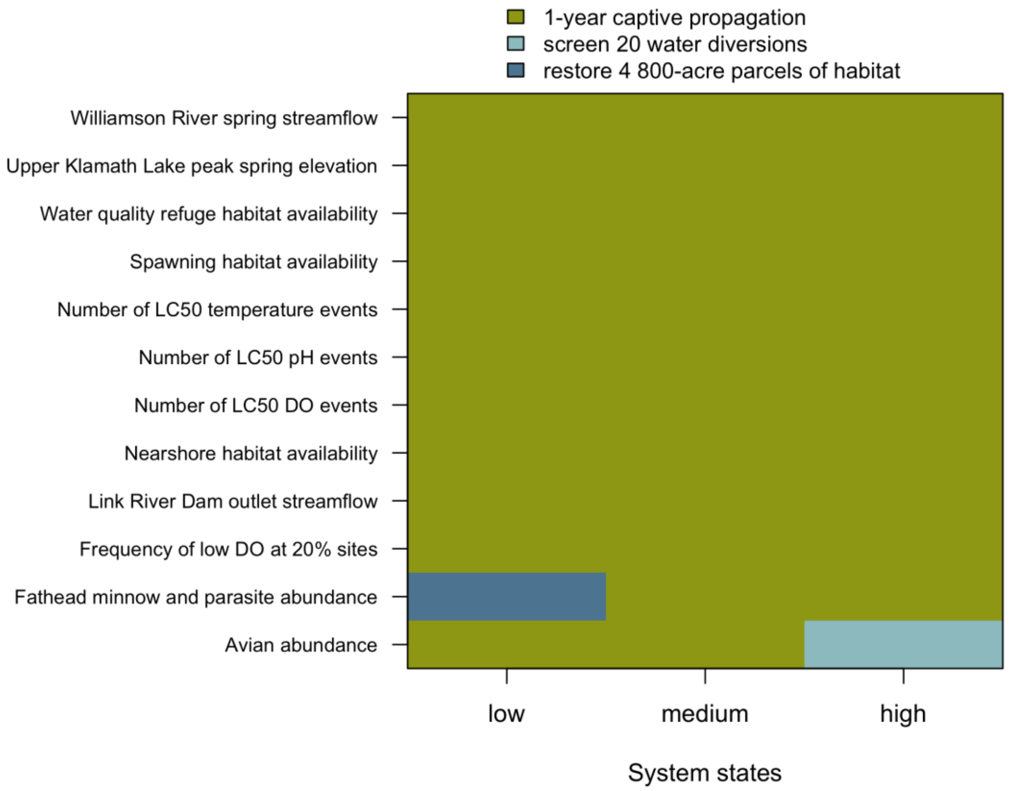

Figure 13. System state-dependent policy plot of optimal decisions. State values correspond to minimum and maximum values in Table 10. System states (y-axis) are the environmental inputs to the population model life stage survival and fecundity parameter submodels.

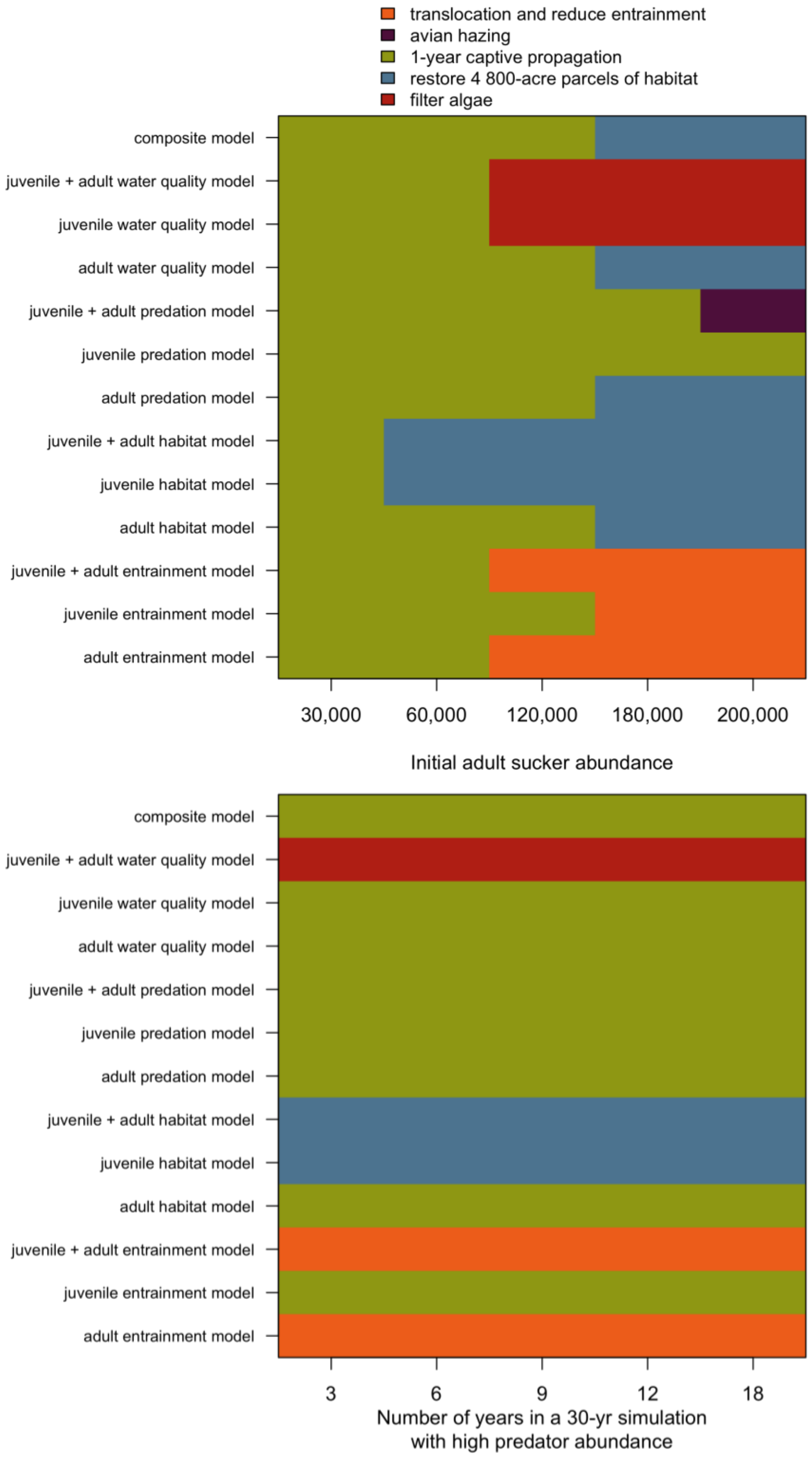

Figure 14. Policy plot of alternative model hypotheses (information states) for juvenile and adult Lost River suckers and Shortnose suckers in Upper Klamath Lake vs (top) initial sucker abundance and (bottom) aquatic and avian predator abundance.

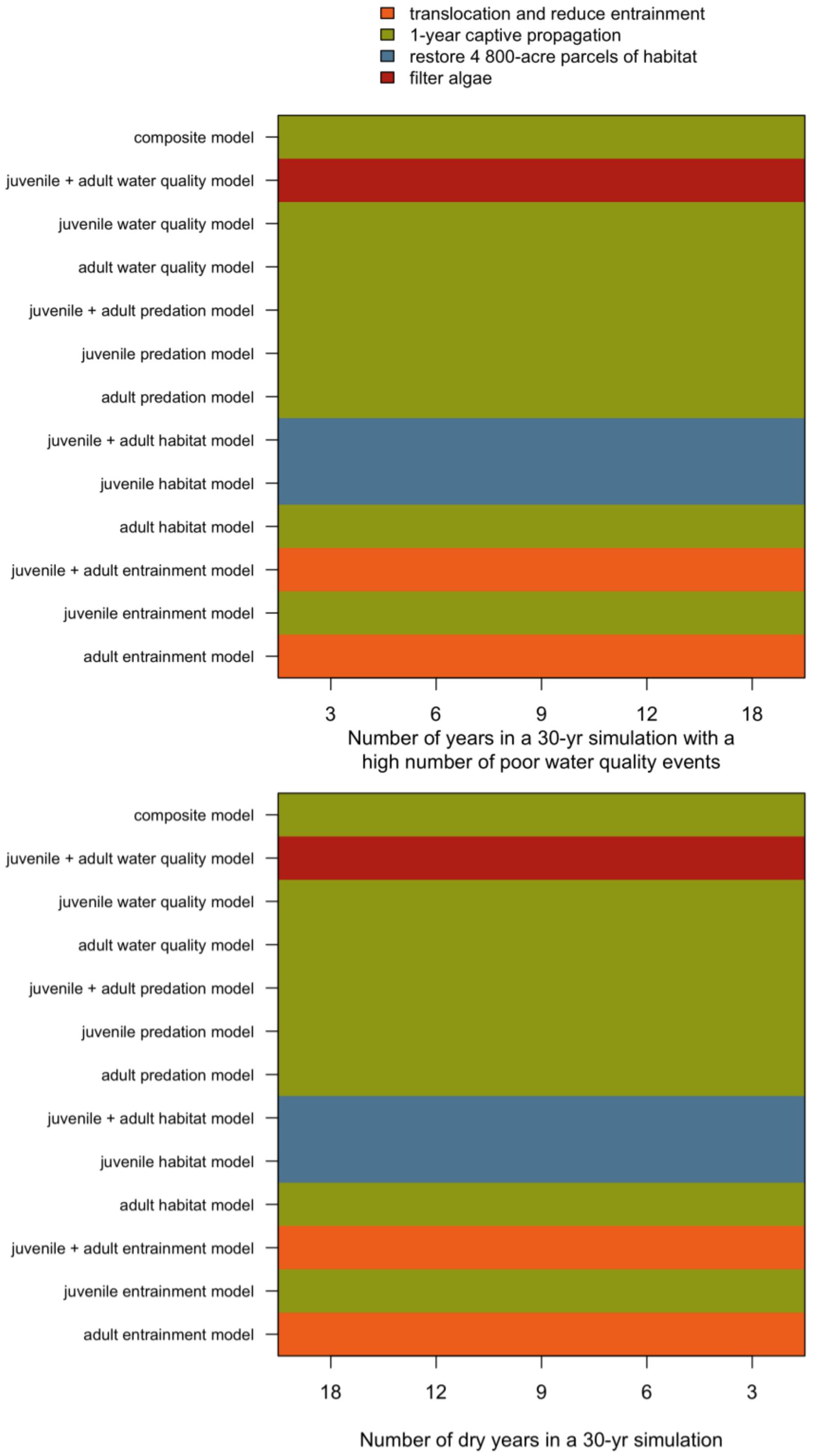

Figure 15. Policy plot of alternative model hypotheses (information states) for juvenile and adult Lost River suckers and Shortnose suckers in Upper Klamath Lake vs. (top) of the frequency of poor water quality and (bottom) frequency of wet years.

7 Tables

Table 1. Stakeholders in the Upper Klamath Basin.

Stakeholder	Type	Activity in Basin
Klamath tribes (Klamath, Modoc, and Yahooskin)	Native tribes	Historically resided in Basin, utilize suckers as food and for cultural uses, has seniority rights with regards to water (KBRA 2010)
U.S. Bureau of Reclamation	Federal Agency	Operates the Klamath Irrigation Project (NMFS & USFWS 2013)
U.S. Fish and Wildlife Service	Federal Agency	Principal listing agency for the Endangered Species Act in Upper Klamath Basin (NMFS & USFWS 2013)
Farmers and Ranchers	Private landowners	Receive water deliveries through Klamath Project for irrigated pasture and agriculture (NRC 2004)
U.S. Geological Survey	Federal Agency	Research and monitoring of water quality and suckers in Basin (NMFS & USFWS 2013)
Environmental Protection Agency	Federal Agency	Manages water quality in Basin (ODEQ 2002)
Oregon Department of Environmental Quality	State Agency	Supports research involved with Environmental Protection Agency regarding water quality requirements (ODEQ 2002)
Federal Energy Regulatory Commission	Federal Agency	Regulates operation of hydroelectric dams (KHSA 2013)
PacifiCorp	Private Company	Operates multiple hydroelectric dams in the Basin (KHSA 2013)
The Nature Conservancy	Conservation organization	Initiates purchasing of land for restoration and conservation (TNC 2010)
The National Research Council	Private nonprofit institution	Evaluates U.S. Fish and Wildlife's assessments of Klamath Project operations (NRC 2004)
State of California North Coast Regional Water Quality Control Board	State Agency	Supports research involved with Environmental Protection Agency regarding water quality requirements (NCRWQCB 2010)
National Marine Fisheries Service	Federal Agency	Principal listing agency for the Endangered Species Act in Lower Klamath Basin (NMFS & USFWS 2013)
Bureau of Land Management	Federal Agency	Cooperating agency for Environmental Impact Statements on Klamath Hydroelectric Settlement Agreement (KHSA 2013)

Table 2. The expected demographic estimates used to parameterize the submodel functions. Age-0 survival was estimated using optimization to calibrate the population model to adult sucker tagging data in Hewitt et al. (2015). Adult survival and fecundity parameters were modified to reflect differences in survival among river and lake-spawning Lost River Suckers and Shortnose Suckers.

Parameter	**river-spawning Lost River sucker**	**Source**
egg survival	0.027	Scoppettone et al. (2000)
larvae survival	0.05	Houde (1994)
age-0 survival	0.005	estimated using optimization
age-1 survival	0.4225	Billman and Crowl (2007)
subadult survival	0.63225	Billman and Crowl (2007)
small adult survival	0.90	Hewett et al. (2014)
large adult survival	0.90	Hewett et al. (2014)
subadult transition duration probability (age at maturity)	0.86	Buettner and Scoppettone (1990)
small adult transition duration probability	0.70	Perkins et al. (2000)
sex ratio (females to males)	0.53	Hewett et al. (2014)
small adult fecundity	75,000	Perkins et al. (2000)
large adult fecundity	139,927	Perkins et al. (2000)

Table 3. Statistical summary of compiled historical environmental data. Environmental variables such as streamflow and lake elevation served as inputs to the population model survival and fecundity parameter submodels.

Environmental variable	Minimum	1st quantile	Mean	3rd quantile	Maximum	USGS gages and data sources
Mean spring streamflow of Williamson River (March – August)	638	843	1055	1113	1942	11502500
Number of high pH events	0	0	0.38	0.10	3.00	422719121571400
Number of low dissolved oxygen events	0	0	0.15	0	2.00	422719121571400
Number of high temperature events	0	0	0	0	0	422719121571400
Mean elevation Upper Klamath Lake (February-June)	4140	4142	4142	4143	4143	USGS 11507001
Proportion of spawning season when lake levels are below low level threshold	0.00	0.04	0.24	0.38	1.00	USGS 11507001
Spring peak Upper Klamath Lake elevation (April-May)	4141	4143	4143	4143	4143	USGS 11507001
Percent of macrophyte habitat available based on May through July lake levels	4141	4142	4142	4142	4143	USGS 11507001
Mean low DO events/year at 20% gages	0.0	1.0	3.7	4.6	15.0	all gages in UKL recording DO
Mean elevation of Pelican Bay from July-September	4139	4140	4140	4140	4141	11505800
Mean August-September streamflow of Link River	524	781	857	981	1031	11507500
Fathead Minnow catch per unit effort	4	47	158	232	475	Markle et al. (2014b)
Avian abundance	0	1830	1830	1862	4473	Evans et al (2015)

Table 4. Functions and parameters used to represent the juvenile alternative hypotheses and estimate the survival of Klamath suckers. Coefficients generated using logistic regressions detailed in Methods section.

Parameter	Estimate	Description
Number of eggs produced	$N_f \times (1 - PROPS_l) \times FEC \times (1 - PROPS_d)$	N_f = number of small and large adult females FEC = average fecundity based on number of small and large females $PROPS_l$ = proportion of spawning season when lake levels are below low level threshold $PROPS_d$ = proportion of decreased spawning duration when lake levels are below low level threshold
Spring streamflow on larval survival	$\frac{1}{1 + e^{-(-4.6468 + -0.0005 \times WR.MAR.AUG)}}$	$WR.MAR.AUG$ = mean spring streamflow of Williamson River March to August
Habitat availability on larval survival	$\frac{1}{1 + e^{-(-3.8918 + 2.0794 \times UKL.MAY.AUG)}}$	$UKL.MAY.AUG$ = percent of macrophyte habitat available based on May through July lake levels
Fathead Minnow predation and parasite prevalence on larval and juvenile survival	$\frac{1}{1 + e^{-(-2.5216 + -0.0023 \times FHM_{t-1})}} \times \left(1 - \left(\frac{e^{-3.4307+0.0283\times FHM_t}}{1 + e^{-3.4307+0.0283 \times FHM_t}}\right) \times \left(\frac{PEN}{100}\right)\right)$	FHM_{t-1} = Fathead Minnow catch per unit effort in year_{t-1} FHM_t = Fathead Minnow catch per unit effort in year_t PEN = severity of parasite prevalence penalty for different life stages
Condition on juvenile survival	$((K_o - K_a) + 1) \times S_a$	K_o = observed condition K_a = average condition S_a = 0.005 for age-0, 0.4225 for age-1, 0.63225 for subadults
Water quality on larval survival	$N_{sp} \times 0.5^{EVT}$	N_{sp} = number of surviving larvae before LC50 water quality event

Table 4. (cont.)

Water quality on juvenile survival	$S_a \times \left(1 - \left(\frac{EVT}{100} \times C\right)\right)$	S_a = 0.005 for age-0, 0.4225 for age-1, 0.63225 for subadults *EVT* = number of poor water quality events, *pH*+*DO*+*Temp* *C* = 100% for age-0, 90% for age-1 and subadults
Avian predation on juvenile survival	$S_a \times (1 - (PRD \times RTO))$	*PRD* = avian predation rate, 0.015+0.0000116**AVIAN* *RTO* = predation ratio for adjusting effect of different life stages, 4 for age-1 juveniles and subadults
Entrainment effect on larval survival	$\frac{1}{1 + e^{-(-2483458 + 3933.8360 \times PEAK + -1.5578 \times PEAK^2)}}$	*PEAK* = Spring peak Upper Klamath Lake elevation (April-May)
Link River streamflow on adult entrainment	$\frac{1}{1 + e^{-(2.4470 + -0.0006 \times LINK)}}$	*LINK* = mean August-September streamflow of Link River

Table 5. Functions and parameters used to represent the adult alternative hypotheses and estimate the survival of Klamath suckers.

Parameter	Estimate	Description
Water quality on adult survival	$S_a \times \left(1 - \left(\frac{EVT}{100} \times C\right)\right)$	S_a = 0.90 for river-spawning Lost River sucker adults 0.92 for lake-spawning Lost River sucker adults 0.84 for Shortnose sucker adults *EVT* = number of poor water quality events, *lowDO20* *C* = 60% for small adults, 30% for large adults
Water quality refuge availability on adult survival	$0.001 \times (((1.00005 \times PEL.JUL.OCT) - 4140.384)^3) + 0.88$	*PEL.JUL.OCT* = mean elevation of Pelican Bay from July-September
Avian predation on adult survival	$S_a \times (1 - (PRD \times RTO))$	*PRD* = avian predation rate, 0.015+0.0000116**AVIAN* *RTO* = predation ratio for adjusting effect of different life stages, 3 for small adults, 2 for large adults
Link River streamflow on adult entrainment	$\frac{1}{1 + e^{-(2.4470 + -0.0006 \times LINK)}}$	*LINK* = mean August-September streamflow of Link River

Table 6. Demographic parameter differences between species/spawning groups. All younger stages from egg to subadult demographic parameters did not have differences between species/spawning groups.

Parameter	**river-spawning Lost River sucker**	**lake-spawning Lost River sucker**	**Shortnose sucker**	**Source**
small adult survival	0.90	0.92	0.84	Hewett et al. (2014)
large adult survival	0.90	0.92	0.84	Hewett et al. (2014)
subadult transition	0.80	0.80	0.70	Buettner and Scoppettone (1990)
small adult transition	0.70	0.70	0.50	Buettner and Scoppettone (1990), Terwilliger et al. (2010) and Perkins et al. (2000)
sex ratio	0.53	0.53	0.73	Hewett et al. (2014)
small adult fecundity	75,000	75,000	21,544	Buettner and Scoppettone (1990), Terwilliger et al. (2010) and Perkins et al. (2000)
large adult fecundity	139,926	139,926	43,450	Buettner and Scoppettone (1990), Terwilliger et al. (2010) and Perkins et al. (2000)
initial adult abundance	93,600	9,773	15,679	NMFS & USFWS (2013); Hewitt et al. 2015, Klamath Sucker Extinction Prevention Plan

Table 7. Parameters used in utility function. Utility scores are calculated for each decision alternative using proportional scoring of the model simulation objectives 1) management costs and 2) end adult sucker abundances, combined using a weighted sum ranging from 0 to 1 with the highest utility being the optimal decision.

Parameter Descriptions	**Value**
Minimum end of simulation river-spawning Lost River sucker abundance	51
Maximum end of simulation river-spawning Lost River sucker abundance	608,614
Minimum end of simulation lake-spawning Lost River sucker abundance	1
Maximum end of simulation lake-spawning Lost River sucker abundance	23,389
Minimum end of simulation Shortnose sucker abundance	0
Maximum end of simulation Shortnose sucker abundance	39,033
Minimum management costs	$0
Maximum management costs	$460 M
Objective weight for river-spawning Lost River sucker end adult abundance	0.25
Objective weight for lake-spawning Lost River sucker end adult abundance	0.25
Objective weight for Shortnose sucker end adult abundance	0.25
Objective weight for management costs	0.25

Table 8. List of decision alternatives and 30-year cost estimates. Decision alternative simulation time horizon is 30 years. Each simulation scenario consists of choosing one decision alternative for an entire simulation and that single decision is then initiated in the model on a yearly basis. If the decision has a specific lifespan (i.e., alum treatment lasts for 20 years), then that decision is initiated once at the beginning of the simulation. If a decision has a maximum value (screen water diversions) then that decision is initiated every year until the maximum is reached.

Decision Alternative	**30-Year Cost**	**Source**
No action	$ 0	-
Translocation and entrainment reduction	$ 11.5 M	Klamath Sucker Extinction Prevention Plan, not yet published
Avian hazing	$ 45.8 M	DCCO Draft EIS 2014
Controlled propagation program: 1-year rearing	$ 62.8 M	Klamath Sucker Extinction Prevention Plan, not yet published
Controlled propagation program: 2-year rearing	$ 125.6 M	1-year rearing × 2
Controlled propagation program: 3-year rearing	$ 188.4 M	1-year rearing × 3
Screen 1 water diversion/year (20 max)	$ 0.4 M	Nobriga et al. 2004
Restore 1 800--acre parcel/year for habitat (4 parcels max)	$ 90.0 M	Stillwater Sciences 2013
10-year barge based algae filtration project	$ 11.1 M	Stillwater Sciences 2013
Dredge the entire Upper Klamath Lake	$ 460.0 M	Stillwater Sciences 2013
Treat entire Upper Klamath Lake with alum	$ 180.0 M	Stillwater Sciences 2013
Build 1 400-acre treatment wetland/year (4 parcels max)	$ 17.0 M	Stillwater Sciences 2013

Table 9. Mean values of simulated environmental variables in stochastic decision model. Environmental variables served as inputs to the population model survival and fecundity parameter submodels.

Description	**Environmental variable**	**Mean (SD)**	**Stochastic values realized using**
Mean Williamson River flow March-August (cfs)	*WR.MAR.AUG*	1053 (355)	Gamma distribution
Probability of pH event in Williamson River Delta	*pH*	0.15 (0.38)	Binomial distribution probability 0.05
Probability of DO event Williamson River Delta	*DO*	0.01 (0.09)	Binomial distribution probability 0.025
Probability of temp. event Williamson River Delta	*Temp*	0 (0)	Binomial distribution probability 0.00005
Mean UKL elevation February-June (m)	*UKL.FEB.JUN*	4142.11 (0.60)	Gamma distribution
Proportion of spawning season lake elevation below threshold	*PROPS*	0.26 (0.22)	$-0.43 \times UKL.FEB.JUN + 1761.35$
Peak spring UKL elevation (m)	*PEAK*	4142.76 (0.52)	$0.87 \times UKL.FEB.JUN + 549.93$
Mean UKL elevation May-August	*UKL.MAY.AUG*	4141.89 (0.33)	$0.55 \times UKL.FEB.JUN + 1870.89$
3+ consecutive low DO day events at 20% of gauges	*lowDO20*	3.7 (4.1)	Poisson-Gamma distribution

Table 9. (cont.)

Mean Pelican Bay lake elevation July-October (m)	*PEL.JUL.OCT*	4139.84 (0.23)	$0.71 \times UKL.MAY.AUG + 1198.26$
Mean Link River flow August-September (cfs)	*LINK*	857 (36)	$110 \times UKL.MAY.AUG + 453727$
Mean Fathead Minnow abundance (CPUE)	*FHM*	162 (148)	Poisson-Gamma distribution
Mean Pelican and Cormorant abundance in UKL nesting sites	*AVIAN*	1393 (1040)	*PROPS*<0.2, uniform distr. 0-1,000 *PROPS*>0.2&<0.4, uniform distr. 1,000-2,000 *PROPS*>0.4&<0.6, uniform distr. 2,000-3,000 *PROPS*>0.6&<0.8, uniform distr. 3,000-4,000 *PROPS*>0.8, uniform distr. 4,000-5,000

Table 10. Model input values corresponding to system states used in evaluating state dependent policies. System states correspond to minimum, average, and maximum values based on USGS river and lake gages. Predator abundances based on published reports.

Description	**Environmental variable**	**States**		
		low (minimum)	**medium (average)**	**high (maximum)**
Williamson River spring streamflow (cfs)	*WR.MAR.AUG*	637.6	1053.3	1941.6
Number of LC_{50} pH events	*pH*	0	0.15	3
Number of LC_{50} DO events	*DO*	0	0.01	2
Number of LC_{50} temperature events	*Temp*	0	0	0
Spawning habitat availability (m)	*UKL.FEB.JUN*	4140.5	4142.1	4142.8
Upper Klamath Lake peak spring elevation (m)	*PEAK*	4141.2	4142.8	4143.3
Nearshore habitat availability (m)	*UKL.MAY.AUG*	4140.9	4141.9	4142.7
Frequency of low DO at 20% sites	*lowDO20*	0	3.7	15
Water quality refuge habitat availability (m)	*PEL.JUL.OCT*	4139.0	4139.8	4140.7
Link River Dam outlet streamflow (cfs)	*LINK*	524.0	857.8	1031.3
Fathead minnow and parasite abundance (CPUE)	*FHM*	4	162	475
Avian abundance	*AVIAN*	0	1393	4473

Table 11. Alternative models representing hypotheses about Klamath sucker ecosystem dynamics.

Alternative Model Hypotheses	**Model Weights**
Composite Model: all models equal weight	$adult = 0.25\times WQM_a + 0.25\times PM_a + 0.25\times HM_a + 0.25\times EM_a$ $juvenile = 0.25\times WQM_j + 0.25\times PM_j + 0.25\times HM_j + 0.25\times EM_j$
Water Quality Model (*WQM*): poor water quality is main factor limiting recovery	$adult = 0.625\times WQM_a + 0.125\times PM_a + 0.125\times HM_a + 0.125\times EM_a$ $juvenile = 0.625\times WQM_j + 0.125\times PM_j + 0.125\times HM_j + 0.125\times EM_j$
Water Quality Model, juveniles (WQM_j): poor water quality is main factor limiting juvenile recovery	$adult = 0.25\times WQM_a + 0.25\times PM_a + 0.25\times HM_a + 0.25\times EM_a$ $juvenile = 0.625\times WQM_j + 0.125\times PM_j + 0.125\times HM_j + 0.125\times EM_j$
Water Quality Model, adults (WQM_a): poor water quality is main factor limiting adult recovery	$adult = 0.625\times WQM_a + 0.125\times PM_a + 0.125\times HM_a + 0.125\times EM_a$ $juvenile = 0.25\times WQM_j + 0.25\times PM_j + 0.25\times HM_j + 0.25\times EM_j$
Predation Model (*PM*): predation is main factor limiting recovery	$adult = 0.125\times WQM_a + 0.625\times PM_a + 0.125\times HM_a + 0.125\times EM_a$ $juvenile = 0.125\times WQM_j + 0.625\times PM_j + 0.125\times HM_j + 0.125\times EM_j$
Predation Model, juveniles (PM_j) juvenile predation is main factor limiting recovery	$adult = 0.25\times WQM_a + 0.25\times PM_a + 0.25\times HM_a + 0.25\times EM_a$ $juvenile = 0.125\times WQM_j + 0.625\times PM_j + 0.125\times HM_j + 0.125\times EM_j$
Predation Model, adults (PM_a): adult predation is main factor limiting recovery	$adult = 0.125\times WQM_a + 0.625\times PM_a + 0.125\times HM_a + 0.125\times EM_a$ $juvenile = 0.25\times WQM_j + 0.25\times PM_j + 0.25\times HM_j + 0.25\times EM_j$
Habitat Model (*HM*): habitat is main factor limiting recovery	$adult = 0.125\times WQM_a + 0.125\times PM_a + 0.625\times HM_a + 0.125\times EM_a$ $juvenile = 0.125\times WQM_j + 0.125\times PM_j + 0.625\times HM_j + 0.125\times EM_j$
Habitat Model, juveniles (HM_j): juvenile habitat is main factor limiting recovery	$adult = 0.25\times WQM_a + 0.25\times PM_a + 0.25\times HM_a + 0.25\times EM_a$ $juvenile = 0.125\times WQM_j + 0.125\times PM_j + 0.625\times HM_j + 0.125\times EM_j$
Habitat Model, adults (HM_a): adult habitat is main factor limiting recovery	$adult = 0.125\times WQM_a + 0.125\times PM_a + 0.625\times HM_a + 0.125\times EM_a$ $juvenile = 0.25\times WQM_j + 0.25\times PM_j + 0.25\times HM_j + 0.25\times EM_j$
Entrainment Model (*EM*): entrainment is main factor limited recovery	$adult = 0.125\times WQM_a + 0.125\times PM_a + 0.125\times HM_a + 0.625\times EM_a$ $juvenile = 0.125\times WQM_j + 0.125\times PM_j + 0.125\times HM_j + 0.625\times EM_j$
Entrainment Model, juveniles (EM_j): juvenile entrainment is main factor limited recovery	$adult = 0.25\times WQM_a + 0.25\times PM_a + 0.25\times HM_a + 0.25\times EM_a$ $juvenile = 0.125\times WQM_j + 0.125\times PM_j + 0.125\times HM_j + 0.625\times EM_j$
Entrainment Model, adults (EM_a): adult entrainment is main factor limited recovery	$adult = 0.125\times WQM_a + 0.125\times PM_a + 0.125\times HM_a + 0.625\times EM_a$ $juvenile = 0.25\times WQM_j + 0.25\times PM_j + 0.25\times HM_j + 0.25\times EM_j$

Table 12. Utility and mean and standard deviation (in parenthesis) of estimated end adult abundance of Klamath suckers for each decision alternative ordered by decreasing utility with the optimal decision at the top. Utility scores are calculated for each decision alternative using proportional scoring of the model simulation objectives 1) management costs and 2) end adult sucker abundances, combined using a weighted sum ranging from 0 to 1 with the highest utility being the optimal decision.

Decision alternatives	**Utility**	**river-spawning Lost River suckers**	**lake-spawning Lost River suckers**	**Shortnose suckers**	**Cost**
Initial Adult Abundance	-	90,000	10,000	15,000	-
1-year captive propagation	0.316	38,457 (5,112)	5,046 (633)	4,759 (320)	$62.8 M
Translocation and reduce entrainment	0.309	45,220 (6,502)	3,979 (528)	581 (80)	$11.5 M
Screen 20 water diversions	0.305	34,153 (5,000)	3,597 (551)	428 (59)	$420 K
No action	0.304	32,858 (4,778)	3,524 (538)	418 (57)	$0
Restore 4 800-acre parcels of habitat	0.303	80,399 (13,990)	5,968 (1,016)	759 (112)	$90 M
Filter algae (3 10-year projects)	0.303	37,491 (5,566)	3,784 (584)	455 (63)	$11.1 M
Build 4 400-acre treatment wetlands	0.299	37,422 (5,555)	3,780 (584)	455 (63)	$17 M
Avian hazing	0.287	37,979 (5,322)	4,050 (591)	480 (64)	$45.75 M
2-year captive propagation	0.275	37,694 (5,050)	4,844 (620)	4,004 (256)	$125.6 M
3-year captive propagation	0.248	38,059 (5,086)	4,915 (628)	5,027 (334)	$188.4 M
Alum treatment for entire Upper Klamath Lake	0.211	37,434 (5,455)	3,825 (585)	458 (63)	$180 M
Dredge entire Upper Klamath Lake	0.062	40,389 (5,923)	3,994 (614)	482 (66)	$460 M

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