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Do impassable dams and flow regulation constrain the distribution of green sturgeon in the Sacramento River, California?

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Summary

Conservation of the threatened green sturgeon *Acipenser medirostris* in the Sacramento River of California is impeded by lack of information on its historical distribution and an understanding of how impassable dams and altered hydrographs are influencing its distribution. The habitat preferences of green sturgeon are characterized in terms of river discharge, velocity, channel gradient, and air temperature associated with 2590 sightings of green sturgeon in the Klamath and Rogue rivers using the Mahalanobis distance D^2, a multivariate measure of distance from the mean habitat conditions associated with the sightings. D^2 was then calculated for reaches of the Sacramento and San Joaquin rivers and their tributaries under historic and current (2007) hydrographs to assess where and when habitat conditions in the Sacramento–San Joaquin basin are similar to those known to support green sturgeon. The model for current habitat conditions was validated with observations of acoustically-tagged green sturgeon at large in the basin in 2007. The model predicts that in the absence of impassable dams and altered hydrographs, green sturgeon would utilize the mainstem Sacramento and San Joaquin rivers, and several major tributaries including portions of the lower Feather River, American River, and Yuba River. While dams block access to about 9% of historically available habitat, it is likely that the blocked areas contained relatively high amounts of spawning habitat because of their upstream position in the river network. Flow regulation below the reservoirs has mixed effects on habitat suitability for green sturgeon, with many reaches showing increased suitability in winter and spring, but with some reaches showing decreased suitability in many months, particularly late spring through early autumn. Overall, it appears that the main effect of construction of large water-storage reservoirs in the Sacramento–San Joaquin river basin has been to curtail the distribution of green sturgeon within this basin.

Introduction

The Sacramento–San Joaquin river basin is currently the subject of several large-scale ecosystem restoration programs that aim to recover anadromous fish populations, including the North American green sturgeon *Acipenser medirostris*. The green sturgeon is known to spawn in only three rivers: the Rogue River in southern Oregon and the Klamath and Sacramento rivers in northern California. Like most sturgeons worldwide (Pikitch et al., 2005; Rosenthal and Pourkazemi, 2006), green sturgeon are of conservation concern. The species as a whole is covered by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Raymakers and Hoover, 2002) and is categorized as Near Threatened by the IUCN (St. Pierre and Campbell, 2006). The northern distinct population segment (NDPS) that spawns in the Rogue and Klamath rivers is considered a Species of Concern by the US National Marine Fisheries Service, and the southern distinct population segment (SDPS) of green sturgeon that spawns in the Sacramento River is listed as a threatened species under the US Endangered Species Act.

To be effective, restoration plans need to be based on a solid understanding of how the ecosystem functioned prior to anthropogenic alterations (Harwell et al., 1996); basic to this is an understanding of the distribution of organisms within the ecosystem and the factors that control their distribution. The historical distribution of green sturgeon in the Sacramento-San Joaquin is poorly documented, but Adams et al. (2007) summarizes information that suggests that they may have been distributed above the locations of present-day dams on the Sacramento and Feather rivers. Information on the historical or current distribution of green sturgeon in the San Joaquin River and its tributaries is entirely lacking. It is known that mature green sturgeon enter rivers in late winter to late spring and migrate inland to spawning sites (Erickson and Webb, 2007; Heublein et al., 2009). After spawning, *A. medirostris* may leave the river or, more commonly, spend the summer and autumn in deep pools before departing the river with the onset of winter rains (Erikson et al., 2002; Heublein et al., 2009).

For Sacramento River green sturgeon, dams are hypothesized to be a major factor in their decline (Adams et al., 2007). The Sacramento-San Joaquin river basin has been heavily developed for water storage and conveyance, and all but the smallest tributaries have impassable dams at fairly low elevations. These dams may have reduced the amount and altered the spatial distribution of spawning, rearing and holding habitat available and by restriction to the mainstem Sacramento River, making *A. medirostris* more vulnerable to environmental catastrophes. The main purpose of most of these dams is to store water collected during the winter rainy and spring snow-melt seasons for use in the dry summer and autumn. Dams therefore alter stream hydrographs in ways that may alter the suitability of downstream reaches for various green sturgeon life stages. At present, flow requirements of salmonids factor into the determination of flow regimes, but the requirements of green sturgeon are not considered.

Habitat modeling offers one way to better understand the distribution of animals. The basic idea is to link easily-measured habitat attributes to observations of presence (and absence, under some approaches) with some sort of statistical model, and then use the model to predict the distribution of the animal from maps of the habitat attributes. Some approaches, such as logistic regression, require both presence and absence data, while others, such as bioclimatic envelopes and Mahalanobis distance D^2, require only presence data (Manly et al., 2002). Johnson and Gillingham (2005) found that methods based on presence-absence and presence-only data had similar predictive accuracy, outperforming a method based on expert opinion, and produced broadly similar maps of habitat suitability. Of the presence-only based methods, Farber and Kadmon (2003) argued that Mahalanobis D^2 was more accurate than envelope-based methods because Mahalanobis D^2 can capture the typically oblique rather than rectilinear nature of species niches and use all of the sightings data, rather than only the most extreme observations. Also, for rare species, presence-only methods avoid the problem of interpreting absences – for rare species, suitable habitat patches may be unoccupied when surveyed.

In the Mahalanobis D^2 approach, habitat suitability is quantified as a distance from a multivariate mean that is estimated from habitat attributes associated with sightings of the organism under study (Clark et al., 1993). An implicit assumption of this approach is that the mean of the habitat attributes is equivalent to optimal habitat conditions, and that habitats with a smaller distance from the mean are more suitable than habitats with a larger distance. Any piece of habitat can be characterized by its distance from the mean, and if it is within some specified distance of the mean habitat conditions associated with presence of the organism (e.g. within the range of distances associated with the sightings data), it can be deemed suitable habitat. The potential distribution of an organism can then be evaluated by mapping the locations of suitable habitat elements. The Mahalanobis D^2 approach has been used in many studies of terrestrial organisms (e.g. Clark et al., 1993; Knick and Dyer, 1997; Corsi et al., 1998), but to date, it has rarely been used for aquatic environments [for example, Degraer et al. (2008) studied the distribution of marine benthic communities], and to our knowledge, never in a fluvial setting.

In this paper, we use the Mahalanobis distance approach to assess whether the distribution of green sturgeon in the Sacramento–San Joaquin river basin is constrained by impassable dams, and whether water management improves or impairs the distribution of habitat below these impassable dams. We utilize sightings and habitat data from 2590 observations of green sturgeon in the Rogue and Klamath rivers, and characterize habitat by discharge, velocity, channel gradient, and air temperature (a proxy for water temperature). Hydrological data for unregulated (historical) and regulated (present-day) flows are used. The resulting models predict the spatial and temporal distribution of green sturgeon in the Sacramento–San Joaquin basin prior to and post hydrologic development, thus allowing us to assess how impassable dams and altered hydrographs may be constraining distribution. We validate the model predictions by comparing the cumulative distribution function (cdf) of D^2 values from relocations of acoustically-tagged green sturgeon in the Sacramento River in 2007 to the cdf of D^2 from the sightings from the Klamath and Rogue rivers.

Materials and methods

Study area

Sightings data were obtained from the Klamath River in northern California and from the Rogue River in southern Oregon. Habitat models based on these sightings data were applied to the Sacramento and San Joaquin rivers and their tributaries in California's Central Valley. Fig. 1 shows a map of the study area.

Sightings data

We used 2590 geo-referenced 'sighting' events (any method of detecting the presence of a green sturgeon) to characterize the habitat preferences of the adults. These sighting events generally occurred between March and December of 2000–2005 in the Rogue, Klamath and Trinity rivers. Sighting events were not selected to reflect a particular behavior (spawning, holding, migration, etc.), as this was generally not known, but were used to define the range of environmental conditions known to support green sturgeon throughout a significant portion of their freshwater range.

Sightings data come from gillnet captures, angling and telemetry relocations. Telemetry data were subsampled to produce one sighting per fish per day. The Oregon Department of Fish and Wildlife and the Wildlife Conservation Society provided capture locations (gillnet sets and angling) during the years 2000–2004 ($n = 165$) for the Rogue River. The second group of Rogue River sightings was from capture locations and relocations via radio and acoustic telemetry studies conducted in 2000–2004, $n = 1209$ (Erikson et al., 2002; Erickson and Webb, 2007). Sightings in the Klamath and Trinity rivers were provided by the Yurok Tribal Fisheries Program and consisted of capture locations (gillnet sets) and relocations via radio and hydroacoustic telemetry studies in 2002–2005, $n = 1216$.

Habitat characteristics

Green sturgeon habitat was characterized by river discharge, velocity, gradient and air temperature, a proxy for water temperature. Hydrological and geomorphic variables were obtained from the enhanced National Hydrologic Dataset, NHD Plus (Region 18, version 1-1; McKay et al., 2008). NHDPlus is a 1 : 100 k hydrography GIS dataset containing mean annual flow volume and mean annual velocity estimates with digital-elevation-model-derived contributing area and gradient data for each stream segment. Individual stream segments generally ranged from 1-5 km in length and were the unit of analysis in this study.

To estimate monthly flow and velocity in the absence of storage, diversions and transfers, we used data describing monthly unimpaired flow volumes for 26 mainstem locations in our study area during water years 1920 through 1992 (California Department of Water Resources (CDWR) (1994). For each of the 26 watersheds, the monthly flow rates of stream segments upstream and downstream of the mainstem data point were calculated applying the following equation (Gordon et al., 2004):

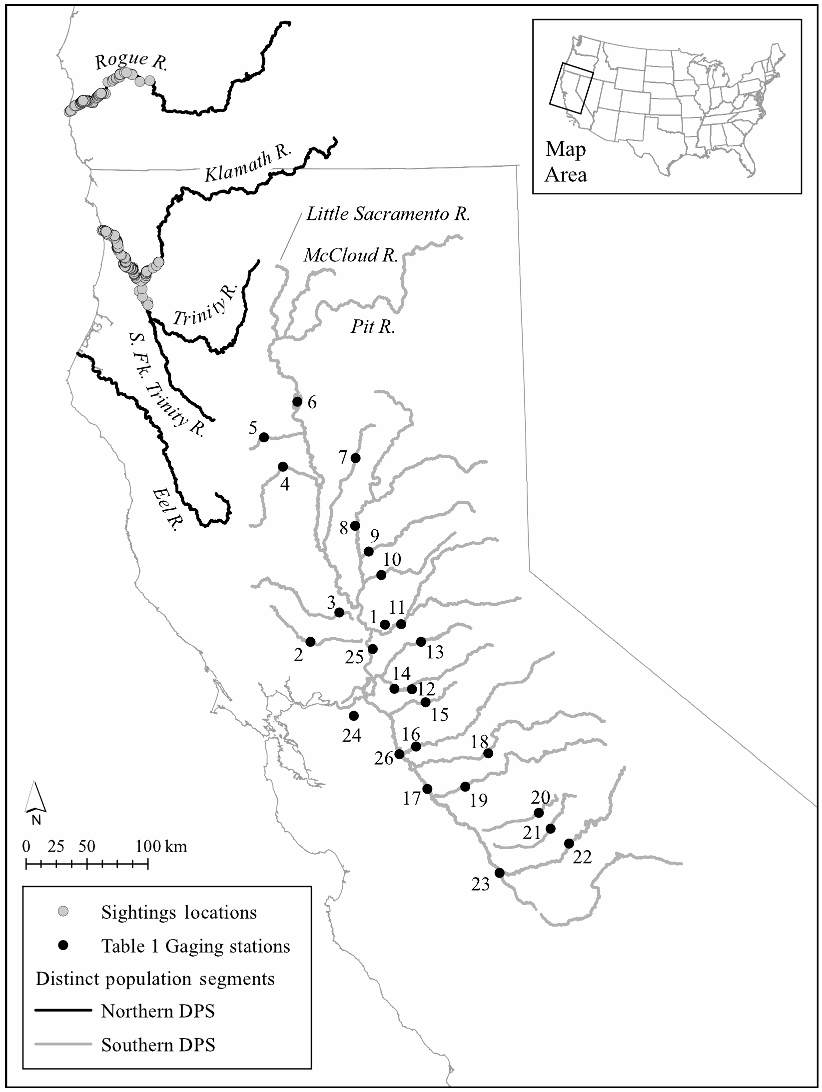

Fig. 1. Map of study area displaying sightings data, locations of gauging stations described in Table 1, labeled by DWR Region and the two Distinct Population Segments defined by the US National Marine Fisheries Service. Disconnected stream segments are an artifact of the NHD Plus dataset and did not affect the analysis

$$Q_{i,m} = \frac{Q_{s,m}}{M_s} M_i, \tag{1}$$

where $Q_{i,m}$ is the calculated monthly mean flow rate of stream segment i during month m. M_s is the mean annual flow rate of the mainstem stream segment s, from the NHDPlus dataset. $Q_{s,m}$ is the historical monthly mean flow rate of the mainstem stream segment s, during month m, from the CDWR dataset. M_i is the mean annual flow rate of tributary stream unit i, from the NHDPlus dataset. Monthly mean velocities were calculated using equations relating stream segment contributing area, stream segment gradient, mean annual discharge and the modeled monthly mean discharge rates from above (Jobson, 1996; McKay et al., 2008).

Historical monthly mean air temperatures were calculated as the mean of 1.25 arc-minute average monthly maximum and average monthly minimum PRISM (Parameter-elevation Regressions on Independent Slopes Model) air temperature grids (Daly et al., 2002). Stream segment air temperatures were assigned through the spatial intersection of the GIS hydrology and the monthly mean air temperature grids.

Mahalanobis distance

The Mahalanobis distance (D^2) is a unitless measure of distance between the multivariate mean of a sample dataset and any data point having measured values for the same variables (Mahalanobis, 1936). In this study, we estimated the gradient, discharge rate, water velocity and air temperature for 2590 sighting events to describe the environmental conditions known to support green sturgeon in terms of a mean vector m and a covariance matrix C. We then estimated the distance from m of each available habitat unit (x) in the Central Valley, CA, using the following equation:

$$D^2 = (x - m)^{\mathrm{T}} C^{-1} (x - m) \tag{2}$$

When all variables are normally distributed, D^2 is approximately distributed as a chi-square random variable, and D^2 values can be converted into probabilities. Because stream velocity, discharge and gradient remained distinctly non-normal after log transformation, we estimated the cdf of the sightings data empirically to scale the D^2 values for the sightings data. The cdf of the Rogue and Klamath sightings D^2 values were used to identify the ranges of D^2 for which a stream segment could be considered similar. Results for each month were mapped in a GIS and intersected with the most downstream impassable dams to identify currently accessible habitat (Goslin, 2005).

Validation

To test the validity of our model, we compared the distribution of predicted green sturgeon habitat during 2007 to the observed distribution of acoustically-tagged green sturgeon within our study area as shown by hydrophone detections during that year. Thirty one tagged green sturgeon were present in the Sacramento–San Joaquin River in 2007, and detected on an array of 123 hydrophones extending throughout the accessible portion of the Sacramento River and the Sacramento–San Joaquin delta (see Heublein et al. (2009) and Lindley et al. (2008) for details on the tagging and telemetry study).

Flow conditions for 2007 were estimated from flow data from the United States Geologic Survey (USGS) and California Data Exchange Center (CDEC) gauging stations (Table 1). Flow data were obtained from stations located as close as possible to the original mainstem locations used to construct the historical model. Flow quantities and velocities for each stream segment were calculated using the same methods as above.

Table 1
Gaging stations used to develop monthly mean impaired flows

DWR Region	Watershed	Station ID	Data Type
1	Sacramento Valley Floor	11447360	USGS historical impaired average
2	Putah Creek	11454000	2007 USGS measured
3	Cache Creek	11452500	2007 USGS measured
4	Stony Creek	BLB	2007 CDEC measured
5	Sacramento West Side	11379500	2007 USGS measured
6	Sacramento River Near Red Bluff	11377100	2007 USGS measured
7	Sacramento East Side	11389775	2007 USGS measured
8	Feather River	GRL	2007 CDEC measured
9	Yuba River	11421000	2007 USGS measured
10	Bear River	11424000	2007 USGS measured
11	American River	11446500	2007 USGS measured
12	San Joaquin East Side	11312000	USGS historical impaired average
13	Cosumnes River	11335000	2007 USGS measured
14	Mokelumne River	11325500	USGS historical impaired average
15	Calaveras	MRS	2007 CDEC measured
16	Stanislaus River	11303000	2007 USGS measured
17	San Joaquin Valley Floor	11274538	2007 USGS measured
18	Tuolumne River	11289650	2007 USGS measured
19	Merced River	CRS	2007 CDEC measured
20	Chowchilla River	11259000	USGS historical impaired average
21	Fresno River	11258000	USGS historical impaired average
22	San Joaquin River	11251000	2007 USGS measured
23	Tulare Basin Outflow	MEN	2007 CDEC measured
24	San Joaquin Valley West Streams	11337600	2007 USGS measured
25	Sacramento Outflow	11447650	2007 USGS measured
26	San Joaquin Outflow	11303500	2007 USGS measured

Monthly air temperature grids for 2007 were calculated as the mean of average monthly maximum and average monthly minimum PRISM air temperature grids produced for the year 2007.

Results

Sightings of green sturgeon in the Klamath and Rogue rivers showed clear evidence for habitat selection (Fig. 2). Sightings were associated with higher discharges, higher velocities, and lower gradients, consistent with a preference for mainstem river reaches and an avoidance of smaller tributaries. Sightings were not associated with the coldest temperatures (less than 5°C).

Figure 3 shows the cumulative distribution of D^2 for the sightings data collected on the Rogue and Klamath rivers. The median D^2 was 3.65, the 95th percentile was 9.48, and the maximum was 22.46.

The model using historical flows predicts that green sturgeon habitat was widely distributed in the Sacramento River, San Joaquin River, and some of the larger tributaries to the Sacramento River, including the Feather River, the American River and lower reaches of the Pit, McCloud and Little Sacramento rivers (Fig. 4). Of the 100,352 kms of riverine habitat available within the Sacramento-San Joaquin basin, as identified in the NHDPlus dataset, approx. 957 $\pm$ 154 km (mean $\pm$ SD) have D^2 values less than the maximum D^2 of the green sturgeon sightings. Keswick Dam blocks access to approx. 39 $\pm$ 14 km of habitat in the Pit, McCloud and Little Sacramento, Nimbus Dam blocks access to approx. 22 $\pm$ 8 km of habitat in the American River, Oroville Dam blocks access to approx. 16 $\pm$ 4 km of habitat in the Feather River, Friant Dam blocks approx. 12 $\pm$ 4 km of habitat in the San Joaquin River and Daguerre Dam blocks approx. 4 $\pm$ 2 km of habitat in the Yuba River.

Results of the model using hydrologic conditions from 2007 show that alteration of flow regimes has complex effects on the suitability of stream habitats for green sturgeon. In the winter and spring (January–June and November–December), most habitat units in the Sacramento, Feather and American rivers under impaired flows become more similar to the mean vector of the sightings, while the remainder become less similar (Fig. 5). In July through October, the cdf of D^2 values is quite similar for both the unimpaired and impaired hydrographs. Even during months when most stream reaches have small D^2 under impaired hydrographs, some have much larger D^2 values. These stream reaches are mostly in the San Joaquin River, in which flows are greatly reduced (to near zero in some reaches) for much of the river channel between the confluence of the Merced River and Friant Dam.

The predicted distribution of green sturgeon habitat under current flow regimes is consistent with the observed distribution of acoustically-tagged green sturgeon. On average, D^2 of habitat units used by green sturgeon in the Sacramento were farther from the mean vector than those used by green sturgeon in the Klamath and Rogue rivers, but 98.8% of the Sacramento sightings were within the range of D^2 values observed for the Klamath and Rogue rivers (Fig. 3).

Discussion

Consistency of our results

The predicted habitat distributions under current and historical conditions are consistent with relocation data for acous-

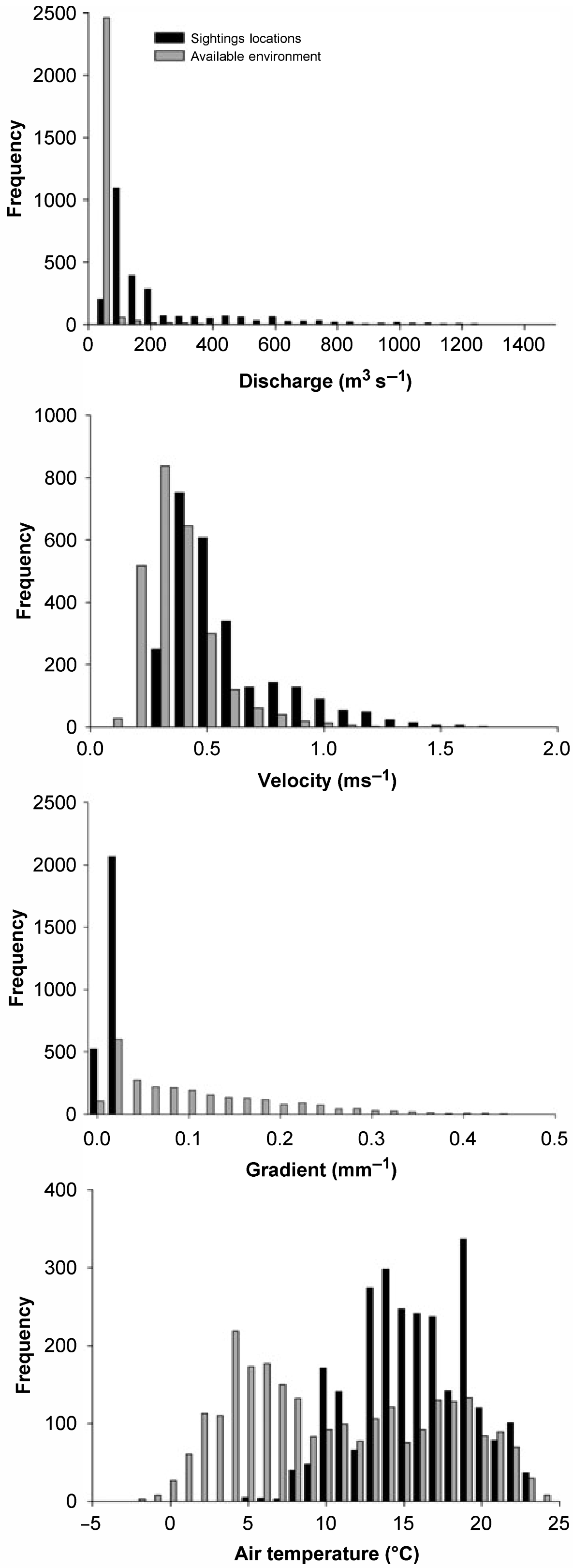

Fig. 2. Frequency distributions of available (light gray bars) and utilized (dark gray bars) habitat values in Klamath–Trinity and Rogue river basins. Habitat selection indicated by differences in frequency distributions

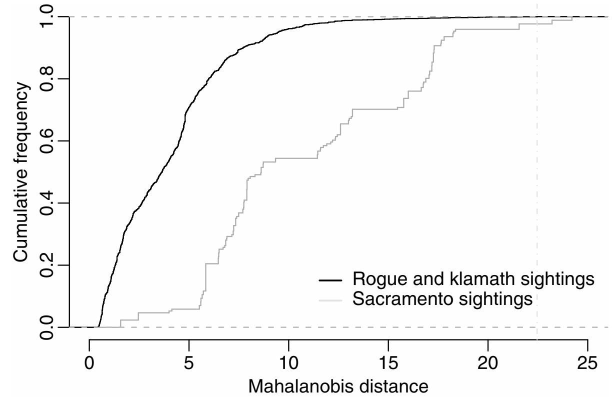

Fig. 3. Cumulative distribution of D^2 for sightings data collected in Klamath–Trinity and Rogue rivers (black line) and sightings data collected in 2007, Sacramento River (gray line). In both cases, D^2 measures multivariate distance from mean of sightings data from Klamath–Trinity and Rogue rivers. Vertical dashed line = D^2 value of 22.46

tically-tagged green sturgeon, with previous statements in the literature about its distribution in the Sacramento–San Joaquin basin, and with recent anecdotal observations. For example, Moyle (2002) stated that green sturgeon spawn above and below the Red Bluff Diversion Dam on the mainstem Sacramento River and in the lower Feather River. In recent years, adults have been observed in the lower Feather River and Yuba River near Daguerre Point dam (A. Seesholtz, California Department of Water Resources and G. Reedy, South Yuba River Citizens League, pers. comm.). Historically, at least one very large adult green sturgeon was caught by an angler fishing in Lake Shasta in 1977 (presumably trapped above the dam for more than 30 years), as evidenced by a photograph that is displayed in the Shasta Dam visitors center (mistakenly labeled as a white sturgeon; pers. comm., R. Chase, U.S. Bureau of Reclamation). The identification of large stretches of the San Joaquin River as suitable habitat contrasts with the absence of any records of green sturgeon in this river (Adams et al., 2007), although historical sampling may have been inadequate to document use of this river by green sturgeon.

Effect of impassable dams

Adams et al. (2007) hypothesized that significant amounts of historically-utilized spawning habitat may be blocked by Shasta Dam and Oroville Dam on the Feather River, substantially reducing the productive capacity and greatly simplifying the spatial structure of the Sacramento River *A. medirostris* population. Our model results support this hypothesis. It is generally believed that spawning areas are at the upstream-most reach of the green sturgeon's spawning migration, and that they may move some distance back downstream after spawning and before migrating back to sea (Benson et al., 2007; Erickson and Webb, 2007). The Shasta Dam and reservoir blocks access to reaches of the Pit, McCloud and Little Shasta rivers that contained apparently suitable habitat for green sturgeon. Similarly, Oroville Dam and reservoir block some areas of suitable habitat on the middle fork of the Feather River, and Daguerre Point Dam blocks some habitat on the Yuba River. These same dams have been implicated in the extirpation of many populations of winter- and spring-run chinook salmon (Yoshiyama et al., 1998; Lindley et al., 2004).

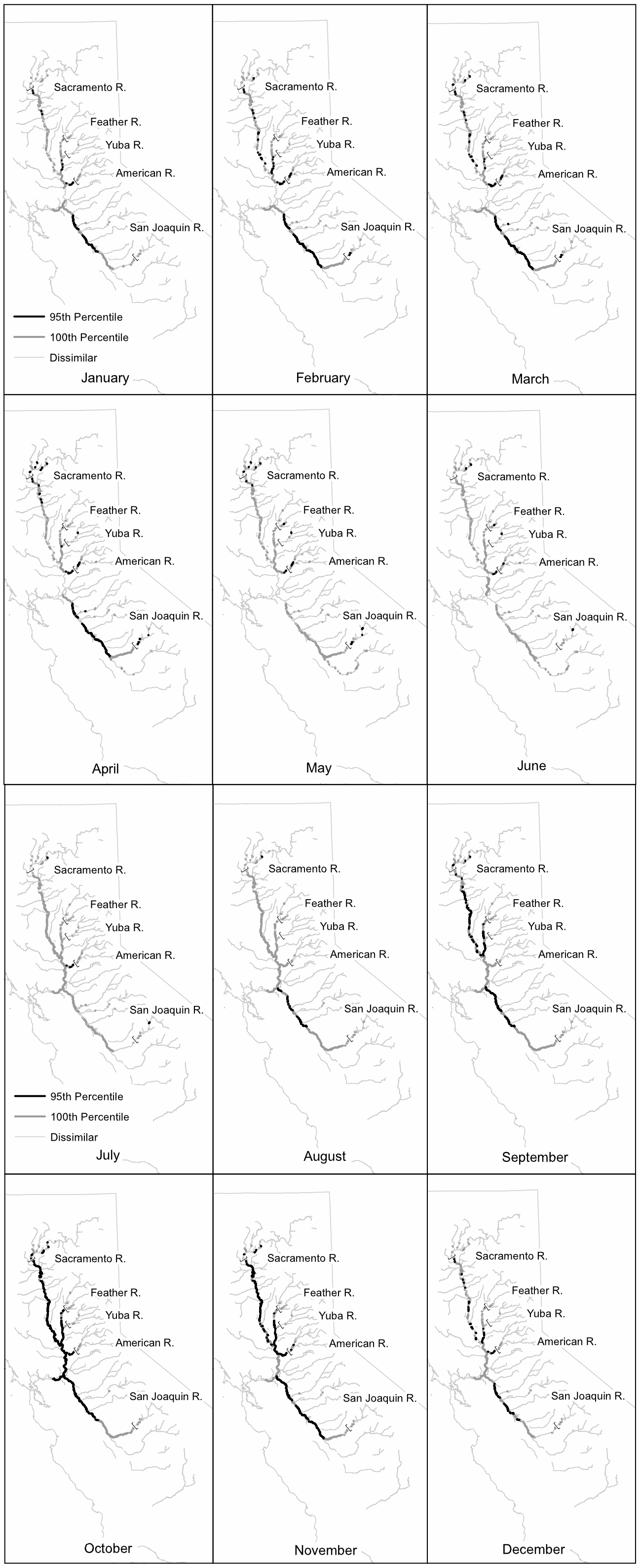

Fig. 4. Predicted location of green sturgeon *A. medirostris* habitat by month under average historical flow regimes and without man-made migration barriers. Heavy black lines = habitat is within 95th percentile of observed D^2 associated with sightings in Klamath and Rogue rivers (similar); wide gray lines = habitat less than maximum observed D^2 associated with sightings in Klamath and Rogue rivers but in the final 5th percentile (similar); narrow gray lines = stream reaches with D^2 greater than that observed in association with sightings (dissimilar). Bracket symbols = impassable dams

Our model also predicts the existence of suitable habitat on the American River and the San Joaquin River. We are not aware of any historical accounts of green sturgeon in either of these rivers. At present, much of the predicted habitat on the American River is above Nimbus Dam, and long sections of the San Joaquin River are de-watered by Friant Dam, thus it is

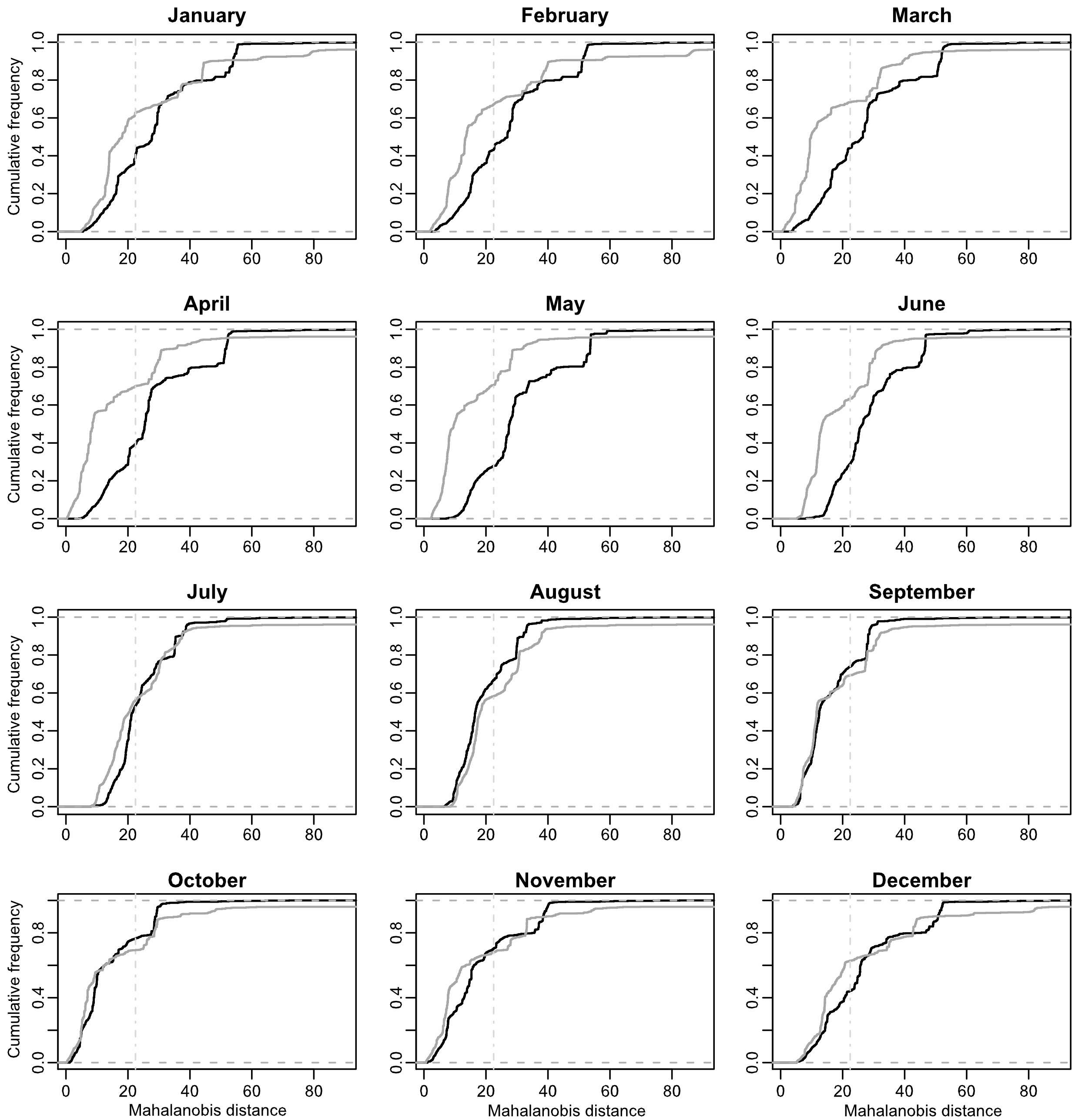

Fig. 5. Influence of altered hydrographs on suitability of green sturgeon *A. medirostris* habitat below impassable dams, Sacramento–San Joaquin basin. Black lines = cumulative distribution of D^2 under the historical, unimpaired hydrographs; gray lines = cumulative distribution of D^2 for impaired hydrology observed in 2007. When the gray line is to the left of the black line, current (2007) conditions are more similar to the mean of sightings data collected in Klamath–Trinity and Rogue rivers

perhaps not surprising that there are no contemporary accounts of the fish in these rivers. If these rivers did once support green sturgeon spawning, then their current restriction to the mainstem Sacramento River and perhaps lower Feather River must be viewed as a significant risk factor for this population.

Effect of altered flow regimes

Taken at face value, our results suggest that flow regulation improves habitat suitability for adult green sturgeon in most river reaches below impassable dams, except in August and September. This occurs because in some reaches below dams, winter and spring discharge is lower than it would be in the absence of regulation, and therefore closer to the mean of the flows associated with the sightings data. There are, however, several reasons to be cautious in accepting the conclusion that flow regulation may be benefiting *A. medirostris* in their remaining habitats below dams. Reservoirs and dams trap sediments and reduce peak flows, altering channel morphology and the distribution of sediments, with potentially profound effects on spawning, rearing and holding habitats for green sturgeon. Indeed, flow regulation has been implicated in the decline of many sturgeon populations in North America (e.g., Beamesderfer and Farr, 1997; Kynard, 1997; Duke et al., 1999). Another issue is the effect of reservoirs on stream temperature. Air temperature is insensitive to changes in river temperature caused by reservoir operations. Generally, reservoir releases make downstream reaches cooler in the summer and warmer in the winter relative to what would be predicted from air temperature. This error, if corrected, would likely lead to lower D^2 estimates for many regulated reaches in summer months, when air temperatures are relatively high.

Considerations for future work

While our results appear reasonable and consistent with available information, there are some cautions to bear in mind and improvements are possible. The major weakness of the D^2 approach is that the D^2 statistic describes distance from a unimodal mean, and increasing D^2 is interpreted as declining habitat quality. It is certainly conceivable that suitability in relation to some habitat metrics, such as flow, may be an asymptotic function, where D^2 increases with an increase in the metric, but actual suitability might remain constant or even increase at levels greater than the mean (Knick and Rotenberry, 1998). It would therefore be inappropriate to use our model to design flow regimes for green sturgeon without more work to verify the relationship between flow and habitat suitability.

By necessity, our model used just a few readily-available habitat measures to characterize green sturgeon habitat, which could possibly be better described by more detailed habitat measures, such as depth, riverbed rugosity and sediment size, water temperature, the presence of hydraulics etc, as well as by behavioral state (e.g. spawning versus post-spawning residence), although Creque and Rutherford (2005) found that habitat measures derived from GIS were better predictors of trout density than site-level field measurements. Such measures would require detailed observations of both habitat and green sturgeon behavior.

Finally, our model dealt only with mature green sturgeon. Other life stages, especially larvae and juveniles, may use very different habitats, and these habitats may have been altered more by the effects of dams and flow regulation than the spawning, holding and migratory corridor habitats that our model addresses. Unfortunately, very little information is available on the habitat requirements and utilization patterns for these early life stages. While expensive and logistically challenging, much work is needed to further advance our understanding of the habitat requirements and potential distribution of green sturgeon.

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