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ARTICLE

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Abstract
We analyzed remote detection data from PIT-tagged Lost River Suckers *Deltistes luxatus* at four shoreline spawning areas in Upper Klamath Lake, Oregon, to determine whether spawning of this endangered species was affected by low water levels. Our investigation was motivated by the observation that the surface elevation of the lake during the 2010 spawning season was the lowest in 38 years. Irrigation withdrawals in 2009 that were not replenished by subsequent winter–spring inflows caused a reduction in available shoreline spawning habitat in 2010. We compared metrics of skipped spawning, movement among spawning areas, and spawning duration across 8 years (2006–2013) that had contrasting spring water levels. Some aspects of sucker spawning were similar in all years, including few individuals straying from the shoreline areas to spawning locations in lake tributaries and consistent effects of increasing water temperatures on the accumulation of fish at the spawning areas. During the extreme low water year of 2010, 14% fewer female and 8% fewer male suckers joined the shoreline spawning aggregation than in the other years. Both males and females visited fewer spawning areas within Upper Klamath Lake in 2010 than in other years, and the median duration at spawning areas in 2010 was at least 36% shorter for females and 20% shorter for males relative to other years. Given the imperiled status of the species and the declining abundance of the population in Upper Klamath Lake, any reduction in spawning success and egg production could negatively impact recovery efforts. Our results indicate that lake surface elevations above 1,262.3–1,262.5 m would be unlikely to limit the number of spawning fish and overall egg production.

Management of reservoirs in the arid western USA balances human water use with the ecological needs of sensitive aquatic species. High demand and low supply of water in this region necessitate tight water budgets. In fact, in many parts of the western USA available water supply is fully appropriated for human use (Anderson and Woosley 2005). Climate change adds to the complexity of water allocation in arid climates by reducing snow pack, causing earlier runoff, and reducing water storage capabilities (Kooperman et al. 2009). Concerns over water allocation are of particular importance for fishes in arid portions of the western USA where endemism is common and many populations of freshwater fishes are declining (Chapin et al. 2001). As such, there is a critical need in this region to understand the minimum amount of water required to sustain sensitive species and essential ecological functions (Anderson and Woosley 2005). Reduced lake or

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reservoir surface elevations can reduce spawning habitat, rearing habitat, and water quality.

Upper Klamath Lake, Oregon, is managed to provide irrigation water to agricultural lands in the Upper Klamath Basin as part of the federally operated Klamath Project, with consideration for species listed under the U.S. Endangered Species Act (USFWS 1988). The average depth of the lake is 2.7 m and the lake surface elevation varies within a range of about 1.5 m. The gradual slope of the littoral zone near the shoreline causes the surface area to be very sensitive to changes in lake surface elevation (NRC 2004). Irrigation withdrawals combined with evaporation and downstream flow can lead to depleted water supplies within the irrigation season and in the following year if subsequent winter and spring inputs are below average. For example, water used in the summer of 2000 was not replenished by winter and spring precipitation causing lower-than-average lake surface elevation during 2001. As a result, separate Biological Opinions issued by the U.S. Fish and Wildlife Service and the National Marine Fisheries Service recommended that the U.S. Bureau of Reclamation maintain minimum lake surface elevations for endangered Lost River Suckers *Deltistes luxatus* and Shortnose Suckers *Chasmistes brevirostris* and minimum downstream flows in the Klamath River for threatened Coho Salmon *Oncorhynchus kisutch* (USFWS 2008; NMFS 2010). To meet these obligations, the U.S. Bureau of Reclamation curtailed water deliveries to irrigators, resulting in substantial agricultural and economic losses. In a follow-up report, the National Research Council concluded that the sucker Biological Opinion contained insufficient evidence to support minimum lake surface elevation requirements (NRC 2004). Water withdrawals in 2009 were again greater than the recharge that occurred in the subsequent winter and spring, resulting in lake surface elevations in the spring of 2010 that were the lowest in the last 38 years. The 38-year average lake surface elevation for Upper Klamath Lake for dates between March 1 and June 1 is 1,262.6 m above mean sea level, whereas the average for the same time period in 2010 was 1,262.1 m (USGS 2014; Figure 1).

Lost River Suckers are an obligate lake-dwelling fish (family Catostomidae) endemic to the Upper Klamath Basin of southern Oregon and northern California (Scoppettone and Vinyard 1991). These fish, like other lake suckers in the western USA, are negatively affected by water diversions,

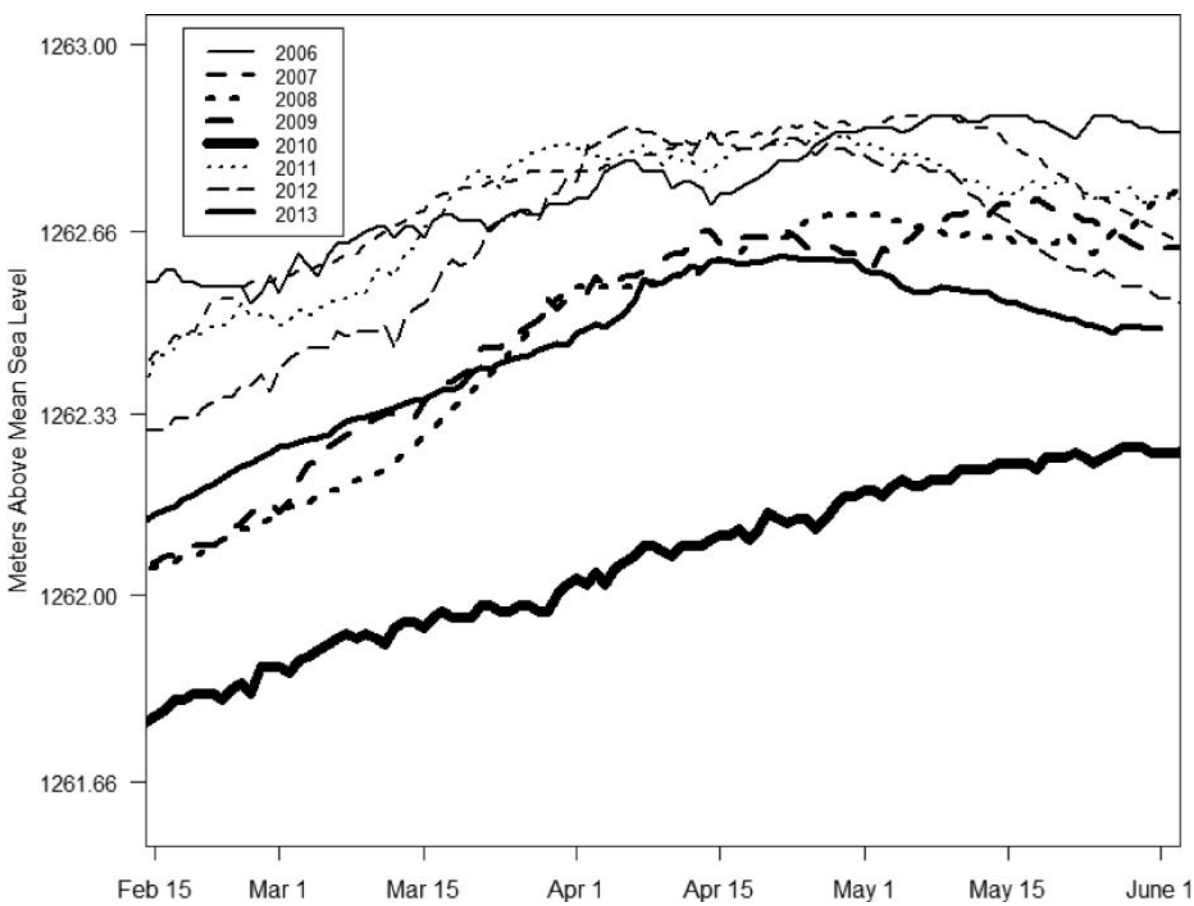

FIGURE 1. Upper Klamath Lake surface elevation at U.S. Geological Survey station 11507001 (shown in Figure 2). Elevations are in meters above mean sea level in the U.S. Bureau of Reclamation datum.

interactions with nonnative species, and habitat degradation (Belk et al. 2011; Rasmussen 2011). Lost River Suckers live up to 50 years and can grow to 800 mm FL and 3.5 kg (Moyle 2002; Terwilliger et al. 2010). These long-lived fish were once extremely abundant in the lakes and rivers of the upper basin, but declining abundance and decreasing range prompted their being listed as endangered by the U.S. Fish and Wildlife Service in 1988 (USFWS 1988). A number of distinct Lost River Sucker populations have been extirpated throughout their historical range (NRC 2004). Presently, the largest remaining sucker population resides in Upper Klamath Lake, Oregon (Hewitt et al. 2012). Most fish in the spawning aggregations are between 20 and 25 years old (Hewitt et al. 2012). This lack of diversity in age structure and a near absence of fish 1–7 years of age is strong evidence of ongoing recruitment failure in this population.

Most Lost River Suckers in Upper Klamath Lake make annual spawning migrations up the Williamson and Sprague rivers between February and May (Hewitt et al. 2012). A smaller distinct subpopulation spawns during the same time period in the vicinity of several groundwater upwelling areas along the eastern shoreline of the lake and includes at least 10,000 individuals (Janney et al. 2008; Hewitt et al. 2012; Figure 2). Due to strong fidelity to spawning sites located in either the lake or its tributaries (Janney et al. 2008), the Lost River Suckers that use these shoreline spawning areas are considered to be a distinct management unit for recovery planning purposes (USFWS 2012).

Lost River Suckers arrive at shoreline spawning areas each year when lake water temperature reaches approximately 6°C (Hewitt et al. 2012). As is typical of western lake suckers, a Lost River Sucker spawning event lasts less than 6 s in which a single female is commonly flanked by two males (although up to seven males have been observed). Gametes are released over gravel substrate where water depth is typically between about 0.2 and 0.6 m (Scoppettone et al. 1983; Sigler et al. 1985; Perkins et al. 2000b; Reiser et al. 2001). Males often remain at the spawning area between spawning events whereas females often retreat to deeper water offshore, returning to spawn every few minutes (Perkins et al. 2000b).

The relationships among lake surface elevation, shoreline spawning habitat availability, and Lost River Sucker spawning patterns are unclear. A better understanding of these relationships will help resource managers ensure that adequate lake surface elevations are maintained during months when suckers are spawning. We quantified the relation between declining lake surface elevation and the area of known spawning habitat rendered unusable at the four main lakeshore spawning areas. We also used detections of suckers with PIT tags by remote underwater antennas at shoreline spawning areas to compare 2010 spawning activity to seven other recent years. The goal of these comparisons was to determine whether spawning activity was negatively affected in 2010 due to low lake surface elevations.

STUDY AREA

Upper Klamath Lake was naturally impounded by a rock reef, but in 1921 the U.S. Bureau of Reclamation built the Link River Dam to control lake surface elevations. Prior to construction of the dam, water surface elevations varied between 1,261.9 m and 1,262.9 m, and annual fluctuations averaged roughly 0.6 m (NRC 2004). The channels cut into the natural reef to facilitate flows to the dam enabled water surface elevations to be lowered an additional 1.2 m. Recent water management practices generally produce water surface elevations in Upper Klamath Lake that are roughly 0.5 m higher in the spring and 0.5 m lower during summer and fall compared with predam elevations (USFWS 2008).

Spawning habitat along the eastern shoreline of Upper Klamath Lake consists of small, discrete areas where groundwater upwells from the base of Modoc Rim. Most known spawning occurs at four specific locations: Cinder Flat, Ouxy Spring, Silver Building Spring, and Sucker Spring. Bottom elevations in spawning areas range from about 1,261.5 m to 1,263.0 m (Reiser et al. 2001). These areas are characterized by water less than 0.75 m deep (Buettner and Scoppettone 1990), primarily gravel and cobble substrate, and to a varying extent, groundwater inflow. As with other species of western lake suckers, groundwater upwelling appears to be an important characteristic of Lost River Sucker spawning habitat (Sigler et al. 1985). Sucker Spring is the largest of the four spawning areas and has more groundwater inflow than Ouxy Spring or Silver Building Spring. Upwelling groundwater temperature at these areas ranges from 12°C to 16°C, which is within the range of spawning temperatures for other catostomids (Sigler et al. 1985; Hamel et al. 1997). Cinder Flat, the second largest spawning area, is an exception in that it has virtually undetectable groundwater influence but substantial spawning activity.

METHODS

We hypothesized that shoreline-spawning Lost River Suckers would skip spawning or reduce spawning activity when lake surface elevation was low and a substantial amount of spawning substrate was not adequately submerged. Based on observations of spawning activity and presence of embryos, we presumed that Lost River Suckers require at least 0.2 m of water to spawn (Buettner and Scoppettone 1990; Reiser et al. 2001). To address our hypotheses we first determined the area of known spawning habitat that was too shallow for use by spawning suckers at each of the four main spawning areas as a function of lake surface elevation. To ensure that skipped spawning was not confused with straying to the only other known spawning habitat (i.e., the Williamson and Sprague rivers; Figure 2), we examined encounter histories of fish detected by PIT tag antennas or physically captured at both river and shoreline spawning areas. Spawning activity for fish at the shoreline areas was assessed based on the amount of

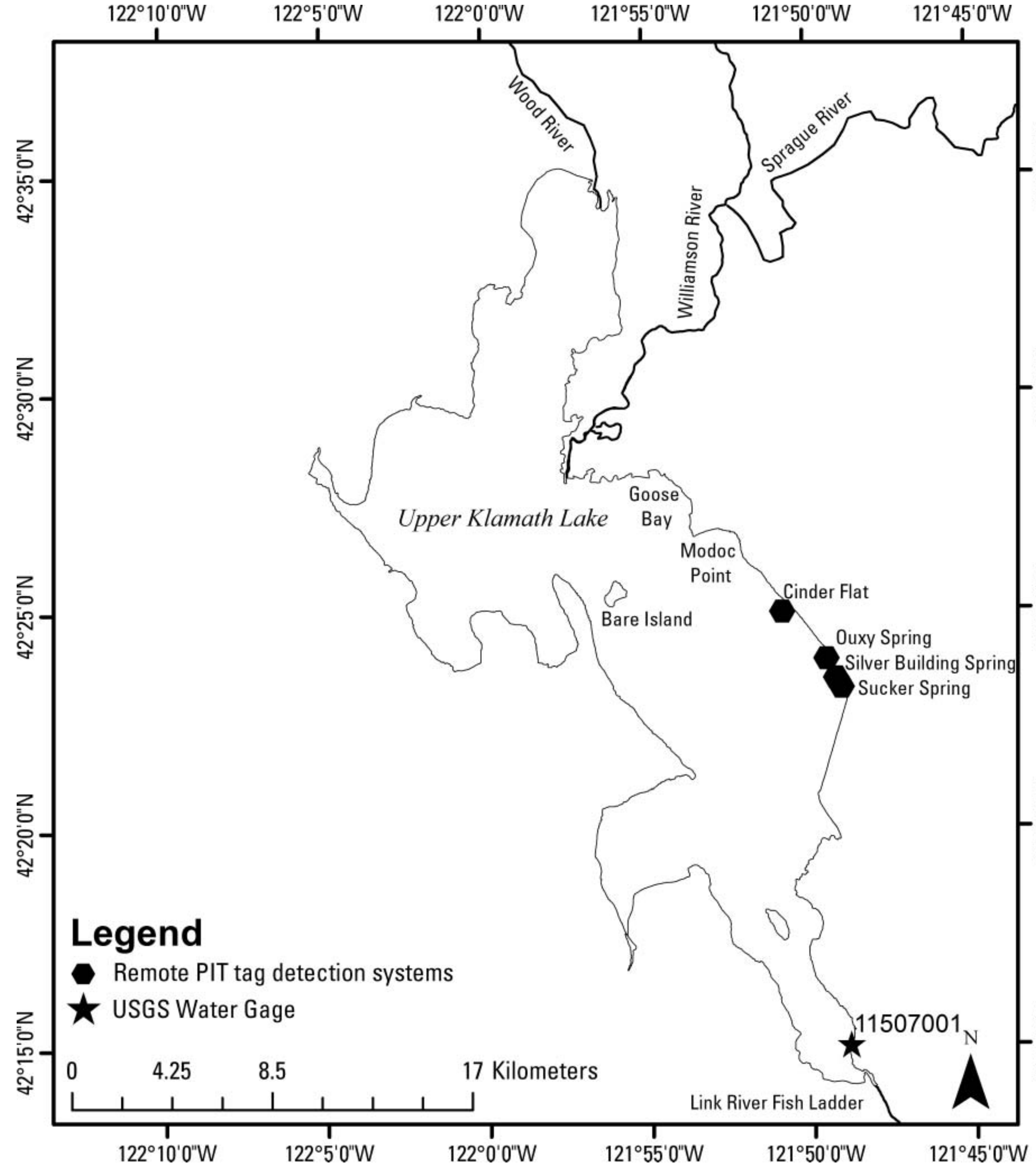

FIGURE 2. Upper Klamath Lake in south-central Oregon. Tributaries with known Lost River Sucker spawning activity, the locations of remote PIT tag detection systems at shoreline spawning areas, and the location of U.S. Geological Survey water station 11507001 are shown.

time spent at a spawning area, the number of spawning areas visited, and the distance between spawning areas used within a spawning season.

Lake surface elevation and water temperature.—We used lake surface elevation data from the U.S. Geological Survey (USGS) Upper Klamath Lake station 11507001 (http://waterdata.usgs.gov/or/nwis/uv/?site_no=11507001&PARAmeter_cd=00062,72020; Figure 2). These data are reported in the U.S. Bureau of Reclamation Vertical Datum (USBRVD) that was established locally for reporting lake elevation (Carpenter et al. 2009). Data were queried for the period between March 1 and June 1 each year, encompassing the period of time during which 99% of Lost River Suckers were detected by remote PIT tag antennas. Mean daily water temperature data were acquired from USGS station 11507500 at the Link River near Klamath Falls, Oregon (http://waterdata.usgs.gov/or/nwis/dv/?site_no=11507500&agency_cd=USGS&referred_module=qw).

Habitat availability assessment.—Physical profiles of the spawning areas were generated in ArcMap 10.0 (ESRI, Redlands, California) using two sources of data. Bare earth Light Detection and Ranging (Lidar) data collected at 1-m resolution and vertically accurate to 0.1 m were acquired from Oregon Department of Geological and Mineral Industries (ODGMI 2011). The Lidar data do not effectively penetrate below the water surface; therefore, additional elevation data were collected using a Trimble Zephyr 2 antenna (accurate to 1 dm) to profile the offshore edges of the spawning areas, which are typically inundated. These manually collected elevation data were corrected based on the Plum Point bench mark (http://www.ngs.noaa.gov/cgi-bin/ds_mark.prl?PidBox=NY0468) located 1,267.8 m above mean sea level and less than 1 km from Sucker Spring.

Lidar data were converted from raster form to points centered on each pixel and merged with manually collected elevation data to produce interpolated 0.1-m contours. Combined data were converted from the North American Vertical Datum of 1988 to USBRVD (following Carpenter et al. 2009) so that data could be compared with lake surface elevation from the USGS station. Polygons were drawn to encompass each spawning area based on where Lost River Suckers have been visually observed spawning since at least 2000. Contours were laid over polygons outlining known spawning habitat at each of the four spawning areas. We calculated the area of the known spawning habitat that became unusable as lake surface elevation declined. We restricted our assessment to lake surface elevations higher than 1,261.4 m because of data limitations and lake surface elevations lower than 1,263.0 m because that is the maximum possible lake surface elevation (full pool).

Remote PIT tag detection systems.—Lost River Suckers that spawn at the shoreline areas were sampled with trammel nets and implanted with PIT tags from 2005 to 2013. Suckers were redetected on remote underwater detection systems beginning in 2006 (Figure 2). Methods for this ongoing population dynamics research project are described in detail in Hewitt et al. (2010). Briefly, adult suckers were captured in 30.5-m trammel nets set in a semicircle around areas of concentrated spawning at shoreline spawning areas from February to May each year. Around 5,800 adult suckers were implanted with 12-mm, 0.1-g, full-duplex, 134.2-kHz PIT tags in the ventral abdominal musculature anterior to the pelvic girdle (Biomark, Boise, Idaho). We additionally used data from Lost River Suckers tagged in the Williamson and Sprague rivers or other locations in Upper Klamath Lake that were detected at shoreline spawning areas. Tagged suckers were detected with two or three flat plate antennas located at each shoreline spawning area and with antennas located at various locations in the Williamson and Sprague rivers (Figure 2). Transceiver software at each detection station was set to record an individual tag no more than once within specified time intervals (between 30 min and 2 h) to avoid exceeding data storage capacity. To verify consistency in detection efficacy, antenna current was checked on a daily basis and recalibrated when needed. This ensured that the maximum distance from each antenna at which a tag could be detected was always between 0.20 and 0.25 m.

Frequency of skipped spawning.—We used Cormack–Jolly–Seber (CJS) live-recapture models (Williams et al. 2002; Nichols 2005) to obtain maximum likelihood estimates of annual reencounter (p) and apparent survival (Φ) probabilities. Methods for developing encounter histories and analysis models are given in detail in Hewitt et al. (2010, 2012). Because CJS models simultaneously estimate annual survival and reencounter probabilities, the reencounter probabilities provide direct information about the live proportion of the subpopulation that joined the spawning aggregations in each season. Specifically, the estimated reencounter probability is the joint probability that a fish returned to an Upper Klamath Lake shoreline spawning area and the probability that a fish at the shoreline spawning areas was detected. We assumed that among-year differences in the probability of detecting fish that were present were negligible. This was a valid assumption considering the coverage of the antennas and the limited area of spawning habitat. Changes in sampling intensity can affect reencounter probabilities, but the consistency of our monitoring efforts minimized such effects. In models where p is not constrained to be constant across years, the terminal estimates of p and Φ are confounded in the CJS likelihood and cannot be separately estimated; thus, we only report estimates of p for 2006–2012. To provide parameter estimates that are specific to the shoreline spawning Lost River Sucker subpopulation, we excluded individuals from the analysis that were detected on river antennas (Hewitt et al. 2012).

Movement among spawning areas.—We examined encounter data for each fish to determine whether a reduction in the number of spawning areas visited or the distance between spawning areas visited was associated with low lake surface elevation. The numbers of spawning areas visited by male and female Lost River Suckers were summarized for each spawning season. We calculated the proportions of fish that visited each pairing of the four spawning areas within a given spawning season to assess how lake surface elevation was related to the distance suckers traveled between spawning areas.

To determine whether fish that skipped spawning at the shoreline areas in a given year instead migrated into lake tributaries to spawn, we investigated the histories of the few fish that were presumed to belong to the shoreline subpopulation but strayed into the tributary spawning areas. We considered the histories of the 15 fish that were detected only at shoreline spawning areas in at least two spawning seasons and were detected in one of the tributaries in only a single year. We did not include data from 25 fish that were detected at the shoreline areas and in the tributaries in multiple spawning seasons because it was unclear what subpopulation they belonged to. We also excluded fish that were detected in both the river and at the shoreline areas in the same year. We tallied the number of shoreline-to-river strays according to the year in which they were detected in a tributary.

Spawning duration.—Because Lost River Suckers that spend less time in the spawning areas are expected to have less chance of being detected in a season, we summarized the proportion of fish in each year that were detected only once on the remote antennas. We also estimated differences in the amount of time suckers spent at spawning areas among years by calculating the time between the first and last detection of each fish in each year. Fish that were both remotely detected and physically captured were excluded from this analysis to eliminate any behavior bias that might have occurred from handling. Fish that were detected only once in a year were assigned a duration of 1 h for this analysis. We did not include data from 2006 because noon and midnight were not differentiated in the data. We considered the effect of sex on duration of time spent on the spawning areas and graphically displayed data in notched box plots. Nonoverlapping notches, which were calculated as ±1.58 times the interquartile range divided by the square root of the sample size, indicated highly significant differences (Chambers et al. 1983).

RESULTS

Lake Surface Elevation and Water Temperature

Lake surface elevation increases during the spawning season each year due to increased input from snowmelt. During the 8 years of this study mean lake surface elevation was lowest in 2010, highest in 2006, 2007, and 2011, and intermediate in 2008, 2009, and 2013 (Figure 1). Lake surface elevation in 2012 was intermediate to high for most of the spawning season, but declined after May 15. Lake surface elevations did not exceed 1,262.3 m during the spawning season of 2010, and levels were approximately 0.3 m lower than in 2008, 2009, and 2013 and between 0.6 m to 0.9 m lower than in all other years.

As expected, water temperature generally increased over the spawning season each year (Figure 3). Fish arrived at spawning areas when lake water temperatures first exceeded about 6°C, and accumulated fastest when water temperatures were increasing. Fish accumulated unusually early in 2007 when water temperature increased rapidly in March (Figure 3). In contrast, most fish did not start arriving until April in 2012 because of cool March water temperatures. When lake water temperatures drop after the spawning season has begun, the arrival of fish at the spawning areas slows down (Hewitt et al. 2012). Decreases in water temperature in late March and early April of 2008, 2010, and 2011, after fish had begun to arrive at the spawning areas, temporarily slowed down the arrival of fish and resulted in relatively longer spawning seasons.

Habitat Availability Assessment

All known spawning habitat was useable at full pool (1,263.0 m), but some habitat at each spawning area became unusable as lake surface elevation decreased (Figure 4). As lake surface elevation declined below about 1,262.5 m the spawning habitat was lost more rapidly at Sucker Spring, whereas habitat was lost less rapidly at Ouxy Spring across the range of lake elevations in our analysis (Figure 4). The amount of spawning habitat lost at Silver Building Spring was similar to Ouxy Spring for most lake surface elevations, but no spawning habitat remained at Silver Building Spring when the lake elevation declined below 1,262.0 m. Spawning habitat at Cinder Flat is not negatively impacted until lake surface elevation declines below 1,262.6 m because there is no habitat above that elevation. The area of potential spawning habitat rendered unusable at the average lake surface elevation in 2010 (1,262.1 m) was about four times greater than in intermediate water years (1,262.6 m) and about 10 times greater than in high water years (1,262.8 m). This corresponds to approximately 354.8 m^2 more spawning habitat in intermediate water years and 420.5 m^2 more habitat in high water years than in 2010.

Tagging and Detection Summary

We detected 2,658 male and 3,220 female PIT-tagged Lost River Suckers at the shoreline spawning areas at least once between 2006 and 2013. Between 643 and 2,414 female and 676 and 1,793 male Lost River Suckers were detected in each year from 2006 to 2013 (Table 1). When fish that were handled in the same year they were remotely detected were censored from the spawning duration analysis to avoid effects of handling stress, the resulting data set included tag detections for between 481 and 2,045 females and between 468 and 1,320 males in each year.

Reencounter Probabilities

Model selection statistics from previous analyses have consistently supported CJS models for shoreline spawning Lost River Suckers that include separate estimates of reencounter probability for each sex in each year (Hewitt et al. 2010, 2012). Excluding the estimates for 2010, estimated reencounter probabilities between 2006 and 2012 always exceeded 0.97 for females (average = 0.973) and 0.98 for males (average = 0.984) (Figure 5). In each of these years nearly all of the PIT-tagged fish that were alive in the subpopulation were reencountered at some point during the spawning season. The complementary estimates of apparent annual survival (2006–2011) were 0.92 or greater for females and 0.88 or greater for males, in line with expectations given the life span of Lost River Suckers (up to 50 years: Terwilliger et al. 2010; Hewitt et al. 2012). Reencounter probabilities for both sexes were substantially lower in 2010 than in other years of the study, 0.83 (95%

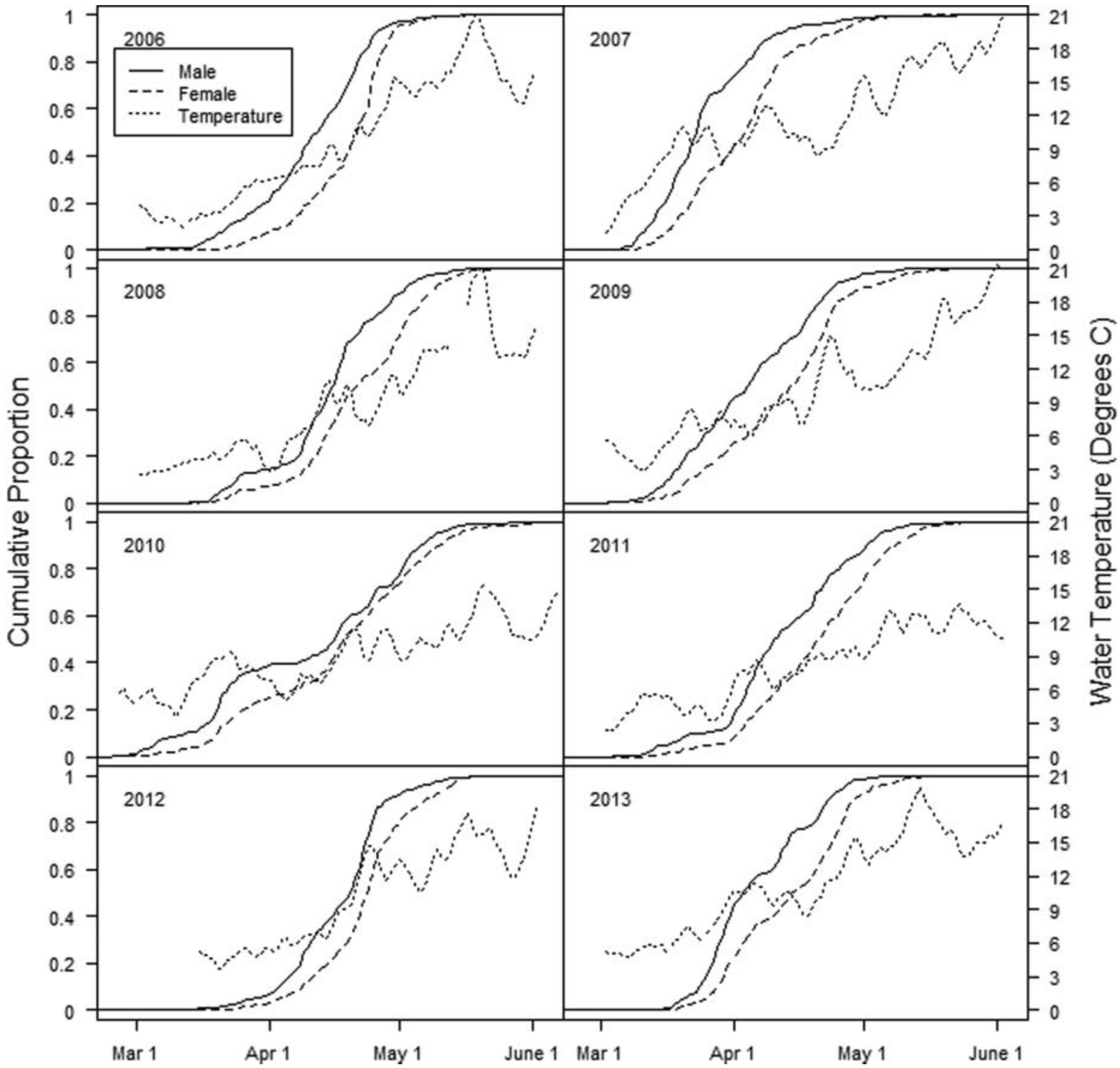

FIGURE 3. Cumulative proportion of first detections of male and female Lost River Suckers detected each year at the shoreline spawning areas in Upper Klamath Lake, Oregon. Water temperature (°C) at the Link River Dam outlet from Upper Klamath Lake is given for reference. Note that all spawning areas are combined.

CI = 0.81–0.85) for females and 0.90 (95% CI = 0.88–0.92) for males (Figure 5). These are the lowest estimates for both sexes since we implemented remote detection systems at the shoreline spawning areas and are 0.14 and 0.08 less than average for females and males, respectively.

Within-Season Movement among Spawning Areas

Detection data indicate that both male and female Lost River Suckers move among shoreline spawning areas within a season, and males are more likely to visit more spawning areas than are females (Figure 6). Between 4% and 21% of females and 9% and 32% of males were detected at all four spawning areas in a year (Figure 6). From 23% to 43% of females and from 23% to 44% of males were detected at only one spawning area in a single year. The proportion of males and females detected at all four spawning areas in 2010 was about half of the next lowest year, and the proportion detected at only a single spawning area was higher in 2010 than in any other year (Figure 6). The number of fish that visited a pairing of any two spawning areas appeared to be dependent on the distance between the areas. That is, fewer fish of either sex moved between Cinder Flat and the other areas than among Sucker, Silver Building, and Ouxy springs (Figure 2; Tables 2, 3). Furthermore, the number of fish moving between Cinder Flat and the other spawning areas was lowest in 2010.

Very few PIT-tagged Lost River Suckers that were encountered at the shoreline areas in at least 2 years strayed to the

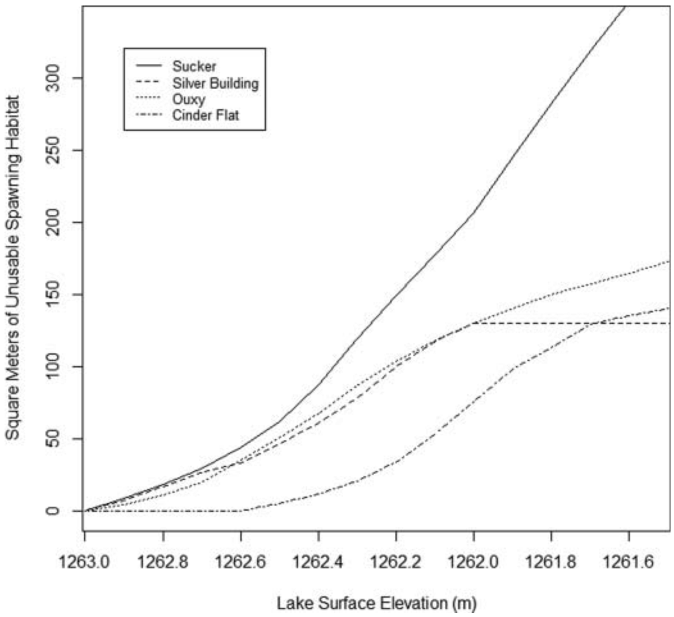

FIGURE 4. Area of unusable spawning habitat at four Upper Klamath Lake shoreline Lost River Sucker spawning areas as a function of lake surface elevation. The locations of the four spawning areas are shown in Figure 2. Elevations are in meters above mean sea level in the U.S. Bureau of Reclamation datum. There is no spawning habitat at Cinder Flat above 1262.6 m.

TABLE 1. Number of female and male Lost River Suckers tagged with PIT tags that were encountered each year at shoreline spawning areas in Upper Klamath Lake from 2006 to 2013. Handled fish included those that were newly tagged or tagged in a previous year and physically recaptured. Only fish that were not handled in a year that they were detected were included in analysis of duration of time spent at spawning areas. The percentages of female and male Lost River Suckers tagged with PIT tags that were detected only once within a year are also given.

Year	Handled	Not handled	Percentage (%) detected only once
		Female	
2006	162	481	1.87
2007	349	602	1.99
2008	283	962	4.78
2009	425	1,167	4.8
2010	166	1,346	15.68
2011	452	1,571	4.07
2012	546	1,739	4.31
2013	369	2,045	5.38
		Male	
2006	208	468	0.83
2007	289	549	1
2008	204	739	1.14
2009	426	745	1.54
2010	286	945	6.76
2011	699	935	0.95
2012	614	1,139	1.32
2013	473	1,320	1.47

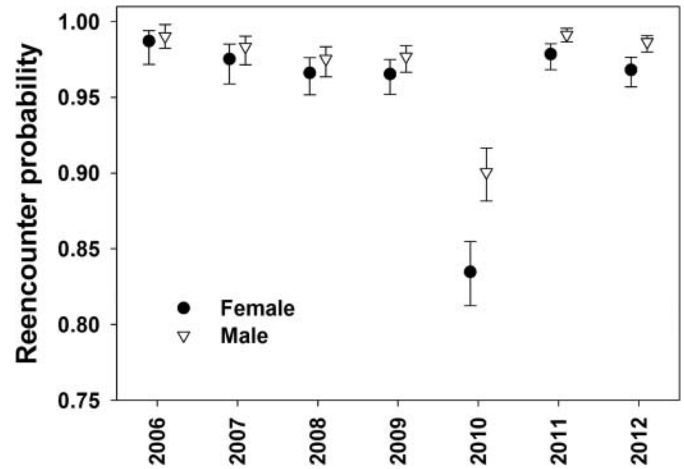

FIGURE 5. Reencounter probabilities estimated from Cormack–Jolly–Seber models fitted to data for tagged Lost River Suckers at shoreline spawning areas in Upper Klamath Lake, Oregon, from 2006 to 2012. Model selection indicated that reencounter probability was different between sexes, so we reported females and males separately. Vertical bars represent the 95% CI.

Williamson and Sprague rivers. Either zero or one male and between one and three females were encountered as strays in a river during any given year including 2010. Furthermore, none of the individuals that were detected at the shoreline spawning areas in all years except 2010 were detected in either of the rivers in 2010.

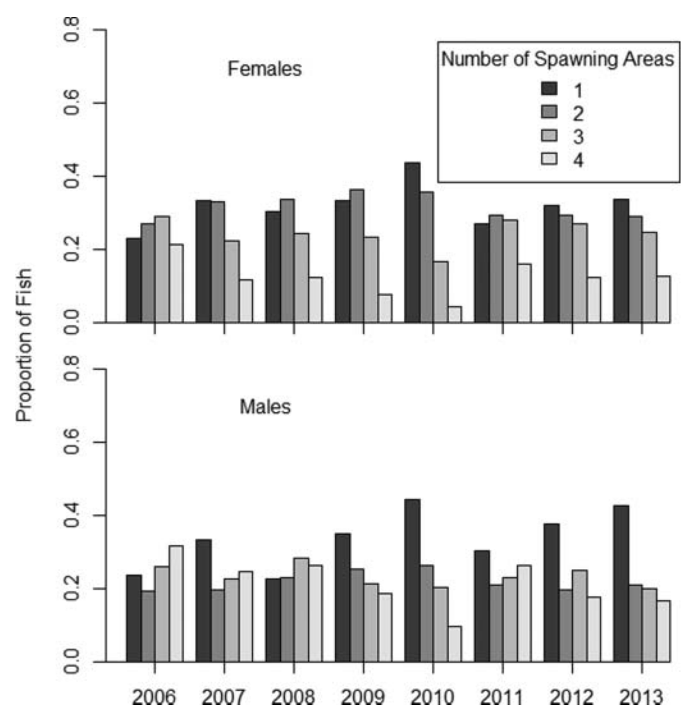

FIGURE 6. Proportion of female (top panel) and male (bottom panel) Lost River Suckers that were detected at one, two, three, or four of the shoreline spawning areas in each spawning season from 2006 to 2013.

TABLE 2. Proportion of male Lost River Suckers detected at each spawning area, listed as the column heading that were also detected at the spawning area, listed in column one in each year from 2006 to 2013. The locations of the spawning areas within Upper Klamath Lake are shown in Figure 2.

Spawning area	Cinder Flat	Ouxy Spring	Silver Building Spring	Sucker Spring
		2006		
Cinder	1.00	0.60	0.53	0.70
Ouxy		1.00	0.77	0.89
Silver			1.00	0.95
Sucker				1.00
		2007		
Cinder	1.00	0.47	0.47	0.58
Ouxy		1.00	0.76	0.83
Silver			1.00	0.93
Sucker				1.00
		2008		
Cinder	1.00	0.52	0.55	0.66
Ouxy		1.00	0.78	0.87
Silver			1.00	0.92
Sucker				1.00
		2009		
Cinder	1.00	0.40	0.34	0.61
Ouxy		1.00	0.64	0.90
Silver			1.00	0.96
Sucker				1.00
		2010		
Cinder	1.00	0.26	0.28	0.45
Ouxy		1.00	0.58	0.82
Silver			1.00	0.90
Sucker				1.00
		2011		
Cinder	1.00	0.47	0.46	0.58
Ouxy		1.00	0.75	0.84
Silver			1.00	0.94
Sucker				1.00
		2012		
Cinder	1.00	0.31	0.44	0.51
Ouxy		1.00	0.77	0.82
Silver			1.00	0.90
Sucker				1.00
		2013		
Cinder	1.00	0.31	0.35	0.45
Ouxy		1.00	0.72	0.80
Silver			1.00	0.91
Sucker				1.00

TABLE 3. Proportion of female Lost River Suckers detected at each spawning area listed as the column heading that were also detected at the spawning area listed in column one in each year from 2006 to 2013. The locations of the spawning areas within Upper Klamath Lake are shown in Figure 2.

Spawning area	Cinder Flat	Ouxy Spring	Silver Building Spring	Sucker Spring
		2006		
Cinder	1.00	0.57	0.51	0.69
Ouxy		1.00	0.70	0.86
Silver			1.00	0.93
Sucker				1.00
		2007		
Cinder	1.00	0.37	0.39	0.61
Ouxy		1.00	0.59	0.78
Silver			1.00	0.91
Sucker				1.00
		2008		
Cinder	1.00	0.39	0.47	0.56
Ouxy		1.00	0.69	0.73
Silver			1.00	0.81
Sucker				1.00
		2009		
Cinder	1.00	0.34	0.27	0.68
Ouxy		1.00	0.44	0.83
Silver			1.00	0.94
Sucker				1.00
		2010		
Cinder	1.00	0.29	0.23	0.54
Ouxy		1.00	0.37	0.80
Silver			1.00	0.88
Sucker				1.00
		2011		
Cinder	1.00	0.42	0.47	0.64
Ouxy		1.00	0.69	0.80
Silver			1.00	0.90
Sucker				1.00
		2012		
Cinder	1.00	0.32	0.50	0.59
Ouxy		1.00	0.71	0.78
Silver			1.00	0.87
Sucker				1.00
		2013		
Cinder	1.00	0.31	0.40	0.55
Ouxy		1.00	0.68	0.82
Silver			1.00	0.91
Sucker				1.00

Spawning Duration

Several lines of evidence indicated that Lost River Suckers spent less time at spawning areas in 2010 than in other years of the study. A greater proportion of suckers were only detected on a single occasion in 2010 than in other years (Table 1). In years other than 2010, no more than 5% of the females and 2% of the males were detected only once, whereas 16% of females and 7% of males were detected only once in 2010 (Table 1). Males arrived at the spawning areas earlier than females (Figure 3) and remained for substantially longer

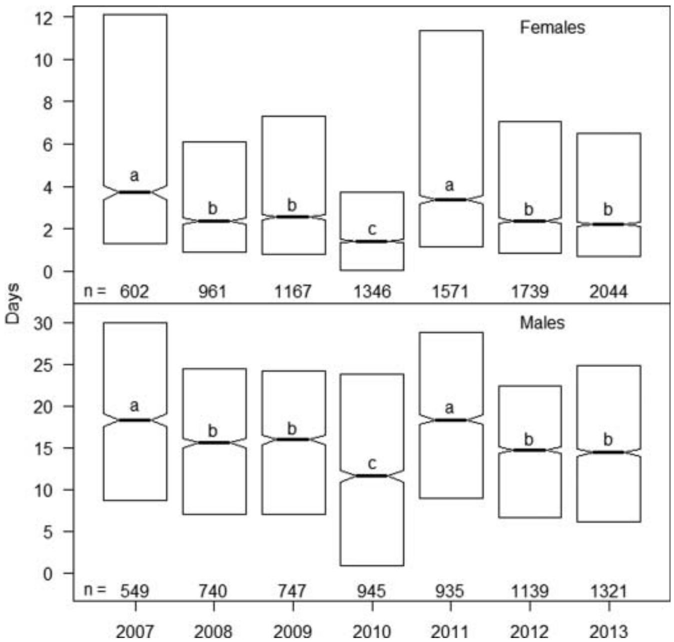

FIGURE 7. Days between the first and last detection of individual female (top panel) and male (bottom panel) Lost River Suckers at the shoreline spawning areas in Upper Klamath Lake, Oregon. Fish that were only detected on one occasion in a year were assigned a detection duration of 1 h. Boxes indicate the central 75% of data. Nonoverlapping notches indicate significant differences among groups. Significantly different groups are indicated by lower case letters. The numbers (n) of fish used in the creation of each box plot are given along the x-axis.

periods of time (Figure 7). The median number of days between the first and last detection of individual males was greater than 14.5 d in all years except 2010; in 2010 the median duration for males was only 11.5 d. The median number of days between the first and last detection of individual females also was lower in 2010 (1.4 d) than in any other year (between 2.2 and 3.7 d). Years with intermediate lake surface elevation (2008, 2009, 2012, and 2013) also produced substantially shorter spawning activity duration than did years with high lake surface elevations (2007 and 2011), but the effect was not as strong as in 2010 (Figure 7).

DISCUSSION

Multiple results from our analysis indicate that conditions for spawning at the shoreline areas were associated with a reduction in Lost River Sucker spawning activity in 2010. During March, April, and May of 2010, lake surface elevation was much lower than in any other year of our study, resulting in less available spawning habitat. An estimated 14% fewer female and 8% fewer male suckers joined the spawning aggregation in 2010 than in the other years. The amount of time Lost River Suckers spent at the spawning areas differed between the sexes and also was less in 2010 than in intermediate water years and much less than in high water years. Although inferences about the effects of low lake surface elevations like those that occurred in 2010 are necessarily limited by the infrequent occurrence of such conditions, the effects on the spawning aggregation in 2010 suggest that such events can negatively affect population dynamics.

The difference in reencounter probabilities between 2010 and other years is most likely due to skipped spawning in 2010. Excluding the estimates for 2010, estimated reencounter probabilities between 2006 and 2012 were high and varied little among years. Estimates in these years indicated that no more than 3% of females and no more than 2% of males either skipped spawning or joined the spawning aggregation but were not detected. Because redetection methods and antenna performance were essentially the same among years, among-year differences in the probability of detecting fish present at the spawning areas were negligible. Therefore, the difference in reencounter probabilities between 2010 and other years provided a conservative estimate of the portion of the subpopulation that skipped spawning.

By examining the encounter histories for fish that were not detected at the shoreline spawning areas in 2010, we determined that those fish did not switch spawning areas and migrate instead to the Williamson or Sprague rivers. This finding is consistent with the strong fidelity that Lost River Suckers have shown for either tributary or shoreline spawning areas in Upper Klamath Lake (Janney et al. 2008; Hewitt et al. 2012). Nonetheless, some of these fish could have spawned at locations that were not monitored or attempted to spawn farther offshore at the shoreline areas where we did not have detection equipment. In the latter case, we considered it unlikely but not impossible that deeper water and muddy substrate in offshore areas was suitable for spawning. Lost River Suckers have never been observed spawning over substrates other than gravel or cobble.

Skipped spawning is a common phenomenon among long-lived catostomids when fish are young, when nutritional condition is poor, or when the mortality or energetic costs associated with spawning are high (Quinn and Ross 1985; Scoppettone et al. 2000; Rideout and Tomkiewicz 2011). Given the nearly homogeneous age and size of fish in this spawning aggregation (Hewitt et al. 2012), young age or small size is very unlikely to be a cause of skipped spawning. We have no direct evidence that nutritional condition was a factor, but a lack of food is unlikely in hypereutrophic Upper Klamath Lake. Due to extremely poor water quality, fish are sometimes diseased during the summer, but they generally do not have signs of impairment during the spawning season (Perkins et al. 2000a; Foott 2004). Nevertheless, some residual poor health may have occurred during the spawning season if water quality conditions were particularly stressful during the previous summer and fish were unable to recuperate. One possible cause of skipped spawning in 2010 is a risk or perceived risk of mortality that outweighed the benefits of spawning. For example, the presence of predators such as American white pelicans

Pelecanus erythrorhynchos, an efficient predator of adult suckers (Scoppettone et al. 2014), may deter fish from approaching the shoreline spawning areas under low water conditions. This is supported by our observations of American white pelicans preying on Lost River Suckers at the spawning areas and recoveries of sucker PIT tags on American white pelican nesting areas.

The amount of time Lost River Suckers spent at the spawning areas differed between the sexes and was shorter in 2010 than in intermediate water years (2008, 2009, 2012, and 2013) and much shorter than in high water years (2007 and 2011). Fish that spend less time overall at the spawning areas are necessarily less apt to be detected on the stationary antennas across multiple areas. Therefore, it is not surprising that movement among sites was detected less often when the duration of time spent at the spawning areas overall was lower. Although we saw an increase in the proportion of fish detected only one time during 2010 compared with other years, it is not clear whether this was simply a result of reduced spawning duration. Most fish were detected many times during a spawning season, and it is possible that fish detected only one time may not have spawned. If true, this would further increase the proportion of fish that functionally skipped spawning in 2010.

Our study refines previous information on the amount of time Lost River Suckers spend at the shoreline spawning areas. Perkins et al. (2000b) reported that 44 of 50 Lost River Suckers of an unspecified sex were recaptured within 10 d of first capture and the longest time between captures of the same fish within a spawning season was 25 d for a male Lost River Sucker. Our results indicated that half of the females spent less than 4 d and half of the males spent less than 20 d at shoreline spawning areas. The duration of time spent in spawning areas by males is similar to the short spawning duration of June Suckers *Chasmistes liorus* that reportedly spend less than 2 weeks at spawning areas (Modde and Muirhead 1994). Remote detection technology used in our study and physical-recapture data used by Perkins et al. (2000b) both underestimated the duration of spawning to some extent. However, due to the frequent detections in our study any underestimation of spawning duration was probably on the order of hours rather than days. The recording delay of 30 min to 2 h for fish detected multiple times limited our ability to measure the length of very short visits, but the infrequency of single detections indicates these were rare.

Water temperature may have affected the arrival timing at shoreline spawning areas, but it did not appear to be associated with the amount of time that individual fish stayed in these areas. Studies of gonadal maturity or the presence of adults or eggs in spawning areas indicate that warmer temperatures are associated with shorter spawning seasons compared with cooler temperatures (Graham and Orth 1986; Hamel et al. 1997). Our results corroborate findings from these studies because the arrival of fish at the spawning areas was prolonged in 2008, 2010, and 2011 when water temperatures dropped after the start of the spawning season. However, the duration of time that individual fish spent at the spawning areas once they arrived was not associated with water temperature. In 2007 when water temperatures increased rapidly in March, nearly all the fish arrived earlier but stayed for the same amount of time or longer than in other years. Water temperatures in 2010 and 2011 were similarly cool throughout the season, but both females and males spent significantly less time at spawning areas in 2010 than in 2011.

The lake level conditions observed in 2010 appeared to have had a greater effect on females than males. A higher percentage of females skipped spawning and the duration of their spawning activity was reduced more than for males. Female suckers may elect to skip spawning more frequently than males given that spawning takes more energy for female suckers than male suckers (Quinn and Ross 1985). However, the loss of a single year's egg production may be compensated with future increases in fecundity. For example, Cui-ui *Chasmistes cujus* reabsorbed eggs in years that they were prevented from spawning, but the older and slower-growing fish compensated with increased fecundity in the following year (Scoppettone et al. 2000). Given that the supply of males is generally not limiting (i.e., several males attend a single female) and males spend more time at spawning areas, participation in the act of spawning by a female is probably more important to the spawning success of the subpopulation than it is for an individual male. A much higher rate of skipping by males compared with females would be needed to equal the same overall reduction in spawning effort. Therefore, the relatively higher rate of skipping by females may have affected the overall spawning success to a greater extent than if the two sexes had been equally discouraged from spawning or if males had been more affected than females.

Considering that fish skipped spawning in the extreme low water year of 2010 and that they spent less time at spawning areas in years with low or intermediate water levels than in years with higher water levels, it is reasonable to conclude that Lost River Sucker spawning activity is not negatively affected by lake surface elevations greater than about 1,262.3–1,262.5 m. Our results indicate that a temporary loss of about 100 m^2 of known spawning habitat may reduce the amount of time fish spend at the spawning areas, but fish will not skip spawning until several hundred square meters of habitat are rendered unusable due to low water level. The U.S. Bureau of Reclamation reports that operation of the Klamath Project from 2013 to 2023 should maintain lake surface elevations during the spawning season above 1,262.3 m in more than 90% of years provided weather predictions are accurate (USBR 2012). However, due to a severe drought in 2012–2013, lake surface elevation was below 1,262.3 m at the start of the spawning season and below 1262.5 until the first week of April in 2013. Nonetheless, the U.S. Bureau of Reclamation operational plan should make it unlikely that low lake surface elevation will impair Lost River Sucker spawning.

Recruitment failure has been identified as the primary limiting factor in the recovery and long-term persistence of Lost River Suckers (Hewitt et al. 2012). Specifically, a near complete absence of immature fish over 1 year of age and nearly no small adults in the spawning aggregations point to a near complete failure within the first year of life. Recruitment failure can be the result of low first-year survival, low egg and larval production, or both. Although the long-term implications of a single year of skipped spawning are unclear, managing to maximize egg production could be beneficial until impediments to recruitment are identified and mitigated.

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