North American Journal of Fisheries Management 36:1254–1268, 2016

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2016.1208123

ARTICLE

Colonial Waterbird Predation on Lost River and Shortnose Suckers in the Upper Klamath Basin

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Abstract
We evaluated predation on Lost River Suckers *Deltistes luxatus* and Shortnose Suckers *Chasmistes brevirostris* by American white pelicans *Pelecanus erythrorhynchos* and double-crested cormorants *Phalacrocorax auritus* nesting at mixed-species colonies in the Upper Klamath Basin of Oregon and California during 2009–2014. Predation was evaluated by recovering (detecting) PIT tags from tagged fish on bird colonies and calculating minimum predation rates, as the percentage of available suckers consumed, adjusted for PIT tag detection probabilities but not deposition probabilities (i.e., probability an egested tag was deposited on- or off-colony). Results indicate that impacts of avian predation varied by sucker species, age-class (adult, juvenile), bird colony location, and year, demonstrating dynamic predator–prey interactions. Tagged suckers ranging in size from 72 to 730 mm were susceptible to cormorant or pelican predation; all but the largest Lost River Suckers were susceptible to bird predation. Minimum predation rate estimates ranged annually from <0.1% to 4.6% of the available PIT-tagged Lost River Suckers and from <0.1% to 4.2% of the available Shortnose Suckers, and predation rates were consistently higher on suckers in Clear Lake Reservoir, California, than on suckers in Upper Klamath Lake, Oregon. There was evidence that bird predation on juvenile suckers (species unknown) in Upper Klamath Lake was higher than on adult suckers in Upper Klamath Lake, where minimum predation rates ranged annually from 5.7% to 8.4% of available juveniles. Results suggest that avian predation is a factor limiting the recovery of populations of Lost River and Shortnose suckers, particularly juvenile suckers in Upper Klamath Lake and adult suckers in Clear Lake Reservoir. Additional research is needed to measure predator-specific PIT tag deposition probabilities (which, based on other published studies, could increase predation rates presented herein by a factor of roughly 2.0) and to better understand biotic and abiotic factors that regulate sucker susceptibility to bird predation.

Piscivorous colonial waterbirds are an integral part of the Upper Klamath Basin ecosystem, and colonies of American white pelicans *Pelecanus erythrorhynchos*, double-crested cormorants *Phalacrocorax auritus*, and other species of fish-eating colonial waterbirds (e.g., gulls *Larus* spp., herons *Ardea* spp., terns *Sterna* spp., and Caspian terns *Hydroprogne caspia*) are present in the region (Shuford 2010). Collectively, the Upper Klamath Basin breeding colonies of American white pelicans

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Received January 19, 2016; accepted June 25, 2016

are the largest colonies on the U.S. west coast (King and Anderson 2005; Shuford 2010). Two species of long-lived catostomid fishes, the Lost River Sucker *Deltistes luxatus* and the Shortnose Sucker *Chasmistes brevirostris*, are also found in the region and are listed as endangered under the U.S. Endangered Species Act (ESA). Numerous factors have been identified as limiting the recovery of sucker populations, including habitat loss, poor water quality, and a lack of juvenile recruitment into the spawning populations (Janney et al. 2008; USFWS 2012; Hewitt et al. 2015). The impacts of predatory birds on ESA-listed sucker populations, however, is currently unknown but may be significant based on the abundance and diversity of piscivorous waterbirds that reside in the Upper Klamath Basin, as well as the relative scarcity of suckers compared with the past. Consequently, avian predation may be a limiting factor for Upper Klamath Basin sucker populations, even if avian predation was not an initial cause of their declines (USFWS 2012).

Samples of Lost River and Shortnose suckers are tagged each year with PIT tags to gather information on their behavior and survival following release (Janney et al. 2008; Hewitt and Hayes 2013; Burdick et al. 2015; Hewitt et al. 2015). The PIT tags allow specific information to be linked to individual fish, such as species, size, age-class (adult, juvenile), and release location. Following release, encounter histories of PIT-tagged suckers are used to evaluate movements, growth, survival, and other demographic characteristics of interest (Hewitt et al. 2015). A portion of these PIT-tagged suckers are consumed by avian predators nesting in the region, and a portion of the ingested PIT tags are deposited (regurgitated or defecated) on the birds' nesting colonies. Electronic recoveries (detections of tags using electronic scanners) of fish PIT tags on waterbird colonies in other regions have been used to evaluate the impact of avian predation on fishes of conservation concern. For example, PIT tags found on bird colonies in the Columbia River basin have been used to measure the relative susceptibility of different fish species, spawning populations, and life histories to bird predation (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005). Recoveries of PIT tag have also been used to identify which individual bird colonies pose the greatest threat to fish survival and to estimate avian predation rates (percentage of tagged fish consumed) (Evans et al. 2012; Frechette et al. 2012; Osterback et al. 2013; Hostetter et al. 2015; Teuscher et al. 2015).

Based on the success of PIT tag predation studies conducted in other regions and the large numbers of suckers that are PIT-tagged each year, we initiated a study to recover sucker PIT tags from bird colonies in the Upper Klamath Basin during 2009–2014 to estimate predation rates. This study primarily investigated the combined impacts of two piscivorous waterbird species, American white pelicans and double-crested cormorants, species that were relatively abundant during 2009–2014 and species capable of consuming both juvenile- and adult-sized suckers. More specifically, the primary objectives of this study were to (1) evaluate the relative susceptibility of suckers to cormorant and pelican predation by fish species (Lost River Sucker, Shortnose Sucker), water body (Clear Lake Reservoir, Upper Klamath Lake), age-class (juvenile, adult), and fish size (FL) and (2) determine which bird nesting colonies posed the greatest risk to sucker survival in the region. Information on bird colony sizes (number of breeding adults) were also evaluated and reported in the context of sucker predation. Finally, we identify several data gaps and critical uncertainties that, if addressed, would result in more accurate measures of avian predation rates and would broaden our understanding of predator–prey interactions in the region.

METHODS

Study area.—We investigated predation on PIT-tagged Lost River Suckers and Shortnose Suckers by American white pelicans and double-crested cormorants breeding on islands located in Upper Klamath Lake, Oregon, and in Clear Lake Reservoir, California, (hereafter, Clear Lake) during 2009–2014 (Figure 1). A total of eight islands or nesting colonies were scanned for PIT tags from suckers following the nesting season: five islands in Upper Klamath National Wildlife Refuge (NWR) and three islands in Clear Lake NWR (Figure 1). Islands in Upper Klamath NWR were small (<0.3 acres [0.12 ha] per nesting site) and consisted largely of mats of bulrush (Cyperaceae) or common tule *Schoenoplectus acutus*. Islands in Clear Lake NWR were larger (0.4 to 9.0 acres [0.16–3.6 ha] per nesting site depending on the island and reservoir water levels) and consisted of rocky or sandy substrate. In addition to scanning nesting colonies in Clear Lake and Upper Klamath Lake, we opportunistically scanned avian nesting, loafing, and roosting sites in other areas (Sheepy Lake and Tule Lake, California; Figure 1; Table A.1 in the Appendix), but because these other areas were only periodically scanned for PIT tags or because these sites were not exclusively used as nesting sites, data were excluded from our analysis of colony-specific predation rates (see below). Lost River Suckers and Shortnose Suckers were annually captured, PIT-tagged, and released into each lake by the U.S. Geological Survey (USGS), Klamath Falls Field Station, as part of an independent study to investigate sucker behavior and survival in the region.

Fish capture, tagging, and release.—Adult Lost River Suckers and Shortnose Suckers in Upper Klamath Lake were tagged with PIT tags beginning in 1991. More intensive tagging efforts in the Upper Klamath Basin began in the mid-1990s, with the most consistent tagging effort occurring for the spawning populations in Upper Klamath Lake and Clear Lake. Juvenile suckers have been captured and PIT-tagged in Upper Klamath Lake since 2008 and in Clear Lake since 2010. A brief description of the USGS-led capture, tagging, and release methods are presented below (see

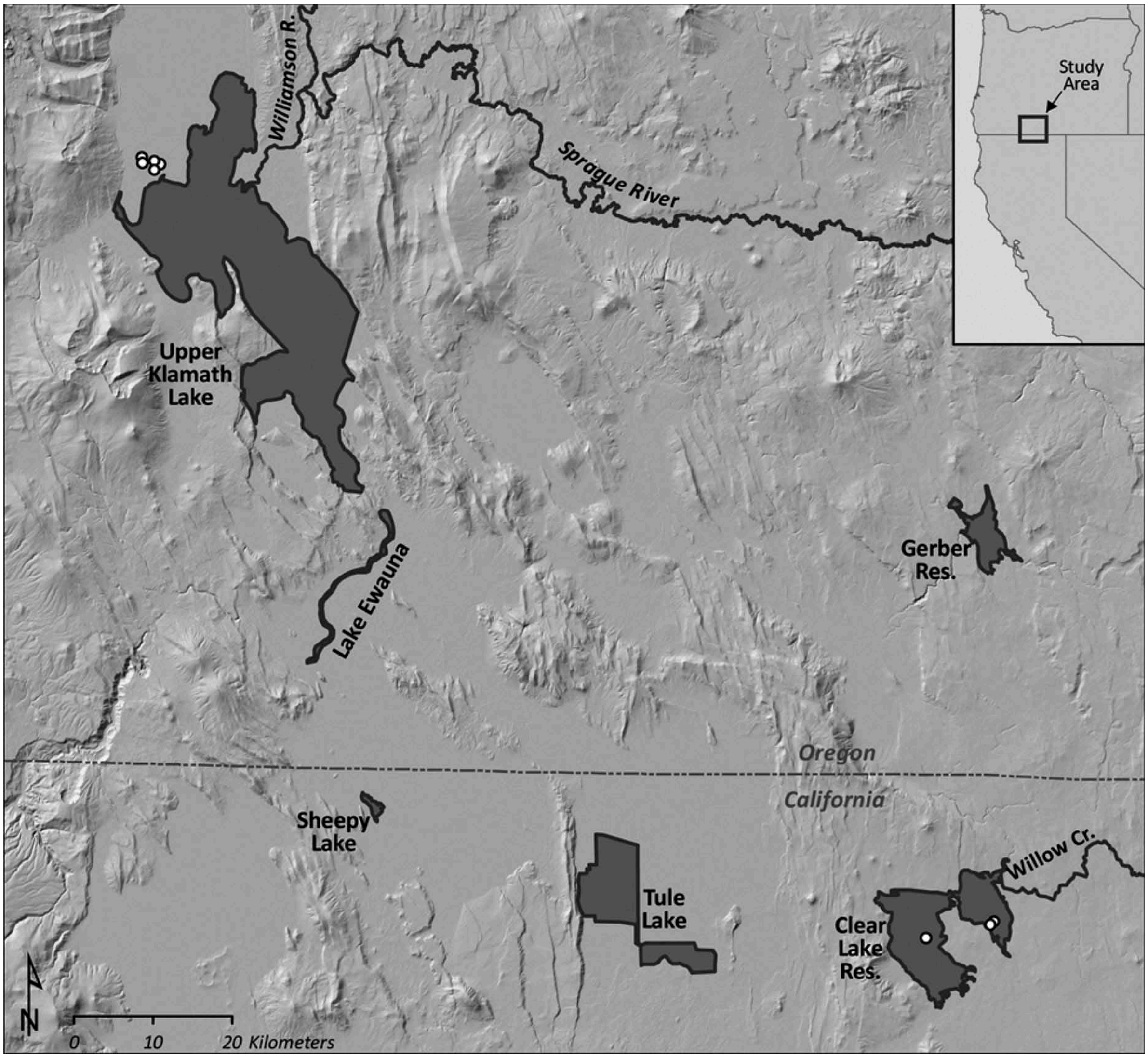

FIGURE 1. Locations of piscivorous waterbird nesting colonies (white dots) scanned for PIT tags implanted in Lost River Suckers and Shortnose Suckers released into Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California, during 2009–2014.

Janney et al. 2008; Hewitt et al. 2010, 2015; Hewitt and Hayes 2013 for detailed descriptions).

Adult Lost River and Shortnose suckers in Upper Klamath Lake were captured for tagging before and during the spawning season (February to June) via trammel nets (1.8 m high, two 30-cm-mesh outer panels, one 3.8-cm-mesh inner panel) set at various sites in the lake. Adult Lost River and Shortnose suckers were also captured in the Williamson and Sprague rivers. River-caught suckers were captured at the Chiloquin Dam fish ladder on the Sprague River during 2000–2008 and at a resistance board weir deployed on the Williamson River starting in 2005. The weir restricted the passage of suckers to two short sections, each fitted with a live trap, and the upstream trap was used to capture fish as they migrated upriver. Large numbers of adult Lost River Suckers were captured and tagged at spring areas along the eastern shoreline of Upper Klamath Lake where a distinct subpopulation spawns, but few adult Shortnose Suckers were captured at the spring areas (Hewitt et al. 2015).

Adult Lost River and Shortnose suckers in Clear Lake were captured using trammel nets similar to those used in Upper Klamath Lake. Suckers in Clear Lake were primarily captured in the west lobe during September and October (Hewitt and Hayes 2013). Nets were set at various locations, but effort was concentrated near the shoreline where catches were consistently the highest. Juvenile suckers in Clear Lake and Upper Klamath Lake were captured using trap nets that were set overnight (see Bottcher and Burdick 2010; Burdick and Rasmussen 2013 for details). Sampling occurred at different times of the year, but generally occurred between May and September.

Adult suckers were identified to species, sexed (Markle et al. 2005), measured (mm FL), and scanned for the presence of a PIT tag. If a PIT tag was not detected, one was inserted into the ventral abdominal musculature anterior to the pelvic girdle. From 1995 to 2004, suckers were tagged with 125-kHz, full-duplex, 12-mm PIT tags. Starting in 2005, 134-kHz, full-duplex, 12-mm tags, which have a greater read range, were used. Juvenile suckers (<300 mm), which cannot be identified to species nondestructively (Markle et al. 2005; Burdick 2013), large enough (FL > 72 mm) for PIT-tagging were tagged if they appeared to be in good condition and water temperature was less than 20°C when captured. Mortality associated with the use of 12-mm PIT tags in juvenile suckers greater than 72 mm FL has been reported to be less than 10% (Burdick 2011).

In addition to physical captures, passive encounters of PIT-tagged suckers using remote underwater antennas were also used to provide information about sucker availability. Remote antenna systems at spawning areas in Upper Klamath Lake (see Hewitt et al. 2015 for a full description of these systems) detected both 125-kHz tags (fish tagged before 2005) and 134-kHz tags (fish tagged during 2005 to 2014). At Clear Lake, remote antennas were used in Willow Creek (beginning in 2006; see Hewitt and Hayes 2013) and in a channel in a shallow strait between the two lobes of Clear Lake (beginning in 2014). Remote arrays in Clear Lake could only detect fish with 134-kHz tags, so predation rate estimates were based only on recoveries of 134-kHz tags at nesting colonies.

*PIT tag recovery on bird colonies.—*Recovery of sucker PIT tags on bird colonies followed the methods of Evans et al. (2012). In brief, PIT tags deposited by birds on nesting colonies were recovered in situ after birds dispersed from their breeding colonies following the nesting season (September–November). Colony sites were scanned using pole-mounted PIT tag antennas and portable transceivers. The PIT tags were detected by scanning the entire area occupied by birds during the nesting season, and at least two passes or complete sweeps of the nesting site were conducted each year. The orientation or directionality of antennas relative to the nesting substrate changed among passes to increase the number of unique detections obtained during a scanning session (Ryan et al. 2003). The area occupied by birds was determined based on aerial photographs of the colony taken during the nesting season.

*Bird colony sizes.—*The methods of Adkins et al. (2014) were used to determine the size (number of breeding adults) of the colonies scanned for sucker PIT tags during 2009–2014. In brief, colony sizes were estimated based on the number of adult birds visible in aerial photographs taken during the nesting season, and two to three aerial surveys were conducted each nesting season. Peak colony size was based on the number of adults present during late incubation (June), the stage of the nesting cycle when the greatest numbers of breeding adults are generally found on the colony (Gaston and Smith 1984). In cases where birds at a given nesting site abandoned the site prior to late incubation (i.e., all nesting attempts failed), photographs of the colony taken earlier in the nesting season, if available, were used to estimate colony size. Photographs were taken with a high-resolution, digital, single-lens reflex (SLR) camera from a fixed-wing aircraft. Counts were conducted with the aid of digital imaging software to delineate the number and species (cormorant, pelican) of each bird in each photograph. Aerial photography also provided limited data on nesting success (based on the presence or absence of young) at each nesting site in each year.

*Predation impacts.—*Impacts of piscivorous colonial waterbirds on sucker survival were evaluated using a hierarchical Bayesian model to estimate predation rates as the proportion of available tagged fish consumed by birds (Hostetter et al. 2015). To evaluate relative differences in sucker susceptibility to avian predation, predation rates were compared by sucker species (Lost River Suckers, Shortnose Suckers), age-class (adult, juvenile), water body, and year (2009–2014).

Accurate predation rate estimates based on PIT tag recoveries from bird colonies generally incorporate three probabilities: (1) the probability that an available PIT-tagged fish is consumed by a bird, (2) the probability that a consumed PIT tag is deposited on the bird's nesting colony, and (3) the probability that the deposited PIT tag is detected by researchers following the nesting season (Hostetter et al. 2015). For example, PIT tags can be regurgitated or defecated at loafing, staging, or roosting sites used by birds during the nesting season, resulting in deposition probabilities that are <1.0 (Osterback et al. 2013; Hostetter et al. 2015; Tauscher et al. 2015). Tags deposited by birds on their nesting colony can also be blown off the colony, destroyed (rendered nonfunctional) during the course of the nesting season, or missed (i.e., not detected) during the scanning process, resulting in detection probabilities that are <1.0 (Evans et al. 2012).

*Fish availability.—*We defined availability as the number of PIT-tagged suckers that were physically captured in nets or traps or that were passively encountered at remote antennas within a year prior to the tag being deposited on a bird nesting colony, but no later than August 31, the presumed end of the nesting season. For instance, all PIT-tagged suckers captured or encountered at remote antenna arrays between September 1, 2008, and August 31, 2009, were considered available to fish-eating birds during the 2009 nesting season. To minimize spurious results that can arise from small sample sizes of tagged fish (Evans et al. 2012), we limited our analyses to groups of ≥100 PIT-tagged suckers per year.

*Detection and deposition probabilities.—*To quantify detection probabilities we used the methods of Evans et al. (2012) and Osterback et al. (2013), whereby PIT tags with known tag codes were used to model detection probabilities at each nesting area (Clear Lake, Upper Klamath Lake) each year.

For nesting colonies in Clear Lake, tags (134 kHz, full-duplex, 12 mm) were intentionally sown (deposited) by researchers before (March) and after (September–October) the nesting season, and the proportion of tags subsequently recovered or detected by researchers was used to estimate detection probabilities (see also Evans et al. 2012). Due to the inaccessibility of nesting sites in Upper Klamath Lake prior to each nesting season we could not sow tags on multiple occasions. Therefore, we estimated detection probabilities for Upper Klamath Lake nesting colonies as the proportion of tags naturally deposited by birds and recovered or detected during the previous nesting season that were also recovered or detected during scanning efforts in the current nesting season (see also Osterback et al. 2013). A comparison of detection rates of researcher-sown tags versus the redetection of naturally deposited tags indicates that the detection probability of naturally deposited tags—tags that have remained on the island for a year or more—was consistently lower than that of researcher-sown tags that have remained on the island for less than a year (i.e., during the course of the nesting season only). Consequently, we used the estimated redetection probability as a lower bound for the probability of detecting tags deposited during the current year (see subsection on *Predation rate calculations* for additional details).

In other tag-based studies of avian predation (e.g., Ryan et al. 2003; Evans et al. 2012; Hostetter et al. 2015), the scanning area has been limited to habitat used by a single bird species. Predator-specific deposition probabilities can then be used to adjust or correct estimates of predation rates (Hostetter et al. 2015). For instance, in a study of double-crested cormorant predation on PIT-tagged juvenile salmonids from the Columbia River basin, Hostetter et al. (2015) estimated an average, annual cormorant PIT tag deposition probability of 0.51 (annual range, 0.43–0.58), indicating that for every 100 consumed tags, 51 were deposited on the colony where researchers could potentially detect them following the nesting season. In the present study, it was not possible to correct or adjust for PIT tag deposition probabilities because the species of predator (cormorant or pelican) was unknown. Furthermore, deposition probability estimates for American white pelicans are currently lacking in published literature and estimates for double-crested cormorants from other colonies may not apply to the colonies in the Upper Klamath Basin. As such, predation rate estimates presented herein were corrected for detection probabilities but not deposition probabilities, resulting in minimum estimates of predation.

Predation rate calculations.—We estimated predation and detection separately for birds nesting in Upper Klamath Lake and Clear Lake. We defined D_{ay} as the estimated number of fish eaten by birds from each area (a) each year (y) for $a \in$ {Clear Lake, Upper Klamath Lake} and $y \in$ {2009, 2010, 2011, 2012, 2013, 2014}. We assumed

$$D_{ay} \approx \text{binomial}\left(n_{ay}, \theta_{ay}\right),$$

where n_{ay} is the number of fish available to be eaten and θ_{ay} is the probability a fish is depredated in study area a in year y. We let ψ_{ay} represent the probability that a tag depredated and deposited in study area a in year y is detected by researchers following the nesting season. We let R_{ay} represent the number of deposited tags that were recovered. Therefore,

$$R_{ay} \approx \text{binomial}(D_{ay}, \psi_{ay}).$$

We used our direct observations of R_{ay} as well as supplemental information (addressed below) related to the detection probability ψ_{ay} in order to make inference about D_{ay} and subsequently about the rate of predation within a study area and year. We defined the predation rate on suckers by birds in study area a in year y to be

$$\text{Predation}_{ay} = D_{ay}/n_{ay}.$$

We referred to the probability of detecting a tag within the first year of its deposition on a colony as the initial deposition year detection probability. The initial deposition year detection probability of scanned area a in year y is expressed as ψ_{ay}. We referred to the probability of redetecting in year y all tags recovered or detected in the previous year as φ_{ay}. We assumed the redetection probability of tags recovered or detected in the immediately preceding year to be less than or equal to the initial year detection probability. Therefore, $\psi_{ay} \approx$ uniform (φ_{ay}, 1) for all a and y. We assumed no further information about redetection probabilities and used uninformative priors to model them. That is $\varphi_{ay} \approx$ uniform (0, 1). For years in which redetection tags were not available, $\psi_{ay} \approx$ uniform ($\max_{!z=y} \varphi_{az}$, 1). This assumption ensured our estimate did not underestimate the actual initial year detection probability (as would likely be the case with a strictly uninformative prior).

For Clear Lake, we have several years (2009, 2010, 2011, and 2013) of additional information to inform our estimates of detection probability from tags that were intentionally sown on nesting colonies on a known date. We let F_{ay} represent the number of found tags out of S_{ay} sown in study area a in year y. We therefore assumed $F_{ay} \approx$ binomial (S_{ay}, ψ_{ay}).

The predation rate model was run using the software JAGS accessed through R version 3.1.2 (RDCT 2014) using the R2jags (Su and Yajima 2012) and dclone (Sólymos 2010) R packages. We ran three parallel chains for 50,000 iterations after a burn-in of 5,000 iterations. Chains were thinned by 20 to reduce autocorrelation of successive Markov chain–Monte Carlo samples, resulting in 6,750 saved iterations. Chain convergence was tested using the Gelman–Rubin statistic (R; Gelman et al. 2014). We reported results as posterior medians along with the 2.5 and 97.5 percentiles, which are the lower and upper limits to what is referred to as the 95% credible interval (95% c.i.).

The methods used to calculate predation rates were based on six key assumptions (A1–A6). The assumptions, along with a description of the potential validity of each assumption, are provided as follows:

(A1) Tagged suckers captured or encountered on remote antennas each year were available as prey to nesting birds for the entirety of the nesting season. This assumption was needed to standardize measures of availability across nesting seasons and assumed that the mortality of a PIT-tagged fish following capture or encounter and prior to consumption by an avian predator was zero. If, however, a significant number or percentage of tagged suckers died before each nesting season, availability would be overstated and consequently would bias predation rates downward. We noted that suckers in Clear Lake were generally tagged in the fall and suckers in Upper Klamath Lake in the spring; thus, Clear Lake sucker mortality before the nesting season may be greater than that of Upper Klamath Lake sucker mortality before the nesting season. As a result, availability of Clear Lake suckers to birds more likely would be overstated and predation more likely would be biased low compared with suckers in Upper Klamath Lake.

(A2) The probability of sucker survival and the probability of tag detection given predation were independent. Lack of independence could potentially bias predation estimates to an unknown degree and overstate estimated precision.

(A3) Captured or encountered suckers were a random and representative sample of all suckers (tagged and untagged) in the population. A difference in predation susceptibility between tagged and untagged fish could bias predation rates and the interpretation of them to an unknown degree.

(A4) Detection probabilities at multiple nesting sites and islands within Clear Lake or within Upper Klamath Lake were equal across scanned sites and islands and tag types (125 kHz and 134 kHz, Upper Klamath Lake only). Considering the comparable nesting substrate within each nesting area (tule mats on islands in Upper Klamath Lake or rocky and/or sandy substrate in Clear Lake) and exposure to similar weather effects, we assumed equal detection probability within each area (i.e., multiple measures of the same variable per area, per year). If individual nesting sites or islands within the same nesting area had significantly different detection probabilities, it could bias predation estimates to an unknown degree. Due to the reduced read range of 125 kHz, 125-kHz tags were likely detected on Upper Klamath Lake colonies at a lower rate than 134-kHz tags (i.e., a lower detection probability of 125-kHz tags on bird colonies). However, only a small proportion (0.06 to 0.25, depending on the sucker species and year) of adult suckers encountered in Upper Klamath Lake were tagged with 125-kHz tags (fish tagged and released before 2005). Furthermore, small numbers of sucker PIT tags (both 125-kHz and 134-kHz tags) were deposited by birds nesting in Upper Klamath Lake relative to the number of tagged fish available (see Results). Consequently, violation of this assumption would lead to only slight underestimation of predation rates.

(A5) The redetection of tags deposited in previous years and recovered in the immediately preceding year was less than or equal to the initial deposition year detection probability. Based on data from previous published studies (Evans et al. 2012; Hostetter et al. 2015) and data collected from sown tags on colonies in Clear Lake (this study, see Results), we believe this assumption is conservative. If, counter to expectation, the redetection probability of tags is greater than the detection probability of tags deposited in the current year, this would further underestimate predation.

(A6) Deposition probabilities were assumed to be 1.0 (i.e., all sucker PIT tags consumed by birds were deposited on a nesting colony). Based on previously published research (Hostetter et al. 2015), this assumption is mostly likely false, and some proportion of ingested sucker PIT tags were egested at off-colony loafing or roosting sites or were rendered nonfunctional during passage through the gastrointestinal tract of a bird. The magnitude of this bias on predation rates in the current study is unknown, but if deposition data collected elsewhere is applicable to nesting colonies in the Upper Klamath Basin, predation rates presented herein could underestimate actual rates by a factor roughly 2.0.

Size selectivity.—To evaluate the relationship between fish size (FL) and susceptibility to avian predation, we compared the size distributions of all available fish with the size distributions of consumed suckers. To minimize the potential confounding effect of growth that may have occurred between the time a PIT-tagged sucker was measured and released and the time it was consumed by a bird, we limited comparisons to suckers consumed in the same year they were measured and released. Data on sucker growth rates indicated that Lost River Suckers in Upper Klamath Lake can grow approximately 10 mm/year, while annual growth rates of Shortnose Suckers are small or unmeasurable once they reach maturity (Hewitt et al. 2012). In Clear Lake, Lost River Suckers can grow approximately 20 mm/year and Shortnose Suckers 15 mm/year (Barry et al. 2009). Consequently, the actual length of suckers at the time of consumption may be slightly greater (right-shifted) than their size at release, but the bias is likely minimal given the low growth rates reported in the literature and because fish were consumed by a bird less than a year after release. Mann–Whitney tests were used to evaluate potential statistical differences in the length of released and depredated suckers. We plotted kernel density estimates of length as side-by-side violin plots in order to visually evaluate differences in length distributions.

RESULTS

Fish Capture, Tagging, and Release

The number of PIT-tagged suckers captured or encountered, and thus available to fish-eating birds, varied by species (Lost River Suckers, Shortnose Suckers), age-class (adult, juvenile), water body (Upper Klamath Lake, Clear Lake) and year (2009–2014; Table 1). During the study period, there were more tagged Lost River and Shortnose suckers available in Upper Klamath Lake than in Clear Lake (Table 1). In Upper Klamath Lake, an average of 24,863 PIT-tagged Lost River Suckers (range, 19,004–29,948) and 6,345 PIT-tagged Shortnose Suckers (range, 5,574–7,212) were available to avian predators during each year of the study period (Table 1). In comparison, an average of 479 PIT-tagged Lost River Suckers (range, 184–725) and 1,993 PIT-tagged Shortnose Suckers (range, 855–3,193) were available to avian predators in Clear Lake (Table 1). The average number of PIT-tagged, juvenile-sized suckers available to avian predators during each year of the study was an order of magnitude less than that of adult-sized suckers; however, adequate sample sizes of tagged juveniles (≥100 PIT-tagged fish) were available for analyses of avian predation rates only in Upper Klamath Lake during 2009, 2011, and 2012 (Table 1).

PIT Tag Recovery on Bird Colonies

The numbers of sucker tags recovered on bird breeding colonies varied by sucker species, age-class, release location, and year. A total of 446 PIT tags from suckers were recovered on bird colonies in the same study year that the fish was released or encountered in either Clear Lake or Upper Klamath Lake (Table 1). Of these, 264 were adult Shortnose Suckers, 170 were adult Lost River Suckers, and 12 were unidentifiable juvenile-sized suckers (Table 1). Tag recovery efforts were not conducted at colonies in Upper Klamath Lake in 2010 and 2011, years in which colony failure occurred (see next section on Bird Colony Sizes), so avian predation rate estimates were not available in these years for these colonies.

A total of 1,291 PIT tags from suckers were recovered from the nesting, loafing, and roosting locations used by piscivorous waterbirds during 2009–2014, regardless of when the PIT tag was placed in the sucker (see Appendix). Tag recoveries date back to fish tagged and released in 1995 and included both juvenile and adult suckers, as well as suckers originating from multiple populations, including Upper Klamath Lake, Clear Lake, and Gerber Reservoir. Recoveries of sucker PIT tags occurred primarily at nesting colonies in Clear Lake and Upper Klamath Lake. Less frequent PIT tag scanning, however, was also conducted at nesting colonies in Tule Lake NWR, California, at Sheepy Lake in Lower Klamath NWR, California, and at select avian loafing and roosting sites in the region (Table A.1). Results from these scans were not included in the main study due to the paucity of tags found (45% or 3.5% of all recovered tags), the lack of detection efficiency data at these sites, and the likelihood that some of the tags were deposited by nonnesting birds or unspecified species of avian predators (Table A.1).

Bird Colony Sizes

Based on the analysis of aerial photography, American white pelicans and double-crested cormorants attempted to nest on islands in both Clear Lake and Upper Klamath Lake during the 2009–2014 study period (Table 2). Birds typically arrived at their breeding colonies in late March to early April, and remained on the colony until mid to late August. The number of breeding birds and the exact location of islands with breeding colonies within each nesting location (Clear Lake, Upper Klamath Lake) varied considerably by year. In general, pelicans were more numerous on nesting colonies in Clear Lake, while cormorants were more numerous on nesting colonies in Upper Klamath Lake (Table 2). On Clear Lake, an average of 859 American white pelicans (range, 128–2,325) and 136 double-crested cormorants (range, 0–197) were counted on nesting colonies during each year of the study period

TABLE 1. Numbers of PIT-tagged Lost River Suckers, Shortnose Suckers, and juvenile suckers (species unknown) available and subsequently recovered (in parentheses) on mixed-species breeding colonies of American white pelicans and double-crested cormorants in Upper Klamath Lake and Clear Lake during 2009–2014. Recoveries represent the total number of suckers consumed from all colonies combined. Tag recoveries only include those tags that were recovered on colonies in the same year the fish was determined to be available to avian predators (see Methods). Dashes (–) denote that fewer than 100 PIT-tagged suckers were available.

Release site	Species	2009	2010	2011	2012	2013	2014
Clear Lake	Lost River Sucker	184 (4)	301 (0)	471 (0)	514 (4)	725 (18)	677 (3)
	Shortnose Sucker	855 (12)	2,399 (4)	3,193 (47)	1,151 (6)	2,044 (48)	2,344 (17)
	Juvenile	–	–	–	–	–	–
Upper Klamath Lake	Lost River Sucker	19,004 (30)	21,391 (1)[a]	23,544 (2)[a]	26,430 (74)	28,863 (17)	29,948 (17)
	Shortnose Sucker	5,574 (24)	7,212 (0)[a]	5,970 (0)[a]	6,685 (76)	6,258 (11)	6,376 (19)
	Juvenile	179 (6)	–	167 (0)[a]	217 (6)	–	–

[a]Tag recovery was conducted at nesting colonies in Clear Lake only.

TABLE 2. Counts of American white pelicans and double-crested cormorants by nesting location (Clear Lake and Upper Klamath Lake) and year. Counts represent the number of adult birds determined from aerial photography. Asterisks (*) denote colony failure, whereby birds attempted to nest but abandoned the site at some point during the nesting season (March–August).

Bird species	2009	2010	2011	2012	2013	2014
Clear Lake[a]						
American white pelicans	2,325	722*	128*	510	1,175	296
Double-crested cormorants	172	0*	77*	286	82	197
Total	2,497	722	205	796	1,257	493
Upper Klamath Lake[b]						
American white pelicans	438	81*	14*	255	152*	247
Double-crested cormorants	1,538	293*	373	885	1,071	1,133
Total	1,976	374	387	1,140	1,223	1,380

[a]Nesting by pelicans and cormorants occurred on up to three different islands (see Figure 1).

[b] Nesting by pelicans and cormorants occurred on up to five different islands (see Figure 1).

(Table 2). On Upper Klamath Lake, an average of 198 American white pelicans (range, 14–438) and 882 double-crested cormorants (range, 293–1,538) were counted on nesting colonies during each year of the study period (Table 2). In 2010 and 2011, extensive breeding failure occurred at many of the nesting colonies in Clear Lake and Upper Klamath Lake (Table 2), whereby birds abandoned their colonies at some point during the nesting season. Colony counts in those two years may not accurately represent the total number of birds that attempted to nest because the colony may have failed or started to fail prior to the first aerial survey.

Depending on the year, Caspian terns, Forster's terns *Sterna forsteri*, great blue herons *Ardea herodias*, black-crowned night herons *Nycticorax nycticorax*, great egrets *A. alba*, California gulls *Larus californicus*, and ring-billed gulls *L. delawarensis* were also visible in aerial photography taken of nesting islands in Clear Lake. For terns and herons, the numbers were small (<20 adults per nesting season). Nesting gulls, however, were more numerous, and some gulls nested amongst nesting pelicans and cormorants, especially at the periphery of the colony, on islands in Clear Lake. There was also evidence that herons were nesting on islands in Upper Klamath Lake, but similar to Clear Lake, the number of herons visible in aerial photography was small (<20 adults per nesting season).

Detection Probabilities

Estimated detection probabilities varied by nesting area (Clear Lake, Upper Klamath Lake) and year, but were generally high (Table 3). Estimates were higher for colonies in Clear Lake (average = 0.76) than for those in Upper Klamath Lake (average = 0.60; Table 3), likely due to differences in nesting substrate (tule mat islands versus rocky–sandy islands). Results confirmed that the detection probabilities of tags intentionally sown and subsequently detected by researchers during the same year were higher than those of tags naturally deposited and redetected the following year. For nesting areas and years in which only redetection rates were available (i.e., those in Upper Klamath Lake), detection probabilities were less precise, as indicated by wider credible intervals (Table 3).

Predation Rates

Results indicated that, relative to their availability, estimated avian predation rates on suckers were highest in Clear Lake by birds nesting at Clear Lake; minimum annual predation rates were as high as 4.6% (95% c.i. = 3.3–6.3%) for Lost River Suckers and as high as 4.2% (95% c.i. = 3.5–5.3%) for Shortnose Suckers (Table 4). Estimated minimum avian predation rates on suckers in Upper Klamath Lake by birds nesting at Upper Klamath Lake were lower than at Clear Lake, and annual estimates were 0.6% (95% c.i. = 0.2–1.0%) for Lost River Suckers and 1.8% (95% c.i. = 1.1–4.1%) for Shortnose Suckers (Table 4). Of the small numbers of juvenile suckers from Upper Klamath Lake that were tagged, 5.7% (95% c.i. = 3.4–10.2%) and 8.4% (95% c.i. = 3.7–22.0%) were consumed by avian predators nesting at Upper Klamath Lake during the 2009 and 2012 nesting seasons, respectively (Table 4). Comparisons of avian predation rates between Lost River Suckers and Shortnose Suckers consumed in the same year indicated that predation rates were generally higher on Shortnose Suckers, and statistically significant differences were observed at Clear Lake in 2011 and at Upper Klamath Lake in 2012 (Table 4).

Results confirmed that pelicans and/or cormorants nesting at Clear Lake commuted to Upper Klamath Lake to forage on suckers, as a small percentage of the PIT tags recovered from Lost River and Shortnose suckers at Clear Lake bird colonies were from fish tagged in Upper Klamath Lake. Interestingly, although fewer than 50 PIT tags from adult Lost River Suckers from the shoreline spawning subpopulation in Upper Klamath Lake were encountered on bird colonies, these fish were more often consumed by birds nesting in Clear Lake than by birds nesting in Upper Klamath Lake. Predation was higher on adult Lost River Suckers from the river spawning subpopulation in Upper Klamath Lake, and these fish were more often consumed by birds nesting in Upper Klamath Lake. There was no evidence that birds nesting at Upper Klamath Lake commuted to Clear Lake to forage on PIT-tagged suckers, as no tags from suckers released in Clear Lake were recovered on bird colonies at Upper Klamath Lake during the study period.

TABLE 3. Estimated detection probabilities (95% c.i.) of PIT tags on bird breeding colonies in Clear Lake and Upper Klamath Lake during 2009–2014. Values were used to adjust predation rate estimates for the proportion of sucker PIT tags deposited by birds on their nesting colonies that were subsequently lost, damaged, or otherwise not detected by researchers following each nesting season. The total number of known tag codes (*n*), i.e., those sown by researchers (Clear Lake only) or naturally deposited by birds (Upper Klamath Lake only), used to model detection probabilities are also provided. Dashes (–) denote that PIT tag scanning did not occur that year.

Location	2009	2010	2011	2012	2013	2014
Clear Lake	0.79 (0.74–0.84) n = 100	0.82 (0.74–0.89) n = 485	0.74 (0.55–0.89) n = 312	0.84 (0.70–0.99) n = 139	0.51 (0.46–0.58) n = 779	0.84 (0.75–0.99) n = 447
Upper Klamath Lake	0.68[a] (0.57–0.88)	–	–	0.44 (0.22–0.71) n = 27	0.70 (0.56–0.93) n = 99	0.59 (0.48–0.76) n = 104

[a]The detection probability estimate was inferred from empirical data collected at nesting sites in Upper Klamath Lake during 2012–2014.

Data regarding the relationships between colony sizes and predation rates on tagged suckers were too few for statistical analyses, with a time series of just 6 years and predation rates not available for both fish species and age-classes in all years. Nevertheless, there was some evidence that predation rates were higher in years when colony sizes were greater (2009 and 2013; Table 2) and lower in years when colony sizes were smaller and colony failure was observed (2010 and 2011; Table 2).

Size Selectivity

Tagged suckers ranging in FL from 72 to 694 mm were consumed by American white pelicans or double-crested cormorants nesting at mixed-species colonies in the same year they were measured and released. The largest sucker consumed was a female Lost River Sucker from Upper Klamath Lake that was measured at 730 mm two and a half years before its tag was detected on a colony in Upper Klamath Lake. Comparisons of the length distributions of available versus depredated suckers and Mann–Whitney tests (W) indicated that depredated suckers tended to be smaller relative to all tagged suckers available to avian predators. For Lost River Suckers tagged in Upper Klamath Lake, depredated suckers (n = 50) had a median FL of 616 mm, whereas available suckers (n = 35,276) had a median FL of 660 mm (W = 1,227,607; P < 0.01; Figure 2). For Shortnose Suckers tagged in Clear Lake, depredated suckers had a median FL of 360 mm (n = 132), whereas available suckers had a median FL of 380 mm (n = 9,217) (W = 804,103; P = 0.01; Figure 2). There was no evidence of size selectivity for Shortnose Suckers tagged in Upper Klamath Lake (n_1 = 60, n_2 = 12,050; W = 383,739; P

TABLE 4. Estimated predation rates (with 95% c.i.) on Lost River Suckers (LRS), Shortnose Suckers (SNS), and juvenile suckers (species unknown) by American white pelicans and double-crested cormorants nesting in mixed-species colonies at Clear Lake and Upper Klamath Lake during 2009–2014. Predation estimates are adjusted to account for on-colony PIT tag detection probabilities but not for on-colony deposition probabilities (see Methods), and are thus minimum estimates of predation on tagged suckers. Dashes (–) denote that sample sizes of available PIT-tagged fish were fewer than 100 or that PIT tag recovery did not occur that year.

Species	2009	2010	2011	2012	2013	2014
Predation on Clear Lake suckers by bird colonies in Clear Lake						
LRS	2.7% (2.2–4.3)	<0.1%	<0.1%	1.0% (0.8–1.8)	4.6% (3.3–6.3)	0.6% (0.4–1.0)
SNS	1.8% (1.4–2.3)	0.2% (0.2–0.4)	2.1% (1.6–3.0)	0.6% (0.5–1.0)	4.2% (3.5–5.3)	0.9% (0.7–1.2)
Juvenile	–	–	–	–	–	–
Predation on Upper Klamath Lake suckers by bird colonies in Upper Klamath Lake						
LRS	0.1% (0–0.2)	–	–	0.6% (0.2–1.0)	<0.1%	0.2% (0.1–0.3)
SNS	0.3% (0.2–0.5)	–	–	1.8% (1.1–4.1)	<0.1%	0.5% (0.4–0.8)
Juvenile	5.7% (3.4–10.2)	–	–	8.4% (3.7–22.0)	–	–
Predation on Upper Klamath Lake suckers by bird colonies in Clear Lake						
LRS	0.1% (0.1–0.2)	<0.1%	<0.1%	<0.1%	<0.1%	<0.1%
SNS	0.3% (0.2–0.4)	<0.1%	<0.1%	0.4% (0.3–0.5)	0.4% (0.2–0.6)	<0.1%
Juvenile	<0.1%	–	<0.1%	<0.1%	–	–

= 0.41; Figure 2). The sample size of depredated juvenile suckers in Upper Klamath Lake (n = 12) was too small for statistical comparison, but it is worth noting that all but 2 of the 12 depredated juvenile suckers were less than 150 mm. Similarly, the sample size of adult Lost River Suckers in Clear Lake (n = 17) was too small for statistical comparison, but a visual examination of the data suggested that larger Lost River Suckers in Clear Lake were less likely to be consumed than their smaller counterparts.

DISCUSSION

This study is the first to estimate predation impacts by nesting piscivorous waterbirds on ESA-listed Lost River Suckers and Shortnose Suckers. Our results indicate that the effects of predation varied by sucker species, sucker size, sucker age-class, bird colony location, and year, demonstrating that predator–prey interactions were dynamic. Estimates of predation rates indicated that, relative to their availability, Shortnose Suckers were often more susceptible to predation by American white pelicans and double-crested cormorants than were Lost River Suckers, although this was not the case for all bird colonies in all years. Of the two nesting areas evaluated, predation rates were consistently higher for pelicans and cormorants nesting at Clear Lake compared with birds nesting in Upper Klamath Lake. Furthermore, pelicans and cormorants nesting at Clear Lake foraged on suckers in both Clear Lake and Upper Klamath Lake. Results from this study also provide evidence that juvenile-sized suckers were more susceptible to avian predation than adult-sized suckers, in cases where adequate sample sizes of both age-classes existed.

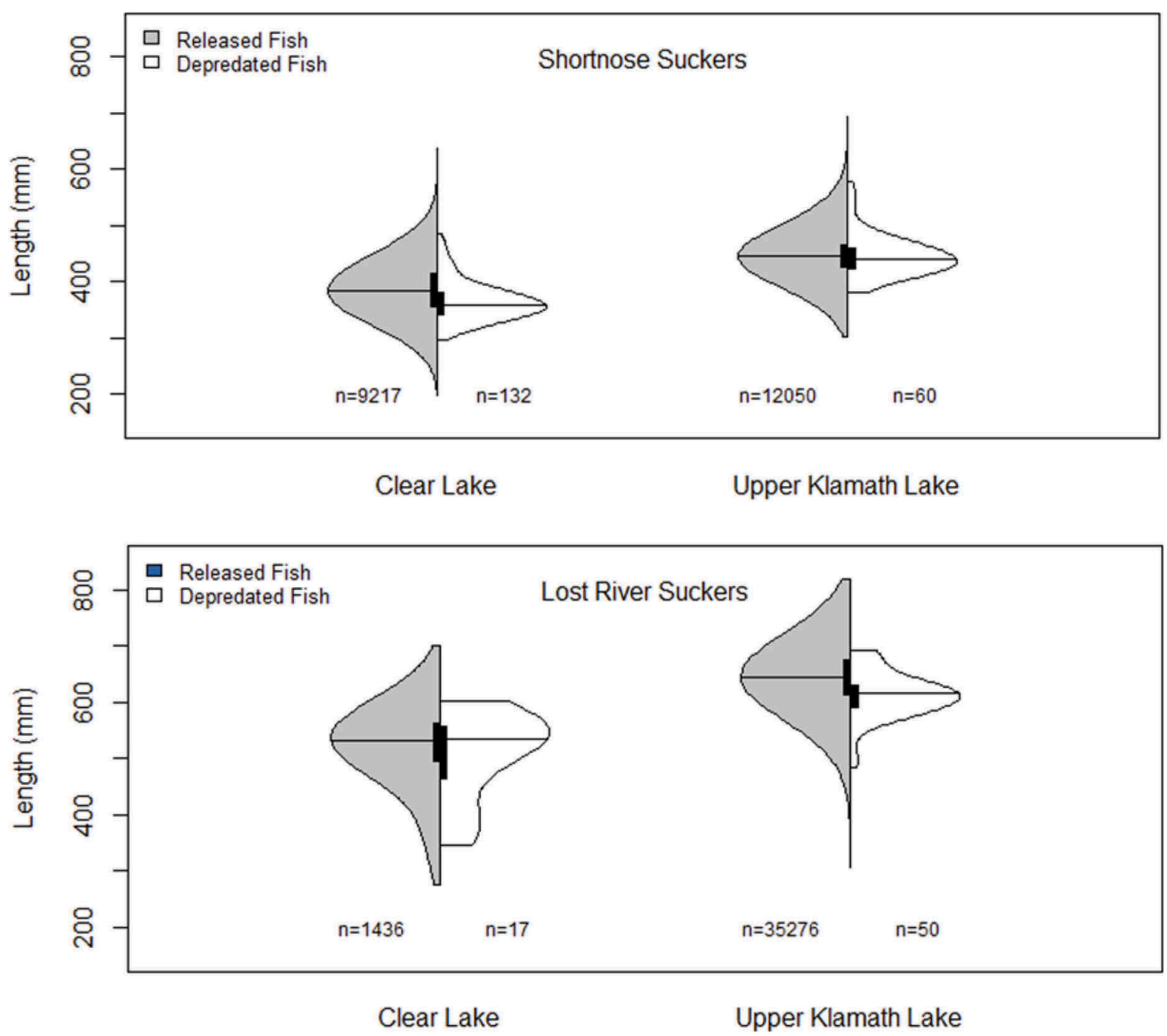

FIGURE 2. Length distributions of Lost River Suckers and Shortnose Suckers measured and released and subsequently consumed by American white pelicans or double-crested cormorants nesting at Clear Lake and Upper Klamath Lake during 2009–2014. Boxes represent interquartile ranges (first to third quartiles). Horizontal lines represent median length.

Avian predation has been identified as a factor regulating fish survival in other parts of the Pacific Northwest (Evans et al. 2012; Osterback et al. 2013; Teuscher et al. 2015), and bird predation has been identified as a limiting factor in the recovery of several ESA-listed salmonid species (USFWS 2005, 2014; USACE 2014). Results of our study indicate that predation by American white pelicans and double-crested cormorants may be a factor limiting recovery of ESA-listed suckers through predation on adult suckers in Clear Lake and juvenile suckers in Upper Klamath Lake. Survival of adult suckers in Upper Klamath Lake, however, does not appear to be limited significantly by avian predation, as estimated avian predation rates were low (<2% of available adults), albeit these estimates represent minimum predation impacts. On average, less than 10% of adult Lost River Suckers and less than 20% of adult Shortnose Suckers in Upper Klamath Lake die annually from all causes combined (Hewitt et al. 2015). Such mortality rates are in line with typical expectations based on the life span of the species. Survival of age-0 and age-1 suckers may be the main impediment to recruitment of new fish into the spawning populations, so further investigation of avian predation on juvenile suckers in Upper Klamath Lake and Clear Lake seems warranted.

In Clear Lake, minimum estimates of predation rates from this study indicate that avian predation may be a significant source of mortality for adult Lost River and Shortnose suckers. Although survival estimates are not yet available for suckers in Clear Lake (Hewitt and Hayes 2013), both species presumably have the potential for survival rates similar to the populations in Upper Klamath Lake. Annual mortality due to avian predation could be 5–10% or more if minimum predation rates are corrected for deposition probabilities and if all avian predators are considered, not just breeding pelicans and cormorants. If mortality due to avian predation is that high, other sources of mortality would have to be small for adult suckers to be surviving at rates similar to those of adult suckers in Upper Klamath Lake. Furthermore, mortality due to avian predation is cumulative over time for age-classes of suckers, and new age-classes are not produced in Clear Lake during drought conditions when access to the spawning area in Willow Creek is limited or entirely inaccessible to adult suckers (Burdick and Rasmussen 2013). Predation on Lost River Suckers in Clear Lake is of particular concern because that spawning population appears to be the smallest spawning population of either species in the Upper Klamath Basin, and few Lost River Suckers in Clear Lake grow large enough to have a size refuge from predation (Hewitt and Hayes 2013).

Results from other studies of avian predation on fish species of conservation concern have linked variation in predation rates to numerous factors, including the availability of alternative prey (Lyons et al. 2014), colony size (Hostetter et al. 2012), and environmental conditions that can affect a predator's ability to capture prey (e.g., turbidity and water levels: Hostetter et al. 2012). Studies also indicate that the intrinsic characteristics of individual fish, such as size and condition (disease, injury, and stress levels), are related to susceptibility to avian predation (Kennedy et al. 2007; Hostetter et al. 2012). In the present study, tagged suckers ranging in size from 72 to 730 mm were consumed. Results provide evidence of some size selectivity across sucker species and age-classes, whereby predation rates were highest on juvenile-sized suckers, followed by Shortnose Suckers, and lastly, the largest species, Lost River Suckers. These findings may be related to the foraging abilities of cormorants and pelicans, whereby smaller-sized suckers were more susceptible to bird predation than larger-sized suckers, particularly the largest Lost River Suckers, such as those from the shoreline spawning subpopulation (up to 800 mm FL: Hewitt et al. 2015). The largest fish a double-crested cormorant can consume depends on the mass and shape of the fish, but is generally considered not to exceed about 450 mm FL (Hatch and Weseloh 1999). Scoppettone et al. (2006) confirmed fish as large as 700 mm in the diet of American white pelicans, while a fish as large as 730 mm was confirmed in the present study. Teuscher et al. (2015) found that American white pelicans nesting at Blackfoot Reservoir, Idaho, were not size selective for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* up to a maximum size of about 600 mm TL, which is not inconsistent with our results for Lost River Suckers. In a study of Caspian tern predation, Hostetter et al. (2012) observed that smaller-sized trout (those less than 250 mm) were more susceptible to tern predation than were larger-sized trout, providing evidence of size selectivity in cases where the distribution of fish lengths in a given species exceeds the maximum size a predator can consume.

Several data gaps were identified in the present study, gaps that if addressed, could result in more accurate measures of avian predation rates on ESA-listed suckers. Specifically, further research is needed to (1) document predator-specific (cormorant, pelican, or other avian predators) impacts, (2) quantify predator-specific PIT tag deposition probabilities, (3) increase the sample size of PIT-tagged juvenile suckers, and (4) investigate the relationship between biotic and abiotic factors on sucker susceptibility to bird predation. In the present study, estimates of colony size were limited to photography taken during just two or three aerial surveys, and because several of the piscivorous waterbird species that nest in the region nested in close proximity to one another, it was not possible to determine which avian predator (double-crested cormorant or American white pelican) was responsible for the deposition of individual PIT tags. More intensive colony surveys (aerial, boat, and land based) coupled with georeferenced tag recoveries may make it possible to associate a tag with a particular species of avian predator.

Studies to quantify predator-specific PIT tag deposition probabilities can be used to generate more accurate estimates of predation rates, those corrected for both detection and deposition probabilities (Hostetter et al. 2015). For instance, by feeding PIT-tagged juvenile salmonids to double-crested cormorants nesting in the Columbia River basin, Hostetter et al. (2015) estimated an average PIT tag deposition rate of 0.51 (annual range, 0.43–0.58), meaning that predation rates corrected for cormorant deposition probabilities were approximately 2.0 times greater than those not corrected for deposition probabilities. Using a similar feeding approach with PIT-tagged trout consumed by American white pelicans nesting in the Blackfoot River basin, Teuscher et al. (2015) estimated a combined detection and deposition probability (a single parameter estimate for both sources of tag nondetection) of 0.30 (annual range, 0.12–0.48). In our study of Upper Klamath Basin nesting colonies, detection probabilities used to correct predation rates on PIT-tagged suckers ranged annually from 0.44–0.84, estimates that are consistently higher than the combined detection and deposition parameter estimates reported by Teuscher et al. (2015). This suggests that some fraction of tag nondetection on pelican colonies is caused by off-colony deposition of tags. Additional research is needed to calculate pelican-specific deposition probabilities, but deposition studies conducted to date in other colonial waterbird species provide strong evidence that a significant proportion of consumed PIT tags are deposited off-colony or are rendered nonfunctional during gastrointestinal digestion by birds (Hostetter et al. 2015).

If deposition data from other predators and colonies are applicable to the mixed nesting colonies in the Upper Klamath Basin, predation rate estimates presented herein would increase by a factor of roughly 2.0. For example, losses of tagged juvenile suckers in Upper Klamath Lake would increase from 6–8% of available fish to approximately 12–16% of available fish if corrected for PIT tag deposition probabilities. Even with an adjustment for deposition probabilities, however, estimated predation rates based on the number of tags recovered from pelican and cormorant colonies in the Upper Klamath Basin would likely still underestimate total avian predation impacts because (1) pelicans and cormorants can remain in the Upper Klamath Basin for several months after the nesting season has ended, (2) immature (nonnesting) or failed (unsuccessful) nesting birds presumably reside and forage on suckers in the region, and (3) other piscivorous waterbirds (e.g., Caspian terns, California and ring-billed gulls, common mergansers *Mergus merganser*, large grebes *Aechmophorus* spp., ospreys *Pandion haliaetus*, and others) may be consuming suckers, albeit impacts to adult-sized suckers from these species are likely small or nonexistent.

In Upper Klamath Lake, a lack of juvenile recruitment is considered a limiting factor in the recovery of both ESA-listed sucker species (Hewitt et al. 2015), and bird predation on juveniles may be a contributing factor to this. Additional research is needed to determine whether the larger proportion of consumed juvenile suckers observed in the present study was related to differences in susceptibility based on the size of the fish, the behavior or spatial distribution of the fish, or is simply an artifact of the small sample sizes of PIT-tagged juveniles. Limited PIT tag data from juvenile sucker tags detected on Clear Lake bird colonies supports the hypothesis that avian predation rates on juvenile suckers may be higher than those on adults. Of the 42 juvenile suckers tagged and released in Clear Lake during July–September 2012, four (9.5%; not corrected for detection probability) were subsequently detected on bird colonies at Clear Lake during fall scanning efforts (Burdick 2013) compared with a predation rate of ≤1.0% for adult suckers at that location during that same year.

Finally, more research is needed to determine whether specific environmental conditions, such as poor water quality, loss of deep water refugia, limited access to spawning tributaries, and/or poor fish condition, are associated with sucker susceptibility to bird predation in the Upper Klamath Basin. Banish et al. (2009) observed poor water quality (low dissolved oxygen, high pH, and outbreaks of the cyanobacterium, *Aphanizomenon flos-aquae*) and habitat conditions in parts of Upper Klamath Lake, which caused suckers to congregate in large numbers in areas where they might have been more susceptible to bird predation. Hewitt and Hayes (2013) noted that spawning runs into Willow Creek, the lone spawning tributary for Shortnose Suckers and Lost River Suckers in Clear Lake, were limited when flows were low in the creek as a result of drought conditions. If suckers on spawning runs are concentrated in the east lobe of the reservoir or at the mouth of the creek when the reservoir water level is also low, as tends to occur during drought conditions, suckers could be more susceptible to avian predation at that location. Hostetter et al. (2012) demonstrated that diseased or injured fish were more susceptible to predation by double-crested cormorants than were apparently healthy fish. If the condition of suckers is compromised during summer, when water quality is poor, or if adult suckers are injured or weaker following spawning, these fish may be more vulnerable to bird predation. Similarly, some fraction of inferred avian predation may actually represent consumption of dead or moribund fish, which would indicate that some fraction of avian predation on suckers is compensatory. Data to address these data gaps and uncertainties would help resource managers better understand the impacts of predation by piscivorous waterbirds on the survival of ESA-listed sucker populations in the Upper Klamath Basin and, using this information, design and implement management initiatives to reduce these impacts, if warranted.

ACKNOWLEDGMENTS

This project was funded by the Bureau of Reclamation (BOR), with support from the U.S. Fish and Wildlife Service (USFWS) and the Klamath Sucker Recovery Implementation Team. We especially thank Kristen Hiatt (BOR) and Josh Rasmussen (USFWS) for their assistance and support. We thank John Beckstrand (USFWS) for his assistance in sowing PIT tags to measure detection efficiency at the Clear Lake NWR colonies and for granting us access and providing transportation to islands in Upper Klamath NWR following the nesting seasons. We thank Tim Lawes of Oregon State University and Aaron Turecek of Real Time Research, Inc., for providing assistance with aerial imagery and colony counts. We thank Alta Harris, Amari Dolan-Caret, and Summer Burdick (U.S. Geological Survey, Klamath Falls Field Station) for invaluable assistance regarding the availability of PIT-tagged suckers. We thank Paul Schmidt of the U.S. Army Corps of Engineers for assistance and support on a related but an independent study of Caspian terns in the region. Finally, this work would not have been possible without the hard work and dedication of numerous field researchers, for which we are grateful. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Appendix: Recoveries of Sucker PIT Tags on Avian Nesting, Loafing, and Roosting Locations in the Upper Klamath Basin

TABLE A.1. Numbers of PIT-tagged Lost River Suckers (LRS), Shortnose Suckers (SNS), and juvenile suckers (Juv.; <300 mm at last capture) recovered on avian nesting and loafing–roosting locations in the Upper Klamath Basin during 2009–2014. Tag recoveries include all sucker PIT tags recovered regardless of the year the sucker was released, the location it was released, or the year the tag was deposited on an avian nesting or loafing–roosting location. Nesting locations represent mixed-species colonies. Not all nesting locations were used as breeding islands in all years. Dashes (–) denote that scanning for PIT tags did not take place that year; totals for all years at each site are indicated in bold font. Data from the artificial islands on Tule Lake and Sheepy Lake (see Figure 1) were as reported by Bird Research Northwest (2015).

	2009			2010			2011			2012			2013			2014			Total		
Location	LRS	SNS	Juv.	LRS	SNS	Juv.	LRS	SNS	Juv.	LRS	SNS	Juv.	LRS	SNS	Juv.	LRS	SNS	Juv.	LRS	SNS	Juv.
Nesting																					
Clear Lake:																					
Site 1 (east lobe)	45	158	8	17	34	4	3	68	0	43	117	4	44	122	1	22	58	8	**174**	**557**	**26**
Site 2 (east lobe)	–	–	–	–	–	–	1	3	0	1	11	0	1	23	0	0	12	0	**3**	**49**	**0**
Site 3 (west lobe)	–	–	–	1	15	1	–	–	–	0	23	1	1	16	1	7	37	1	**9**	**91**	**4**
Upper Klamath Lake:																					
Tule site 1	3	5	3	–	–	–	–	–	–	7	9	2	1	0	0	2	0	0	**13**	**14**	**5**
Tule site 2	16	16	10	1	0	1	–	–	–	3	4	5	2	0	1	1	0	1	**23**	**20**	**18**
Tule site 3	11	7	3	–	–	–	–	–	–	–	–	–	5	0	0	2	2	0	**18**	**9**	**3**
Tule site 4	8	11	7	0	0	2	–	–	–	5	4	1	5	1	1	4	3	1	**22**	**19**	**12**
Tule site 5	–	–	–	–	–	–	–	–	–	57	53	7	–	–	–	20	20	0	**77**	**73**	**7**
Sheepy Lake:																					
Unnamed island	1	3	0		–	–	–	–	–	3	2	0	–	–	–	–	–	–	**4**	**5**	**0**
Man-made island	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	–	–	–	**0**	**0**	**1**
Tule Lake:																					
Unnamed island	–	–	–	0	0	0	–	–	–	–	–	–	–	–	–	1	1	1	**1**	**1**	**1**
Man-made island	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**	**0**
Loafing–roosting																					
Clear Lake:																					
Unnamed island	–	–	–	0	4	0	–	–	–	0	1	4	0	5	0	–	–	–	**0**	**10**	**4**
Shoreline	–	–	–	–	–	–	–	–	–	–	–	–	0	1	0	0	2	0	**0**	**3**	**0**
Upper Klamath Lake:																					
Shoreline	–	–	–	0	0	1	–	–	–	0	2	2	–	–	–	–	–	–	**0**	**2**	**3**
Williamson River	–	–	–	0	0	3	–	–	–	4	3	0	–	–	–	–	–	–	**4**	**3**	**3**