Colonial Waterbird Predation on Lost River and Shortnose Suckers Based on Recoveries of Passive Integrated Transponder Tags

Final Technical Report

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ABSTRACT

We evaluated predation on Lost River suckers (*Deltistes luxatus*) and shortnose suckers (*Chasmistes brevirostris*), both listed under the Endangered Species Act (ESA), from American white pelicans (*Pelecanus erythrorhynchos*) and double-crested cormorants (*Phalacrocorax auritus*) nesting at mixed-species colonies on Clear Lake Reservoir, CA and Upper Klamath Lake, OR during 2009-2014. Predation was evaluated by recovering (detecting) passive integrated transponder (PIT) tags that were implanted in suckers, consumed by pelicans or cormorants, and subsequently deposited on the birds’ nesting colony. Data from PIT tag recoveries were used to estimate predation rates (proportion of available tagged suckers consumed by birds) and to evaluate the relative susceptibility of suckers to avian predation in the Upper Klamath Basin. Data on the size of pelican and cormorant colonies (number of breeding adults) were also collected and reported in the context of sucker predation rates.

Results indicate that predation rates varied by sucker species (Lost River, shortnose), sucker age-class (adult, juvenile), bird colony location (Upper Klamath Lake, Clear Lake), and year (2009-2014), demonstrating that predator-prey interactions were dynamic in the system. Tagged suckers ranging from 72 mm to 730 mm were susceptible to cormorant or pelican predation; all but the largest of the tagged Lost River suckers were susceptible to avian predation. Estimates of minimum, annual predation rates ranged from < 0.1% to 4.6% of the available Lost River suckers and from < 0.1% to 4.2% of the available shortnose suckers during the study period. Of the two colony locations evaluated, predation rates on suckers in Clear Lake were generally higher by birds nesting at mixed-species colonies on Clear Lake. Birds nesting on Clear Lake also commuted over 75 kilometers to forage on suckers in Upper Klamath Lake. Conversely, there was no evidence that birds nesting in Upper Klamath Lake foraged on tagged suckers in Clear Lake. Although sample sizes of tagged juvenile suckers were small and limited to fish tagged in Upper Klamath Lake, there was evidence that bird predation on juvenile suckers was higher than on adult suckers, with minimum predation rate estimates on juvenile suckers ranging from 5.7% to 8.4% of available fish per year.

Minimum predation rates presented here suggest that avian predation may be a factor limiting recovery of populations of Lost River and shortnose suckers, particularly juvenile suckers in Upper Klamath Lake and adult suckers in Clear Lake. Additional research is needed, however, to better assess the impacts of avian predation on sucker populations in the Upper Klamath Basin by (1) recovering PIT tags in a manner so that the species of avian predator is known (i.e., pelican vs. cormorant), (2) measuring predator-specific PIT tag deposition probabilities to generate more accurate (instead of minimum) predation rate estimates, (3) increasing the sample of juvenile suckers in the population that are PIT-tagged, and (4) recovering sufficient sample sizes of PIT tags on bird colonies to describe how various biotic and abiotic factors (e.g., fish condition, water levels and quality, and other factors) contribute to sucker susceptibility to avian predation.

INTRODUCTION

Piscivorous colonial waterbirds are an integral part of the Upper Klamath Basin ecosystem, with 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 *Hydroprogne caspia*]) present in the region. Two species of suckers, 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 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. 2014). 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 to the past. Consequently, avian predation may be a significant limiting factor for populations of ESA-listed suckers, even if avian predation was not an initial cause of sucker declines (USFWS 2012).

Samples of Lost River and shortnose suckers are tagged each year with passive integrated transponder (PIT) tags to gather information on their behavior and survival following release (Janney et al. 2008; Hewitt and Hayes 2013; Hewitt et al. 2014; Burdick et al. 2015). PIT tags allow specific information to be attached to individual fish, including 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 parameters of interest (see Hewitt et al. 2014). 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 fish 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 avian predation (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005). PIT tag recoveries have also been used to identify which individual bird colonies pose the greatest threat to fish survival and to estimate avian predation rates (proportion of tagged fish consumed; Evans et al. 2012; Freschetta 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 number of shortnose and Lost River 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, shortnose), spawning population (Clear Lake, Upper Klamath Lake), age-class (juvenile, adult) and length, 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 suckers by American white pelicans and double-crested cormorants breeding on islands located in Upper Klamath Lake, OR and in Clear Lake Reservoir, CA during 2009-2014 (Figure 1). A total of eight islands or nesting colonies were scanned for sucker PIT tags 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 per nesting colony) and consisted largely of mats of bulrush or common tule (Schoenoplectus acutus). Islands in Clear Lake NWR were larger (0.4 to 9.0 acres per nesting site; depending on the island and
reservoir water levels) and consisted of rocky or sandy substrate. 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 (see Fish Capture, Tagging, and Release).

![Map showing the location of piscivorous waterbird nesting colonies (red dots) scanned for PIT tags implanted in Lost River suckers and shortnose suckers released into Upper Klamath Lake, OR and Clear Lake Reservoir, CA during 2009-2014.](image)

**Figure 1**: Map showing the location of piscivorous waterbird nesting colonies (red dots) scanned for PIT tags implanted in Lost River suckers and shortnose suckers released into Upper Klamath Lake, OR and Clear Lake Reservoir, CA during 2009-2014.

**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 Janney et al. 2008; Hewitt et al. 2010; Hewitt and Hayes 2013; Hewitt et al. 2014 for detailed descriptions).
Adult Lost River and shortnose suckers in Upper Klamath Lake were captured for tagging prior to 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 Clear 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 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.

Adult suckers were identified to species and sex (see Markle et al. 2005), measured (fork-length; nearest mm), 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 non-destructively (Markle et al. 2005; Burdick 2013), large enough for PIT-tagging (> 72 mm) 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 fork-length has been reported to be less than 10% (Burdick 2011).

In addition to physical capture and recaptures, passive encounters of PIT-tagged suckers using remote underwater antennas were also used to provide information about sucker availability. Remote antenna systems were used at spawning areas in Upper Klamath Lake beginning in 2005 (see Hewitt et al. [2014] for a full description of these systems). At Clear Lake, remote antennas were used in Willow Creek, the only spawning tributary for Clear Lake, beginning in 2006 (Hewitt and Hayes 2013). In addition, an array of PIT tag antennas was installed across the channel in the shallow strait between the two lobes of Clear Lake in 2014. In contrast to Upper Klamath Lake, PIT tag antenna systems at Clear Lake can only detect 134 kHz tags.

**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 (Destron Fearing FS2001, Biomark HPR). PIT tags were detected by scanning the entire area occupied by birds during the nesting season, with at least two passes or complete sweeps of the nesting site conducted each year. The area occupied by birds was determined based on aerial photographs taken of the colony during the nesting season (see Bird Colony Sizes for details).
**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, with two to three aerial surveys 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-colony (Gaston and Smith 1984). In cases where birds at a given nesting site failed (i.e., abandoned the site) prior to late incubation, photographs taken of the colony earlier in the nesting season, if available, were used to estimate colony size. Photographs were taken with a high-resolution digital SLR camera from a fixed-wing aircraft. Aerial photography also provided limited data on nesting success (presence/absence of young) at each nesting site.

**Statistical Analysis.**—Impacts of piscivorous colonial waterbirds on sucker survival were evaluated using a hierarchical Bayesian model to estimate avian predation rates (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, shortnose), age-class (adult, juvenile), spawning population (Clear Lake suckers, Upper Klamath Lake suckers), and year (2009-2014).

Accurate predation rate estimates based on PIT tag recoveries from bird colonies generally incorporate three parameter estimates as probabilities: (1) the probability that an available PIT-tagged fish was consumed by a bird, (2) the probability that a consumed PIT tag was subsequently deposited on the bird’s nesting colony, and (3) the probability that the deposited PIT tag was detected on-colony by researchers following the nesting season (see Hostetter et al. 2015). The latter two probabilities relate to the fact that not all PIT tags ingested by birds are subsequently deposited on their nesting colony and that not all deposited PIT tags are subsequently found by researchers after the nesting season. For example, PIT tags can be regurgitated or defecated at loafing, staging, or roosting sites utilized by birds during the nesting season, resulting in deposition probabilities < 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 non-functional) during the course of the nesting season, or missed (i.e., not detected) during the scanning process, resulting in detection probabilities < 1.0 (Evans et al. 2012).

**Fish Availability.**—The number of tagged suckers determined to be available to fish-eating birds nesting at Upper Klamath Lake and Clear Lake consisted of all fish physically captured/recaptured or passively encountered at remote antennas within a year prior to the tag being deposited on a bird colony, but no later than August 31, the presumed end of the nesting season. For instance, all PIT-tagged suckers captured/recaptured or encountered at remote antenna arrays between 1 September 2008 and 31 August 2009 were considered available to birds during the 2009 nesting season. Although there were more tagged fish presumed alive (inferred from encounters in subsequent years), these were censored from the analysis to avoid fish which were known to have survived being over-represented in availability and subsequently underestimating predation rates. To minimize spurious results that can arise from small sample sizes of tagged fish (see 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 a modified version of 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 colony and year. For nesting colonies in Clear Lake, tags (134 kHz full-duplex 12-mm) were intentionally sown (deposited) by researchers prior
(March) and after (September-October) the nesting season, and the proportions of those tags that were subsequently recovered were used to estimate detection probabilities (see Evans et al. 2012). To augment this dataset and to address the lack of sown tags at colonies in Upper Klamath Lake, we also estimated the predation probabilities of those tags naturally deposited by birds and recovered/detected during scanning efforts in the previous year (see Osterback et al. 2013). A comparison of detection rates of sown tags versus the redetection of naturally deposited tags indicates that the detection probability of naturally-deposited tags – those that have remained on the island for a year or more – is consistently lower than that of sown tags that have remained on the island for less than 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 from the current year (see Predation Rate Calculations below for additional details).

In other tag-based studies of avian predation, the scanning area has been limited to habitat used by a single bird species (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012; Hostetter et al. 2015). Predator-specific deposition probabilities, which can vary markedly between bird species (Hostetter et al. 2015), can then be used to adjust or correct estimates of predation rates. This was not possible in the present study because double-crested cormorants and American white pelicans nested communally such that tag recoveries could not be assigned to species of avian predator. Consequently, predation rate estimates calculated herein are known to be negatively biased, less than the actual predation rate, because the number of tagged fish consumed by pelicans and cormorants in the study area was not corrected or adjusted for on-colony PIT tag deposition probabilities.

Predation Rate Calculations. – We estimated predation and detection separately for birds nesting in Upper Klamath Lake and Clear Lake via a hierarchical Bayesian framework. We define $D_{ay}$ as the estimated number of fish eaten by birds from each area $a$ each year $y$ for $a \in \{\text{Clear Lake, Upper Klamath Lake}\}$ and $y \in \{2009, 2010, 2011, 2012, 2013, 2014\}$. We assume

$$D_{ay} \sim \text{binomial}(n_{ay}, \theta_{ay})$$

where $n_{ay}$ is the number of fish available to be eaten and $\theta_{ay}$ is the probability a fish is depredated in study area $a$ in year $y$. We let $\psi_{ay}$ 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

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

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

$$\text{predation}_{ay} = \frac{D_{ay}}{n_{ay}}$$

We refer 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 $\psi_{ay}$. We refer to the probability of redetecting in year $y$ all tags recovered in the previous year as $\varphi_{ay}$. We assume the redetection probability of tags in previous years and recovered in the immediately
preceeding year to be less than or equal to the initial year detection probability. Therefore, we say $\psi_{ay} \sim \text{uniform}(\varphi_{ay}, 1)$ for all $a$ and $y$. We assume no further information about redetection probabilities and use uninformative priors to model them. That is, we assume $\varphi_{ay} \sim \text{uniform}(0, 1)$. For years in which redetection tags were not available, we assumed $\psi_{ay} \sim \text{uniform}(\max_{z=y} \varphi_{az}, 1)$. This assumption helps ensure our estimate does not underestimate the actual initial year detection probability (as would probably be the case with a strictly uninformative prior).

For Clear Lake, we have several years (2009, 2010, 2011, 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 can therefore assume $F_{ay} \sim \text{binomial}(S_{ay}, \psi_{ay})$.

We implemented the predation rate model using the software JAGS accessed through R version 3.1.2 (R Core Team 2014) using the R2jags (Su 2012) and dclone (Solymos 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. 2004). We report results as posterior medians along with the 2.5 and 97.5 percentiles, which are referred to as 95% Credible Intervals (95% c.i.).

Methods to calculate estimates of predation rates were based on the following assumptions:

A1. Tagged suckers captured/recaptured or encountered at arrays each year were available as prey to nesting birds for the entirety of the nesting season in that year.

A2. The probability of sucker survival/predation and the probability of tag detection given predation were independent.

A3. Captured/recaptured/encountered suckers are a random and representative sample of all suckers (tagged and untagged).

A4. Detection probabilities within a bird nesting area (Clear Lake, Upper Klamath Lake) were roughly equal across all scanned regions (islands) in that area.

A5. The re-detection of tags from previous years was less than or equal to that of the initial deposition year detection probability.

A6. Deposition probabilities were 1.0 (i.e., all consumed sucker tags were deposited on a birds nesting colony).

The first assumption (A1) is needed to standardize measures of availability across nesting seasons and assumes that the mortality of a PIT- tagged fish following capture/recapture or encounter was zero. If, however, a significant number or percentage of tagged suckers died prior to each nesting season, availability is overstated and consequently biases predation rates down. The capture/recapture and survival of all tagged suckers were assumed to be mutually independent (A2). Likewise, the detection of tags from all depredated suckers was also assumed to be mutually independent. Lack of independence could potentially bias predation estimates to an unknown degree and overstate precision in our estimates. We further assumed that fish captured/recaptured/encountered were equally susceptible to
avian predation as non-tagged fish in each sucker species and population (A3). A difference in predation susceptibility between tagged and untagged fish could result in an unknown level of bias.

Assumption A4 addresses the fact that little information on detection probabilities were available for some of the bird nesting colonies scanned. Considering the comparable nesting substrates within the two nesting areas (tule mats on islands in Upper Klamath Lake or rocky/sandy substrate in Clear Lake) and exposure to similar weather effects, we assumed the detection probability of the various colony sites within each nesting area (Upper Klamath Lake and Clear Lake) to be equal (i.e., multiple measures of the same parameter per area, per year). If individual colony sites had significantly different detection probabilities, however, it could bias predation estimates to an unknown degree. Based on data from previous published studies (Evans et al. 2012; Hostetter et al. 2015) and data collected from colonies in Clear Lake (this study; see results), we believe assumption A5 is conservative. If, counter to expectation, the re-detection probability of tags detected in previous years is greater than that of tags deposited in the current year, this would further underestimate predation.

Finally, the assumption with perhaps the greatest influence on predation rates, we assumed all consumed tags were deposited by a bird on its nesting colony (A6). Based on previously published research (Osterback et al. 2013; Hostetter et al. 2015, Tuescher et al. 2015), however, this assumption is known to be false, and some proportion of ingested sucker PIT tags were egested at off-colony loafing or roosting sites or were damaged/destroyed during passage through the bird’s gastrointestinal tract. Consequently, estimates of predation rates presented here represent minimum estimates, as the estimates are corrected for detection probabilities but not deposition probabilities (see Discussion for additional details regarding the potential consequences of this assumption on predation rate estimates).

Size Selectivity.—To evaluate the relationship between fish size 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, in Upper Klamath Lake, Lost River suckers can grow approximately 10 mm per 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 the fact that fish were consumed by a bird less than a year following release. Mann-Whitney U 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/recaptured or encountered, and thus available to fish-eating birds, varied by species (Lost River, shortnose), age-class (adult, juvenile), nesting location (Clear Lake, Upper Klamath 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 compared with 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 during each year of the study period (Table 1). The average number of PIT-tagged juvenile-sized suckers available for avian predators during each year of the study was an order of magnitude less than that of adult-sized suckers, with adequate sample sizes of tagged juveniles (≥ 100 PIT-tagged fish) available for analyses of avian predation rates only in Upper Klamath Lake during 2009, 2011, and 2012 (Table 1).

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 suckers consumed from all colonies combined. Tag recoveries only include those tags that were recovered on colonies the same year the fish was available to avian predators (see Methods). Dashes indicate that less than 100 PIT-tagged suckers were available.

<table>
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</table>

1 Tag recovery was conducted at nesting colonies in Clear Lake only

PIT tag recovery on bird colonies.— 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/recaptured/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 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 Bird Colony Size), 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/or roosting locations used by piscivorous waterbirds during 2009-2014, regardless of when the PIT tag was placed in the sucker (Appendix A). 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 (Appendix A). 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, CA, at Sheepy Lake in Lower Klamath NWR, CA, and at select avian loafing/roosting sites in the region (Appendix A). Results from these scans were not included in the main study due to the paucity of tags found, the lack of detection efficiency data at these sites, and the likelihood that some of the tags were deposited by non-nesting birds and/or unspecified species of avian predators (Appendix A).

Bird Colony Sizes.— Based on 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-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 2). On Upper Klamath Lake, in comparison, 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.

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 from aerial photography. Asterisks denote colony failure, whereby birds attempted to nest but abandoned the site at some point during the nesting season (March to August).

<table>
<thead>
<tr>
<th></th>
<th>2009</th>
<th>2010</th>
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<th>2013</th>
<th>2014</th>
</tr>
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<tbody>
<tr>
<td><strong>Clear Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American white pelicans</td>
<td>2,325</td>
<td>722*</td>
<td>128*</td>
<td>510</td>
<td>1175</td>
<td>296</td>
</tr>
<tr>
<td>Double-crested cormorants</td>
<td>172</td>
<td>0*</td>
<td>77*</td>
<td>286</td>
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<td>197</td>
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<tr>
<td>Total</td>
<td>2,497</td>
<td>722</td>
<td>205</td>
<td>796</td>
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<td>493</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American white pelicans</td>
<td>438</td>
<td>81*</td>
<td>14*</td>
<td>255</td>
<td>152*</td>
<td>247</td>
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<tr>
<td>Double-crested cormorants</td>
<td>1,538</td>
<td>293*</td>
<td>373</td>
<td>885</td>
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<td>387</td>
<td>1,140</td>
<td>1,223</td>
<td>1,380</td>
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</tbody>
</table>

1Nesting by pelicans and cormorants occurred on up to three different islands (see Figure 1).
2Nesting by pelicans and cormorants occurred on up to five different islands (see Figure 1).

Depending on the year, Caspian terns (Hydroprogne caspia), 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 and year (Table 3). In general, estimates were higher on colonies in Clear Lake compared with colonies in Upper Klamath Lake (Table 3). Results indicate 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 re-detected the following year. For nesting areas and years in which only re-detection rates were available (i.e., those in Upper Klamath Lake), detection probabilities are less precise, as indicated by wider credible intervals (Table 3).
Table 3. Estimated detection probabilities (95% credible intervals) of PIT tags on bird breeding colonies in Clear Lake and Upper Klamath Lake during 2009-2014. Values were used to correct or 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), those sown by researchers (Clear Lake only) or naturally deposited by birds, used to model detection probabilities are also provided. NA denotes that detection probabilities were not available for that year at that location.

<table>
<thead>
<tr>
<th>Nesting Location</th>
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<th>2012</th>
<th>2013</th>
<th>2014</th>
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</thead>
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<td>0.74</td>
<td>0.84</td>
<td>0.51</td>
<td>0.84</td>
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<tr>
<td></td>
<td>(0.74-0.84)</td>
<td>(0.74-0.89)</td>
<td>(0.55-0.89)</td>
<td>(0.70-0.99)</td>
<td>(0.46-0.58)</td>
<td>(0.75-0.99)</td>
</tr>
<tr>
<td>n</td>
<td>100</td>
<td>485</td>
<td>312</td>
<td>139</td>
<td>779</td>
<td>447</td>
</tr>
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<td>NA</td>
<td>0.44</td>
<td>0.70</td>
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<tr>
<td></td>
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<td>NA</td>
<td>(0.22-0.71)</td>
<td>(0.56-0.93)</td>
<td>(0.48-0.76)</td>
</tr>
<tr>
<td>n</td>
<td>27</td>
<td>99</td>
<td>104</td>
<td></td>
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</tr>
</tbody>
</table>

1 The detection probability estimate for Upper Klamath Lake colonies in 2009 (the first year of scanning) was inferred from empirical data collected at nesting sites in Upper Klamath Lake during 2012-2014.

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 avian 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 (Figure 2). Estimated minimum avian predation rates on suckers in Upper Klamath Lake by birds nesting at Upper Klamath Lake were lower than at Clear Lake, with annual estimates as high as 1.0% (95% c.i. = <0.8 – 1.8%) for Lost River suckers and as high as 1.8% (95% c.i. = 1.1 – 4.1%) for shortnose suckers (Figure 2). 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 (Figure 2). 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, with statistically significant differences observed at Clear Lake in 2011 and at Upper Klamath Lake in 2012 (Figure 2).
Figure 2. Estimates of predation rates (proportion of available fish consumed by birds) on Lost River suckers, shortnose suckers, 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. Error bars represent 95% credible intervals.
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. There was no evidence, however, 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.

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 six 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 from 72 mm 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 prior to its tag being detected on a colony in Upper Klamath Lake. Comparisons of the length distributions of available versus depredated suckers 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 had a median fork length of 616 mm, whereas available suckers had a median fork length of 660 mm ($P < 0.001$). For shortnose suckers tagged in Clear Lake, depredated suckers had a median fork length of 360 mm, whereas available suckers had a median fork length of 380 mm ($P = 0.01$; Figure 3). There was no evidence of a similar size difference for shortnose suckers tagged in Upper Klamath Lake (Figure 3). Sample sizes of depredated juvenile suckers in Upper Klamath Lake ($n = 12$) and adult Lost River suckers in Clear Lake ($n=17$) were too small for statistical analyses, but there was suggestive evidence that larger adult 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 rates by fish-eating waterbirds nesting at multiple colonies on ESA-listed Lost River suckers and shortnose suckers. Our results indicate that predation rates varied by sucker species, sucker size, sucker age-class, bird colony location, and year, thus demonstrating that predator-prey interactions in this system 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 compared with 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 generally higher for pelicans and cormorants nesting at Clear Lake compared to 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.

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; USACE 2014; USFWS 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 rates. On average, fewer than 10% of adult Lost River suckers and fewer than 20% of adult shortnose suckers in Upper Klamath Lake die annually from all causes combined (Hewitt et al. 2014). 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 is thought to 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, especially, in Clear Lake seem warranted.

In Clear Lake, minimum estimates of predation rates from this study indicated 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), it can be assumed that the species have the potential for survival rates similar to the populations in Upper Klamath Lake. If annual mortality due to avian predation is roughly 5-10% or more (as implied if minimum predation rates are corrected for deposition probabilities (see below) and if all avian predators, not just breeding pelicans and cormorants, are considered) other sources of mortality would have to be small for suckers to be surviving at rates like those of 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 (Burdick and Rasmussen 2014), when access to the spawning area in Willow Creek is limited or entirely inaccessible to adult suckers. Consequently, results of our study suggest that avian predation may currently be a significant factor limiting recovery of ESA-listed Lost River and shortnose sucker populations in Clear Lake.

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), foraging behavior (BRNW 2015), 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 each individual fish, like its 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 mm to 730 mm were consumed. Results provide evidence of size-selectivity across sucker species and age-classes, whereby predation rates were apparently 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 and possibly other waterbirds (e.g., gulls, terns, and herons), whereby smaller-sized suckers were more susceptible to bird predation than larger-sized suckers, particularly Lost River suckers greater than 730 mm. 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 fork length (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. 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 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 work 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 a PIT-tagged sucker’s demise. More intensive colony surveys (aerial-, boat-, and land-based surveys), 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 could then be conducted to generate more accurate estimates of predation rates, those corrected for both detection probabilities and deposition probabilities. Hostetter et al. (2015) and Teuscher et al. (2015) were able to quantify predator-specific PIT tag deposition rates by feeding PIT-tagged fish to double-crested cormorants and American white pelicans and using the number of the fed tags subsequently deposited on-colony to model deposition probabilities. Hostetter et al. (2015) estimated a deposition rate of 0.51 (95% c.i. = 0.34 – 0.70) of ingested PIT-tagged salmonids by double-crested cormorants nesting on islands in the Columbia River. Teuscher et al. (2015) estimated a deposition and detection probability (a combined estimate for both parameters) of 0.30 (90% c.i. = 0.08 – 0.55) on PIT-tagged salmonids by American white pelicans nesting in the Black River drainage in Idaho. If tag deposition probabilities observed in these studies are applicable to pelicans and cormorants nesting in the Upper Klamath Basin, predation rate estimates presented herein would increase by a factor of approximately 2.0. For example, losses of tagged juvenile suckers in Upper Klamath Lake would increase from approximately 6 - 8% of available fish to about 12 - 16% of available fish. Even with an adjustment for tag deposition probabilities, estimated predation rates based on the number of tags recovered from pelican and cormorant colonies in the Upper Klamath Basin may still underestimate avian predation rates on ESA-listed suckers because (1) pelicans and cormorants can remain in the Upper Klamath Basin for several months after the nesting season has ended, (2) immature (non-nesting) or failed (unsuccessful) nesting birds presumably reside and forage on sucker in the region, and (3) other piscivorous waterbirds species (e.g., Caspian terns, California and ring-billed gulls, common mergansers [Mergus merganser], large grebes [Aechmophorus spp.], and others) may be consuming suckers, albeit impacts to adult-sized suckers from these species are likely small or non-existent.

In Upper Klamath Lake, a lack of juvenile recruitment is considered a limiting factor in recovery of both ESA-listed sucker species (Hewitt et al. 2014), 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, 4 (9.5%) were subsequently detected on bird colonies at Clear Lake during fall scanning efforts.
(Burdick 2013). Although juvenile sucker behavior is not well understood, larvae out-migrate in May and June to areas of the lake that are more suitable for rearing (Cooperman and Markle 2003; Martin et al. 2013), behavior that could increase the susceptibility of juvenile suckers to avian predation.

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. Janney et al. (2008) observed poor water quality and habitat conditions in parts of Upper Klamath Lake, which could cause suckers to congregate in large numbers in areas where they might be more susceptible to bird predation. Barry et al. (2009) noted that access to Willow Creek, the lone spawning tributary for shortnose and Lost River suckers in Clear Lake, was based on spring-time reservoir levels, and that suckers on spawning runs could either be blocked at the mouth of the creek or potentially trapped in the creek due to water levels during drought conditions, perhaps increasing their susceptibility to avian predation. Hostetter et al. (2012) demonstrated that diseased or injured fish were more susceptible to predation by double-crested cormorants compared to 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 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 colonies and for granting us access and providing transportation to islands in Upper Klamath Lake following the nesting seasons. We thank Tim Lawes of Oregon State University and Aaron Turecek of Real Time Research 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. 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.

LITERATURE CITED


Kennedy, B.M., W.L. Gale, and K.G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (Oncorhynchus mykiss) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506–1516


## APPENDIX A

Table A1. Numbers of PIT-tagged Lost River suckers (LRS), shortnose suckers (SNS), and unknown suckers (> 72 mm but < 300 mm at last capture; UNID) recovered on avian nesting locations and loafing/roost 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 of American white pelicans, double-crested cormorants, Caspian terns, Forster’s terns, California gulls, ring-billed gulls, great blue herons, black-crowned night herons, and/or great egrets. Not all locations listed herein were utilized as breeding islands in all years. Dashes denote that scanning for PIT tags did not take place that year. Data from the man-made Corps constructed tern islands are from BRNW (2015).

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<td>SNS</td>
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