**Avian Predation of Juvenile Lost River and Shortnose Suckers in Upper Klamath Lake: An Assessment of Sucker Assisted Rearing Program Releases during 2018–2020**



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## ABSTRACT

To bolster recruitment in Endangered Species Act (ESA) listed Lost River Suckers (*Deltistes luxatus*) and Shortnose Suckers (*Chasmistes brevirostris*) in the Upper Klamath Basin (UKB), the U.S. Fish and Wildlife Service (USFWS) and its partners have implemented the Sucker Assisted Rearing Program (SARP). As part of this program, juvenile suckers were reared in captivity, implanted with passive integrated transponder (PIT) tags (n= 8,857), and released into the Upper Klamath Lake or its tributaries during 2018–2020. Previous research suggests that predation by American White Pelicans (*Pelecanus erythrorhynchos*), Double-crested Cormorants (*Nannopterum auritum*), and Caspian Terns (*Hydroprogne caspia*) may negatively influence sucker survival, particularly predation on juvenile suckers. Estimates of predation impacts from past studies, however, represented minimum estimates of sucker mortality because analyses did not account for the proportion of consumed tags that were deposited by birds on their breeding colony where PIT tag recovery efforts took place. To estimate and account for deposition probabilities, we conducted a field study in which we fed pelicans PIT-tagged juvenile suckers (n = 401). We accounted for deposition probabilities of cormorants and terns by using previously published estimates. Sucker PIT tags were recovered from pelican, cormorant, and tern nesting sites in the UKB following each breeding season and a hierarchical Bayesian model was used to estimate predation rates (percentage of available tagged fish consumed) on SARP releases as well as naturally-reared or wild juvenile suckers and adult suckers that were PIT-tagged in Upper Klamath Lake and Clear Lake Reservoir. Pelican deposition probabilities were estimated at 0.47 (95% credible interval = 0.36–0.60), indicating that for every 100 PIT tags consumed, on average, 47 were deposited by pelicans on breeding colonies. Estimates of predation rates that incorporate corrections for deposition on SARP releases ranged annually from 4.4% (95% credible interval = 2.9–6.8%) to 8.8% (6.2–13.3%) during 2018–2020. Results suggest that colonial waterbird predation impacts on SARP releases likely constituted a small, but unknown, component of total mortality for suckers released into the Upper Klamath Lake system. Predation impacts on SARP juvenile suckers and wild juvenile suckers, which were estimated annually at 4.7% (1.0–13.9%) to 14.9% (7.6–29.3%), were consistently higher than those observed on adult suckers, with predation on adult suckers typically less than 4.0% of available fish annually. Future predation studies may consider models that integrate both live and dead detections of PIT-tagged suckers to generate more accurate and precise estimates of survival following release, as well as models that consider environmental factors that influence sucker susceptibility to colonial waterbird predation. Such models would provide a more holistic understanding of the degree to which avian predation limits the survival of ESA-listed suckers in the UKB.


## BACKGROUND

Piscivorous colonial waterbirds are an integral part of the Upper Klamath Basin (UKB) ecosystem, with breeding colonies of American White Pelicans (*Pelecanus erythrorhynchos, hereafter "pelicans"*), Double-crested Cormorants (*Nannopterum auritum, hereafter "cormorants"*), Caspian Terns (*Hydroprogne caspia,* hereafter "*terns*"), and other species annually present in the region (Shuford 2010). Although western pelican and cormorant populations have been in decline for more than a century, colonies in the UKB are some of the largest in the western region of North America when conditions are favorable (King and Anderson 2005, Shuford 2010). In the past decade, pelican colonies consisting of more than 2,000 breeding adults have been present in Clear Lake Reservoir, CA, and cormorant colonies of more than 1,500 adults have been documented in Upper Klamath Lake, OR (Shuford 2010, Evans et al. 2016). Large colonies of terns have also been documented in the region in recent years, with more than 1,000 breeding adults observed in Sheepy Lake, CA (Roby et al. 2021). Two species of long-lived catostomids, the Lost River Sucker (LRS; *Deltistes luxatus*) and the Shortnose Sucker (SNS; *Chasmistes brevirostris*), are also found in the region and are listed as endangered under the U.S. Endangered Species Act (ESA; USFWS 1988). Numerous factors have been identified as limiting recovery of sucker populations, including habitat loss, poor water quality, low water levels, and a lack of juvenile recruitment into spawning populations (Janney et al. 2008, USFWS 2012, Burdick et al. 2015, Hewitt et al. 2018, Hewitt et al. 2021, Burdick et al. 2020). Recent data also suggest that impacts from colonial waterbirds may be substantial based on the number and percentage of passive integrated transponder (PIT) tags implanted into suckers that were subsequently recovered on bird colonies in the UKB during 2009–2014 (Evans et al. 2016).

To monitor the behavior and survival of LRS and SNS, fish have been PIT-tagged in Upper Klamath Lake and Clear Lake Reservoir for over two decades (Janney et al. 2008, Hewitt and Hayes 2013, Burdick et al. 2015, Hewitt et al. 2018, Hewitt et al. 2021). PIT tags enable specific information to be linked to individual fish, including species, size, age-class (adult, juvenile), release/recapture location, and other information. Until recently, most PIT-tagged suckers have been adults, as fewer than 1,000 juveniles have been captured and tagged since 2009. This is due in part to poor summer survival of juveniles, particularly in Upper Klamath Lake, that has resulted in a prolonged lack of recruitment into adult spawning populations (Burdick et al. 2020, Bart et al. 2020). As part of an effort to recover imperiled LRS and SNS populations and to address concerns regarding juvenile survival, the Sucker Assisted Rearing Program (SARP) was developed by the U.S. Fish and Wildlife Service (USFWS) and its partners in 2015. The program operates under the hypothesis that poor water quality conditions in Upper Klamath Lake reduce survival of young-of-the-year and juvenile suckers (Day et al. 2020). Beginning in 2016, wild-origin sucker larvae have been captured annually at spawning locations in Upper Klamath Lake and its tributaries and reared at off-site facilities for 1–3 years, or until they reach a size determined to offer the best chance of survival in Upper Klamath Lake (Day et al. 2020). Once at a pre-determined age or size, thousands of juvenile suckers have been PIT-tagged and released annually into Upper Klamath Lake beginning in 2018 (Childress et al. 2019).

A portion of PIT-tagged suckers are consumed by avian predators with their corresponding tag deposited (regurgitated or defecated) at nesting sites (colonies) where they can be detected by researchers following the breeding season (Evans et al. 2016). To address concerns over the potential impact of avian predators on ESA-listed suckers, research involving the recovery of sucker PIT tags on bird colonies in the UKB has been on-going since 2009. However, not all PIT tags that are ingested by colonial waterbirds are subsequently deposited on their colony (Evans et al. 2012, Osterback et at. 2013, Hostetter et al. 2015, Teuscher et al. 2015). For instance, a portion of PIT tags consumed by birds are damaged and rendered unreadable following digestion or are regurgitated off-colony at loafing, staging, or other areas used by birds during the breeding season (Hostetter et al. 2015). Evans et al. (2016) measured minimum predation rates (percentage of available tagged fish consumed) on LRS and SNS; estimates that were adjusted for PIT tag detection probabilities (the fraction of tags deposited on-colony subsequently detected by researchers after the nesting season) but not for PIT tag deposition probabilities (the fraction of tags deposited on-colony). Despite being minimum estimates, impacts were substantial on some groups of tagged fish, with predation rates on adult LRS as high as 4.6% in Clear Lake Reservoir and rates on adult SNS as high as 1.8% in Upper Klamath Lake during 2009-2014 (Evans et al. 2016). Results also indicated that predation rates on juvenile suckers in Upper Klamath Lake were higher than that on adults, with a minimum of 5.7% and 8.4% of available juvenile suckers consumed by birds during 2009 and 2012, respectively (Evans et al. 2016). These data were collected on naturally-reared or wild juveniles, while the impacts on suckers reared in captivity was unknown. Given the greater susceptibility of hatchery-reared fish to bird predation observed in other systems (Fritts and Pearsons 2007, Hostetter et al. 2012), and the en masse release of SARP fish into Upper Klamath Lake, predation impacts on SARP releases may be substantial.

Previous research indicates that PIT tag deposition probabilities by colonial waterbirds can be low and vary by predator species. For instance, in a study of cormorant, tern, and California Gull (*Larus californicus*) predation on PIT-tagged salmonids (*Oncorhynchus spp*.), Hostetter et al. (2015) estimated that average annual PIT tag deposition probabilities varied significantly by predator species, with estimates of 0.15 (95% credible interval = 0.11–0.21) for gulls, 0.51 (0.34–0.70) for cormorants, and 0.71 (0.51–0.89) for terns. Integrating deposition probabilities increased predation rate estimates by a factor of 1.4 to 6.7 depending on the predator species; thus, accurate estimates of predation rely on accurate estimates of species-specific deposition probabilities. Although recent studies have suggested that not all PIT-tagged fish consumed by pelicans are deposited on their breeding colonies (Teuscher et al. 2015, Meyer et al. 2016), these studies did not attempt to measure deposition probabilities independent from detection probabilities, so independent parameter estimates of pelican deposition were unavailable for use in mark-recapture-recovery predation models (Evans et al. 2016). Breeding pelicans have been documented foraging > 50 km away from their respective colonies (Knopf and Evans 2004) and based on empirically measured deposition probabilities for other piscivorous waterbirds, deposition probabilities for pelicans foraging in the Upper Klamath Basin are a critical uncertainty in estimating the impacts of pelican predation on juvenile sucker survival (Evans et al. 2016).

Accurate assessment of cause-specific mortality may be paramount to understanding the efficacy of management actions aimed at increasing the survival of ESA-listed suckers in the UKB. The primary goal of this study was to (1) estimate PIT tag deposition probabilities by pelicans and (2) generate accurate estimates of predation rates by pelicans, cormorants, and terns on SARP releases during 2018–2020. We also updated the minimum estimates of predation reported by Evans et al. (2016) on LRS, SNS, and wild juvenile suckers. In keeping with recent research showing a lack of genetic distinctiveness between SNS and Klamath Largescale Suckers (KLS; *Catostomus snyderi*) in Clear Lake Reservoir (Dowling et al. 2016, Smith et al. 2020), updated results for that waterbody combine individuals that were identified as either SNS or KLS into a single "SNS-KLS" group. Collectively, data generated as part of this study can be used to improve the accuracy of PIT tag-based avian predation models and provide information on cause-specific mortality of ESA-listed suckers in the Upper Klamath Basin.

## METHODS

Study Area – We investigated predation on PIT-tagged SARP releases by pelicans, cormorants, and terns nesting on colonies located in Upper Klamath Lake, OR, Clear Lake Reservoir, CA, Tule Lake Sump 1B, CA, and Sheepy Lake, CA during 2018-2020 (*Figure 1*). Piscivorous colonial waterbirds breeding at these sites were previously identified as posing a potential risk to sucker survival in the region (Evans et al. 2016).

All colonies included in the study were located on U.S. Fish and Wildlife Service National Wildlife Refuges (NWR). 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. Islands in Tule Lake and Sheepy Lake were rocky or sandy islands ranging in size from 0.2 acres to 2.3 acres. Pelicans and cormorants nested at colonies in Upper Klamath Lake and Clear Lake Reservoir, whereas pelicans, cormorants, and terns all nested at colonies in Tule and Sheepy lakes (see also Bird Colony Size *below)*.

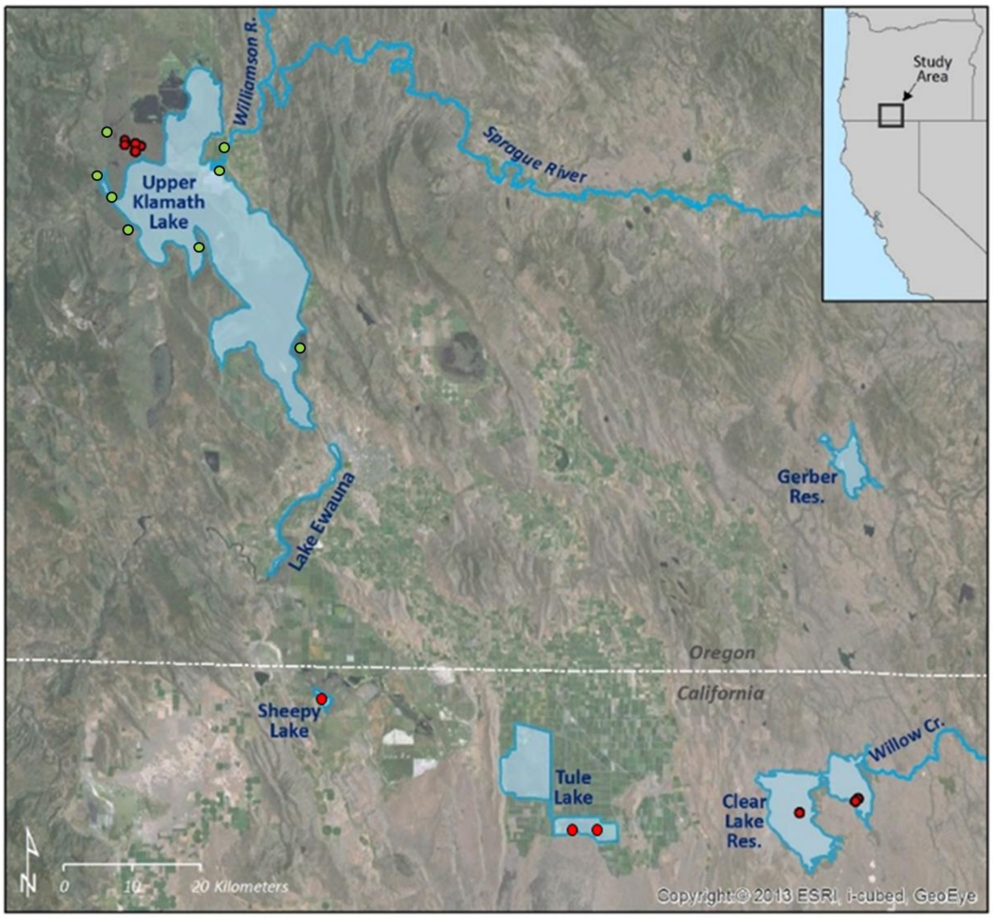


Figure 1. Breeding sites (red dots) used by American White Pelicans, Double-crested Cormorants, and Caspian Terns in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, and Sheepy Lake during 2018–2020. Release sites (green dots) of PIT-tagged SARP juveniles are also provided (see also Appendix, Table A.1).

Availability of PIT-tagged Suckers – The number of suckers available to predation by colonial waterbirds was based on the number of PIT-tagged SARP juveniles released into the Upper Klamath Lake system prior to or during each breeding season in 2018–2020, but no later than 31 August, the presumed end of the breeding season (Evans et al. 2016). For instance, fish released during December 2019 were considered available as prey to birds during the 2020 breeding season. Most SARP fishes were released during March to June, a time period that coincided with the breeding season (see *below*).

Bird Colony Sizes – The methods of Adkins et al. (2014) were used to determine the size (number of adults) of pelican, cormorant, and tern colonies that were subsequently scanned for sucker PIT tags (see PIT Tag Recovery *below*). In brief, colony sizes were estimated based on the number of adult birds visible on-colony in oblique aerial photographs taken during the breeding season (March to August), with one to three aerial surveys conducted each breeding season. Peak colony size was based on the number of adults present during the late egg incubation or early chick rearing period (early June), the stage of the nesting cycle when the greatest number 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 this period, photographs taken of the colony earlier in the breeding 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 colony in each year (see also Evans et al. 2016).

PIT Tag Recovery – Electronic recovery (detection) of sucker PIT tags was conducted at all active colony sites included in the study each year (*Figure 1*). Recovery of sucker PIT tags on bird colonies followed the methods of Evans et al. (2016). 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 breeding season, with two passes or complete sweeps of the nesting site conducted each year. The area occupied by birds was determined from aerial photographs taken of the colony during the breeding season (see *above*). Although recovery efforts were focused on pelican, cormorant, and tern nesting sites, other piscivorous waterbird species (e.g., California Gulls, Ring-billed Gulls [*L. Delawarensis*], Great Blue Heron [*Ardea Herodias*], and other species) were also present at some of these nesting sites in some years. In most cases, the nesting habitat of these other colonial waterbird species was readily identifiable from aerial imagery, but small numbers of these other species could have deposited PIT tags that were included in the study (see *Results* for additional details).

Predation Rate Estimates – Following the previously published methods of Hostetter et al. (2015), a hierarchical Bayesian model was used to estimate predation rates on suckers based on the number of PIT-tagged fish available and the number of tags recovered on Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, and Sheepy Lake colonies during 2018-2020. The probability of recovering a sucker tag on a bird colony is the product of three probabilities: (1) the probability that a tagged fish is consumed (predation probability), (2) the probability that the tag is deposited on the nesting colony (deposition probability), and (3) the probability that the tag is detected by researchers following the breeding season (detection probability; *Figure 2*).

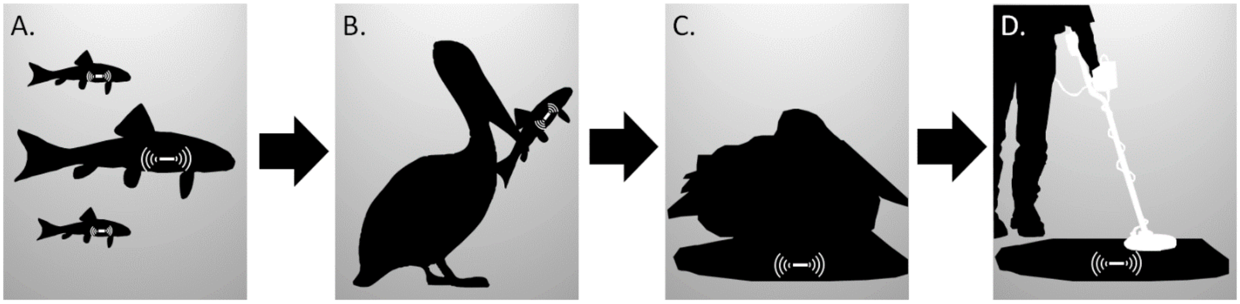


Figure 2. Conceptual model of the tag recovery process in capture-mark-recovery studies of avian predation on fish populations. A. PIT-tagged population of suckers; B. Predation probability – the probability that a tagged sucker is consumed by a breeding bird; C. Deposition probability – the probability that the tag is deposited on the bird's nesting colony; D. Detection probability – the probability that the tag is detected by researchers following the breeding season. Modified figure from Hostetter et al. (2015).

*PIT Tag Detection Probabilities:* Not all PIT tags deposited by birds on their nesting colony are subsequently detected by researchers after the breeding season (i.e., detection probabilities < 1.0; Evans et al. 2012). For example, tags can be blown off the colony during windstorms, washed away during flood events, or otherwise damaged or lost during the breeding season. Furthermore, the detection methods used to find PIT tags on bird colonies are not 100% efficient, with some proportion of detectable tags missed by researchers during the scanning process. Previous research indicates that detection probabilities often vary significantly within and between colonies, variation that necessitates a direct measure of detection probabilities for each colony in each year (Evans et al. 2012; Hostetter et al. 2015; Evans et al. 2016; Payton et al. 2019). To address this, PIT tags with known tag codes were intentionally sown by researchers on colonies in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, and Sheepy Lake each year to estimate PIT tag detection probabilities (hereafter referred to as "control tags"). Control tags were the same size and type as those used to mark SARP releases (12-mm [length] × 2-mm [width], full duplex, 134 KHz). Control tags were sown throughout the areas occupied by nesting birds during the breeding season, identified through aerial imagery (see Bird Colony Sizes *above*). Tags were haphazardly scattered throughout the nesting area used by birds during the breeding season such that the detections (i.e. recoveries) of control tags during scanning efforts each year could be used to model the probability of detecting tags deposited throughout the breeding season using logistic regression. Roughly equal numbers of control tags were sown on each colony each year and sample sizes were selected by considering historical sample sizes (Evans et al. 2016). This approach allows direct comparisons of independent detection probabilities, with similar precision among years (see also Payton et al. 2019).

*PIT Tag Deposition Probabilities:* Not all PIT tags consumed by birds are subsequently deposited on their nesting colonies. Deposition probabilities (i.e. probability that a tag consumed by a bird is deposited on its nesting colony) were previously estimated by intentionally feeding PIT-tagged fish to birds breeding at colonies in the Columbia River Basin by Hostetter et al. (2015), with the proportion of known ingested tags subsequently recovered on cormorant and tern colonies used to estimate predator-specific deposition probabilities. The distribution of the median deposition probability derived from that study was 0.71 (95% credible interval = 0.51–0.89) for terns and 0.51 (0.34–0.70) for cormorants. Results from Hostetter et al. (2015), which included multiple tern and cormorant colonies, indicated that deposition probabilities did not vary significantly within or between years by predator species (cormorants, terns). For the purposes of this study, we assumed deposition probabilities for cormorants and terns reported by Hostetter et al. (2015) were applicable to cormorant and tern colonies in the UKB during 2018–2020. No previously published PIT tag deposition probability estimates, however, were available for pelicans.

To determine what fraction of sucker PIT tags ingested by pelicans were subsequently deposited on their colony, we followed the methods of Hostetter et al. (2015) by directly feeding dead fish implanted with PIT tags to adult pelicans during the breeding season, and then recovered those tags on-colony following the breeding season. Deposition probabilities were estimated by feeding juvenile-sized suckers (fork length range = 173–325 mm) with known tag codes to nesting pelicans on Clear Lake Reservoir throughout the breeding season (*Figure 3*). To account for potentially different levels of colony attendance during the breeding season, multiple feeding periods or trials were conducted based on the colony's chronology, with tagged fish consumed during the nest building, egg incubation, and chick-rearing stages. Suckers used in deposition trials were implanted with the same PIT tag implanted in juvenile SARP releases (12-mm x 2-mm, 134 kHz, full-duplex). A camouflaged boat was used to approach nesting birds and to present them with PIT-tagged suckers (*Figure 3*). Only suckers that were known to have been consumed by an adult pelican were included in the study. Tagged suckers were consumed by adult pelicans throughout the course of each day (range = 0615 to 2042 hrs) during each trial to mimic variable foraging times, and trials were designed to feed as many individual birds as possible.

Figure 3. PIT-tagged suckers (left panel) and observation equipment (center panel) used in deposition trials at the Clear Lake Reservoir American White Pelican colony (right panel) in 2020.

Using these same methods, and as part of a separately funded study, PIT-tagged rainbow trout (*O. mykiss;* fork length range = 112–273 mm) were also fed to American White Pelicans nesting on Badger Island in the Columbia River near Kennewick, WA. Badger Island has been the largest nesting site for pelicans in the Columbia River Basin for the last two decades (Cramer et al. 2021). Similar to studies at Clear Lake Reservoir, PIT-tagged fish were consumed by Badger Island pelicans during three discrete deposition trials that were based on the colony's nesting chronology, with tagged fish consumed throughout all daylight hours and by multiple pelicans during each trial. Results from Badger Island deposition trials are reported herein to assess whether pelican deposition probabilities varied by nesting site (Clear Lake Reservoir, Badger Island) and to bolster sample sizes of tagged fish used to estimate pelican deposition probabilities for use in predation analyses.

Sample sizes of tagged suckers and trout used in deposition studies by pelicans nesting on Clear Lake Reservoir and Badger Island in 2020 are provided below in *Table 1*. Sample sizes of tagged fish used in pelican deposition trials (n = 401; *Table 1*) were similar to those used in cormorant (n = 428) and tern (n

= 456) deposition trials by Hostetter et al. (2015), which should result in similar levels of precision in estimates of pelican deposition relative to cormorant and tern deposition estimates (see *Discussion* for additional details).

Table 1. Sample sizes of consumed and recovered PIT-tagged suckers and rainbow trout by American White Pelicans nesting on an island in Clear Lake Reservoir and on Badger Island in 2020.

| Colony | Trial (dates) | Consumed | Recovered |
|---|---|---|---|
| Clear Lake | 1 (May 8-10) | 55 | 16 |
| | 2 (May 29-31) | 97 | 48 |
| | 3 (July 1-3) | 10 | 2 |
| Badger Island | 1 (May 17-19) | 36 | 5 |
| | 2 (June 5-9) | 95 | 33 |
| | 3 (July 5-10) | 108 | 48 |
| **ALL** | | **401** | **152** |

The probability of a PIT tag being deposited on each colony was then inferred from the binomial process of recovering the experimental tags. That is, for each colony studied, we assumed

$$k_i \sim \text{Binomial}(n_i, \phi * \psi_i)$$

where $k_i$ is the number of PIT tags recovered from the number of tags observed to be consumed ($n_i$) in week *i* and $\psi_i$ represents the probability that a tag, deposited in week *i* is detected following the nesting season. $\psi_i$ was assumed to be a logistic function of week. That is:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 * i$$

where $\beta_0$ and $\beta_1$ are both derived from non-informative priors (normal [0, 1000]).

*Predation Rate Estimates:* Following the methodology of Hostetter et al. (2015), predation rates were modeled independently for each year, each bird species (pelican, cormorant, tern), and each nesting location (Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, Sheepy Lake). The probability of recovering a sucker PIT tag on each colony and year was modelled as the product of the three probabilities described above, the probability that (1) the fish was consumed ($\theta$), (2) the PIT tag was deposited on-colony ($\phi$), and (3) the PIT tag was detected on-colony after the nesting season ($\psi_i$; see also *Figure 2 above*).

Estimation of the probability that a fish was consumed was complicated by two factors: (1) the highly variable number of fish available to predators and (2) the unknown date of consumption for tags recovered from bird colonies. It is generally assumed that predation probabilities vary across time (Payton et al. 2019). In avian predation studies release groups are generally delineated by week. However, fish in this study were released or encountered throughout the year with many weeks lacking adequate sample sizes to measure a predation rate with any meaningful level of precision. We therefore partitioned the year into release groups of one or more weeks with an assumed predation rate constant across the partition. Partition boundaries were determined by weeks in which 100 or more fish were released/encountered and included all consecutive subsequent weeks in which less than 100 fish were released/encountered.

Explicitly, we let $w_1, w_2, \ldots, w_G$ represent the weeks in which 100 or more fish were released/encountered and therefore also represent the temporal boundaries between the *G* release groups. A fish released in week *i* is then considered part of release group $g$ such that $i \in W_g$ where $W_g = \{w_g, w_g + 1, \ldots, w_{g+1} - 1\}$. For each release group *g*, we let the simplex vector $[s_g \quad \theta_{g,0} \quad \theta_{g,1} \quad \cdots \quad \theta_{g,C}]^T$ represent the probabilities that, during the weeks of $W_g$, a fish alive at the beginning of $W_g$ survived ($s_g$), died due to some unexplained reason ($\theta_{g,0}$), or was consumed by a bird from a given colony *c* ($\theta_{g,c}$, for $c \in \{1, \ldots, C\}$, where $C$ is the number of colonies assumed to be foraging in the given year). For fish released/encountered within *g,* we further assume these probabilities to be directly related to the proportion of weeks remaining in *g.* We further assume predation rates for each colony to be similar but not necessarily equal from week to week. We therefore let

$$\theta_{gc} = \theta_{1c} + \sum_{h<g} \epsilon_{c,h}$$

where $\epsilon_{c,h} \sim \mathrm{normal}(0, \sigma_c^2)\ \forall h \in \{1, \ldots, G-1\}$ .

Using the recovery parameters described above, the probability of a fish released/encountered in week $i \in W_g$ being consumed by colony $c$ and recovered following the breeding season can be represented by $\gamma_{g,c}$ and enumerated as

$$\gamma_{i,c} = \frac{|\{j | i \le j < w_{g+1}\}|}{|W_g|} \theta_{g,c} * \bar{\psi}_{c,i} * \phi_c + \frac{|\{j | i \le j < w_{g+1}\}|}{|W_g|} s_g * \chi_{g+1}$$

where

$$\chi_{g+1} = \theta_{g+1,c} * \bar{\psi}_{c,g} * \phi_c + s_{g+1} * \chi_{g+2.}$$

and $\bar{\psi}_{g,c}$represents the arithmetic average probability of detection for tags consumed (and deposited) on colony *c* across all weeks in period *g.*

These assumptions allowed for the identification of temporal variation in predation rates across time while maintaining the integrity of the disparate release/encounter dates for each fish. While survival and probabilities of other mortality are specified in the model, we did not attempt, nor expect to precisely identify, survival rates throughout the year, which are very weakly identifiable, but rather their presence is included to recognize the uncertainty associated with the indeterminate time of predation for any recovered tag. Furthermore, without recapture opportunities subsequent to the breeding season, $s_G$ and $\theta_{G,0}$ are only jointly identifiable.

This parameterization allows to simply model the recovery of tags as

$$\bar{h}_i \sim \mathrm{multinomial}(m_i, \begin{bmatrix} \gamma_{i,1} & \cdots & \gamma_{i,C} & 1 - \sum_C \gamma_{i,C} \end{bmatrix}^T)$$

where $\bar{h}_i$ is a *C+1* length vector, where the *c*th entry enumerated the number of sucker PIT tags recovered from colony *c* (for $c = 1, \ldots, C$) and the final entry equal to the number of unrecovered tags from the available $m_i$ tags observed/released in week *i*.

Informative Beta priors were used to model deposition probability($\phi$). The shape parameters ($\alpha$, $\beta$) are dependent on the predator species (pelican, cormorant, tern) and are assumed to be mutually independent from colony to colony. For pelicans we assumed $\alpha = 6.70$ and $\beta = 7.37$, for cormorants we assumed $\alpha = 15.98$ and $\beta = 15.29$, and for terns we assumed $\alpha = 16.20$ and $\beta = 6.55$. Several of the nesting areas were inhabited by multiple species, with mixed-species breeding areas of pelicans and cormorants on Upper Klamath Lake and Clear Lake Reservoir and a mixed-species nesting area of pelicans, cormorants, and terns on Sheepy Lake (see also *Bird Colony Sizes*). Without data to inform estimates of the impacts of each species independently, we assumed the probability that a tag was deposited by any species to be approximately equal (i.e., we used an average mixed-species deposition probability).

Annual predation rates were defined as the estimated number of PIT-tagged suckers consumed divided by the total number available each week. Annual predation rates were derived as the sum of the estimated number of PIT-tagged suckers consumed each week divided by the total number of PIT-tagged suckers available. Summation of weekly consumption estimates is necessary to accurately reflect variation and autocorrelation of predation rates and thus to create unbiased annual rates with accurate assessments of precision (Hamilton 1994).

Models were analyzed using the software STAN (Stan Development Team 2020), accessed through R version 4.1.0 (R Core Team 2014), and using the rstan package (version 2.21.2; Stan Development Team 2020). To simulate random draws from the joint posterior distribution, we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 4,000 warm-up iterations followed by 4,000 posterior iterations thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013); only chains with zero reported divergent transitions were accepted. Posterior predictive checks compared simulated and observed annual aggregate raw release and recovery numbers to ensure model estimates reflected the observed data. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% Credible Interval) calculated using the HDInterval package (version 0.2.0; Meredith and Kruschke 2016).

*Predation on other suckers:* In addition to SARP juvenile suckers, wild juvenile suckers and adult LRS, SNS, and SNS-KLS were also PIT-tagged or re-encountered (previously tagged) in Upper Klamath Lake and Clear Lake Reservoir by the U.S. Geological Survey (USGS) – Klamath Falls Field Station (see also Hewitt et al. 2018, Hewitt et al. 2021). Tags from these other groups of suckers were also recovered on bird colonies as part of this study and, although not the focus of this study, we provide estimates of predation on these other groups of suckers using the same methods described above on SARP releases. In brief, all wild adult and juvenile PIT-tagged suckers released or re-encountered between 1 September and 31 August were considered available to colonial waterbirds during each nesting season. As with SARP releases, recoveries of these other sucker tags on bird colonies, coupled with estimates of deposition and detection probabilities, were used to generate estimates of predation rates using the model described above. Estimates of predation rates on these other groups of tagged suckers, which date back to 2009, update the minimum estimates of predation reported by Evans et al. (2016) and provide more accurate estimates of historical predation impacts by piscivorous colonial waterbirds on adult and juvenile suckers in the Upper Klamath Basin.

## RESULTS

Availability of PIT-tagged Suckers – The number of PIT-tagged SARP juveniles released into Upper Klamath Lake and its tributaries ranged annually from 2,335 to 3,511 during 2018–2020 (*Table 2*). PIT-tagged SARP fish were released at (1) four sites associated with the 2018 breeding season from March 19 to April 26, 2018, (2) four sites associated with the 2019 breeding season from March 5 to June 26, 2019, and (3) five sites associated with the 2020 breeding season from December 19, 2019 to April 16, 2020 (see also *Figure 1*). The number of PIT-tagged SARP fish released varied considerably by site and year, ranging from 100 to 1,427 tagged suckers per release site, per year (*Appendix, Table A.1*).

Table 2. Numbers of PIT-tagged Sucker Assisted Rearing Program (SARP) juvenile suckers released into Upper Klamath Lake or its tributaries that were subsequently recovered on colonies of American White Pelicans, Double-crested Cormorants, and Caspian Terns in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, and Sheepy Lake. Tag recoveries were not adjusted to account for detection or deposition probabilities and thus represent minimum numbers of consumed tagged fish.

| | | No. Recovered on Avian Colonies | | | |
|---|---|---|---|---|---|
| Year | No. Released | Upper Klamath Lake | Clear Lake Reservoir | Tule Lake Sump 1B | Sheepy Lake |
| 2018 | 2,335 | 32 | | 4 | 1 |
| 2019 | 3,011 | 49 | | | 12 |
| 2020 | 3,511 | 71 | 2 | | 40 |

The numbers of PIT-tagged adult LRS, SNS, and SNS-KLS, and wild juvenile suckers available for use in retrospective analyses of predation varied considerably by sucker taxa, age-class, location, and year (2009–2020) and are provided in *Appendix, Table A2*. In general, sample sizes of PIT-tagged adult suckers were large (several thousand annually) but only small numbers of PIT-tagged wild juveniles (several hundred or less annually) were available for use in predation analyses.

Bird Colony Sizes – Aerial photography showed that pelicans, cormorants, and terns attempted to nest on islands in Clear Lake Reservoir, Sheepy Lake, Tule Lake Sump 1B, and Upper Klamath Lake during the 2018–2020 study period (*Table 3*). The species composition varied by nesting area and year, with pelicans and cormorants nesting on islands in Clear Lake Reservoir and Upper Klamath Lake and pelicans, cormorants, and terns nesting on islands in Tule Lake Sump 1B and Sheepy Lake. Birds typically arrived to breeding colonies in late March to early April and remained on-colony until mid-August, although the exact timing varied each year and depended on colony success (i.e., rearing of young). The islands available to breeding colonies in Sheepy Lake and Tule Lake Sump 1B remained the same in all years, although the number of breeding birds varied each year. While the number of breeding birds varied for colonies located in Clear Lake Reservoir and Upper Klamath Lake, the number of islands with active colonies also varied each year. In general, pelicans were most numerous on nesting colonies in Clear Lake Reservoir; terns were most numerous and evenly represented on nesting colonies in Sheepy Lake and Tule Lake Sump 1B; and cormorants were most numerous on nesting colonies in Upper Klamath Lake. On Clear Lake Reservoir, an average of 618 (annual range = 58–1,166) pelicans, 166 (136–

200) cormorants, and no (zero) terns were counted on colonies each breeding season. On Upper Klamath Lake, an average of 343 (129–510) pelicans, 557 (416–710) cormorants, and zero terns were counted on colonies each breeding season (*Table 3*). On Sheepy Lake, an average of 216 (34–415) pelicans, 404 (366–435) cormorants, and 378 terns (270–544) were counted on colonies each breeding season (*Table 3*). On Tule Lake Sump 1B, an average of 22 (15–36) pelicans, 423 (263–517) cormorants, and 375 terns (72–775) were counted on colonies each breeding season (*Table 3)*. With the exception of Tule Lake Sump 1B colonies, pelican and cormorant chicks were present at all sites in all years. Cormorant chicks were present on Tule Lake Sump 1B colonies in 2019 only. Tern chicks were present in all years an active colony existed on Tule and Sheepy lakes.

Table 3. Peak numbers of American White Pelicans (Pelicans), Double-crested Cormorants (Cormorants) and Caspian Terns (Terns) by nesting location (Clear Lake Reservoir, Upper Klamath Lake, Sheepy Lake, and Tule Lake Sump 1B) and year.

| Bird Species | 2018 | 2019 [a] | 2020 |
|---|---|---|---|
| | | **Clear Lake Reservoir [b]** | |
| Pelicans | 631 | 58 | 1,166 |
| Cormorants | 162 | 136 | 200 |
| Terns | 0 | 0 | 0 |
| **Total** | **793** | **194** | **1,366** |
| | | **Upper Klamath Lake [c]** | |
| Pelicans | 510 | 129 | 391 |
| Cormorants | 544 | 710 | 416 |
| Terns | 0 | 0 | 0 |
| **Total** | **1,054** | **839** | **807** |
| | | **Sheepy Lake** | |
| Pelicans | 199 | 34 | 415 |
| Cormorants | 435 | 412 | 366 |
| Terns | 319 | 270 | 544 |
| **Total** | **953** | **716** | **1,325** |
| | | **Tule Lake Sump 1B** | |
| Pelicans | 36 | 15 | 15 |
| Cormorants | 517 | 263 | 489 |
| Terns | 775 | 278 | 72 |
| **Total** | **1,328** | **556** | **576** |

[a] *Counts derived from imagery acquired several weeks after the peak breeding period and may underestimate colony size.*

[b] *Nesting by cormorants and pelicans occurred on up to three different sites in Clear Lake Reservoir.*

[c] *Nesting by cormorants and pelicans occurred on up to five different sites within Upper Klamath NWR.*

Depending on the location and year, Forster's Terns (*Sterna forsteri*), Great Blue Herons (*Ardea Herodias*), Black-crowned Night-herons (*Nycticorax nycticorax*), Great Egrets (*A. alba*), California Gulls, and Ring-billed Gulls were also visible in aerial photography taken of nesting sites in the UKB. For Forster's Terns and herons/egrets, the numbers were small (< 20 adults per breeding season). Nesting gulls, however, were much more numerous (hundreds to thousands annually) and some gulls nested adjacent to (Clear Lake Reservoir) and amongst (Tule Lake and Sheepy Lake) nesting pelicans, cormorants, and terns. No (zero) gulls, however, nested on islands in Upper Klamath Lake.

PIT Tag Recovery – A total of 211 PIT tags from SARP releases were recovered from pelican, cormorant, and tern colonies during 2018–2020 (*Table 2)*. The number of tags recovered varied by colony location and year, with the majority of tags recovered on nesting sites located in Upper Klamath Lake (n = 152), followed by Sheepy Lake (n = 53), Tule Lake Sump 1B (n = 4) and Clear Lake Reservoir (n = 2). Tags were recovered from fish released at all sites in each year, with a similar proportion of released tags recovered from each release site, within each year (see *Appendix, Table A.1*). Results suggest SARP fish were equally susceptibly to avian predation across all release sites. By year, the largest number of tags (n = 113) were recovered following SARP releases in 2020 (*Table 2*).

Much larger numbers of tags from adult suckers were recovered on bird colonies in the UKB during 2009–2020. For instance, 2,255 tags from adult LRS, SNS, and SNS-KLS have been recovered on avian nesting sites since scanning efforts commenced in 2009 (see *Appendix, Table A.3*). A total of 55 tags from wild juvenile suckers have also been recovered since scanning efforts commenced in 2009 (*Appendix, Table A.3*).

Detection and Deposition Probabilities – Estimated detection probabilities were generally high (greater than 0.80 or 80%) at most nesting areas and years (*Table 4*). Estimates were also relatively consistent across years at the same nesting site. Results suggest that the majority of sucker PIT tags deposited by birds on their nesting colony were subsequently recovered by researchers following the breeding season.

Table 4. Estimated average annual detection probabilities (95% credible interval) of PIT tags on bird colonies in Clear Lake Reservoir, Upper Klamath Lake, Tule Lake Sump 1B, and Sheepy Lake during 2018–2020. Values were used to account 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) sown by researchers to model detection probabilities are also provided.

| Nesting Area | 2018 | 2019 | 2020 |
|---|---|---|---|
| Clear Lake Reservoir | 0.83 (0.68–0.92)<br>n = 200 | 0.88 (0.73–0.96)<br>n = 200 | 0.92 (0.81–0.97)<br>n = 250 |
| Upper Klamath Lake | 0.91 (0.79–0.97)<br>n = 200 | 0.85 (0.68–0.94)<br>n = 125 | 0.86 (0.69–0.94)<br>n = 150 |
| Sheepy Lake | 0.74 (0.61–0.84)<br>n = 75 | 0.89 (0.70–0.96)<br>n = 175 | 0.78 (0.55–0.91)<br>n = 200 |
| Tule Lake Sump 1B | 0.86 (0.63–0.96)<br>n = 50 | 0.91 (0.73–0.98)<br>n = 50 | 0.94 (0.73–0.99)<br>n = 50 |

Trial-specific deposition probabilities for pelicans nesting on Clear Lake Reservoir and Badger Island ranged from 0.30 (95% credible interval = 0.10–0.54) to 0.66 (0.47–0.90; *Figure 4*). There was no evidence that deposition probabilities varied significantly by trial or by colony (Clear Lake Reservoir, Badger Island; *Figure 4*). Average annual deposition probabilities were estimated to be 0.43 (0.31–0.59) and 0.50 (0.36–0.69) at Clear Lake Reservoir and Badger Island colonies, respectively. Average annual deposition probabilities from all trials (n = 6) and colonies (Clear Lake Reservoir, Badger Island) were estimated to be 0.47 (0.36–60). Results indicate that for every 100 tagged fish consumed by pelicans, on average, 47 tags (or 47%) were deposited on breeding colonies.

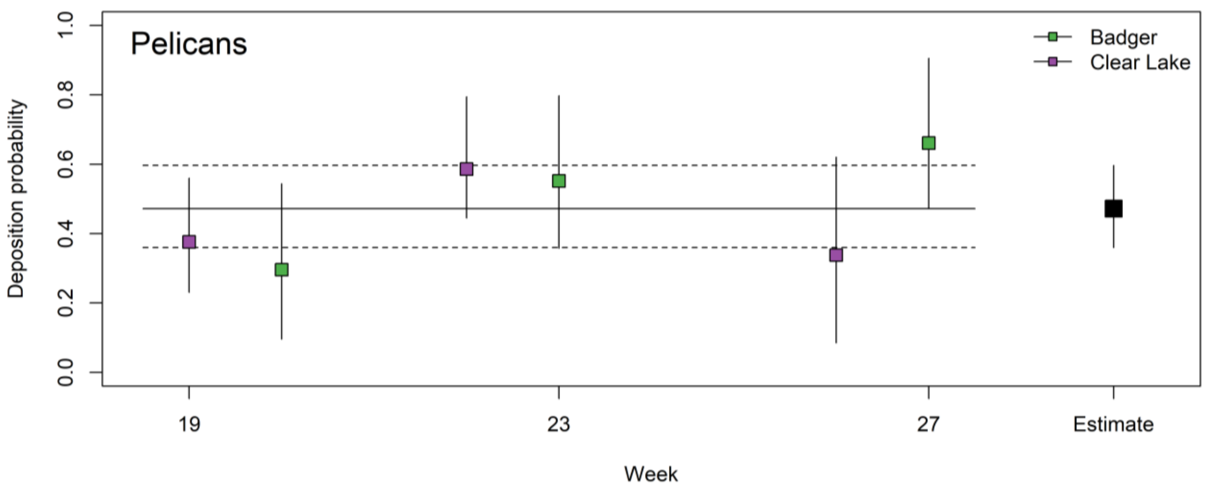


Figure 4. Trial-specific deposition probabilities (95% credible intervals) for American White Pelicans nesting on Badger Island and on Clear Lake Reservoir during 2020. Weeks are those of the Julian calendar. Solid line and black shaded symbol denote the average annual deposition probability estimated (Estimate) across all colonies. Dashed line is the associated 95% credible interval for all colonies. See *Table 1* for sample sizes of consumed PIT-tagged fish by pelican colony and trial.

Predation Rate Estimates – Predation rates on PIT-tagged SARP juvenile suckers, those corrected to account for detection and deposition probabilities, varied by nesting area and year (*Figure 5*). Of the nesting areas evaluated, predation probabilities were consistently the highest by pelicans and cormorants nesting in Upper Klamath Lake, with estimates ranging annually from 3.4% (95% CRI = 2.1–5.7%) to 5.1% (3.5–7.8%; *Figure 5*) during 2018–2020. Higher estimates of predation coincided with the close proximity of nesting sites in Upper Klamath Lake to release locations of SARP juveniles (*Figure 1* and *Appendix, Table A.1*). Predation rates by pelicans, cormorants, and terns nesting on Sheepy Lake were highly variable, ranging annually from 0.2% (< 0.1–0.8%) to 3.1% (1.8–6.9%), and indicated that birds were commuting from Sheepy Lake to forage on suckers in Upper Klamath Lake over 30 km away. Predation rates by pelicans and cormorants nesting on islands in Clear Lake Reservoir and terns nesting in Tule Lake Sump 1B were consistently the lowest of those observed at < 0.3% in all years (*Figure 5*). Clear Lake Reservoir and Tule Lake Sump 1B were the two nesting areas that were the greatest distance from Upper Klamath Lake at over 50 km away. Estimates of predation by all predator species (pelicans, cormorants, and terns) and all nesting areas (Upper Klamath Lake, Clear Lake Reservoir, Sheepy Lake, and Tule Lake) combined (i.e., cumulative impacts) on SARP releases ranged annually from 4.4% (2.9–

6.8%) to 8.8% (6.3–13.3%) during 2018–2020 *(Figure 5*). By year, predation rates were the highest in 2020, but estimates in 2020 were not significantly different from those observed in 2019 (*Figure 5*).

An investigation of predation on SARP juvenile suckers by predator species was limited to sites and years where tags were recovered for an area that was exclusively used by pelicans, cormorants, or terns, conditions that only occasionally occurred during the study period. At Tule Lake Sump 1B in 2018, tags were recovered from an area exclusively used by terns, and despite a large tern colony that year (775 adults; *Table 3*), predation rates were low at 0.3% (0.1–0.8%). At Upper Klamath Lake, tags were recovered from an area exclusively used by cormorants during all three study years, with predation rates ranging from 1.3% (0.7–2.5%) to 3.2% (2.1–5.3%), the highest predator-specific estimates observed. Cormorants were also the most numerous piscivorous waterbird species in Upper Klamath Lake in all three study years (*Table 3)*. In Clear Lake Reservoir, tags were recovered from an area exclusively used by pelicans in all three study years, but predation rates by both pelicans and cormorants were less than 0.3% (*Figure 5*), preventing a meaningful comparison of predation between predator species.

Predation rates by piscivorous colonial waterbirds on adult suckers and wild juvenile suckers in Upper Klamath Lake and Clear Lake Reservoir are provided in *Appendix, Table A.4*. These estimates update the minimum estimates of predation reported by Evans et al. (2016) by accounting for deposition probabilities. In brief, results suggested that predation rates on wild juvenile suckers in Upper Klamath Lake and Clear Lake Reservoir ranged annually from 4.7% (1.0–13.9%) to 14.9% (7.6–29.3%) during 2009–2020 (*Appendix, Table A.4*); estimates that were similar to or higher than those of SARP juvenile suckers. Predation rates on adult LRS, SNS, and SNS-KLS in Upper Klamath Lake and Clear Lake Reservoir ranged from 0.1% (< 0.1–0.2%) to 7.2% (3.9–14.0%) annually during 2009–2020 (*Appendix, Table A.4*). Predation rates on adult suckers, particularly LRS, were generally lower on fish in Upper Klamath Lake compared with Clear Lake Reservoir, with predation on LRS and SNS in Upper Klamath Lake less than 1.0% and 4.0%, respectively, during 2009-2020 (*Appendix, Table A.4*). Estimates were also often, but not always, less than 4.0% on adult suckers in Clear Lake Reservoir, with the highest estimates observed on SNS-KLS and LRS at 6.3% (4.3–11.4%) and 7.2% (3.9–14.0%), respectively, during 2013 (*Appendix, Table A.4*).

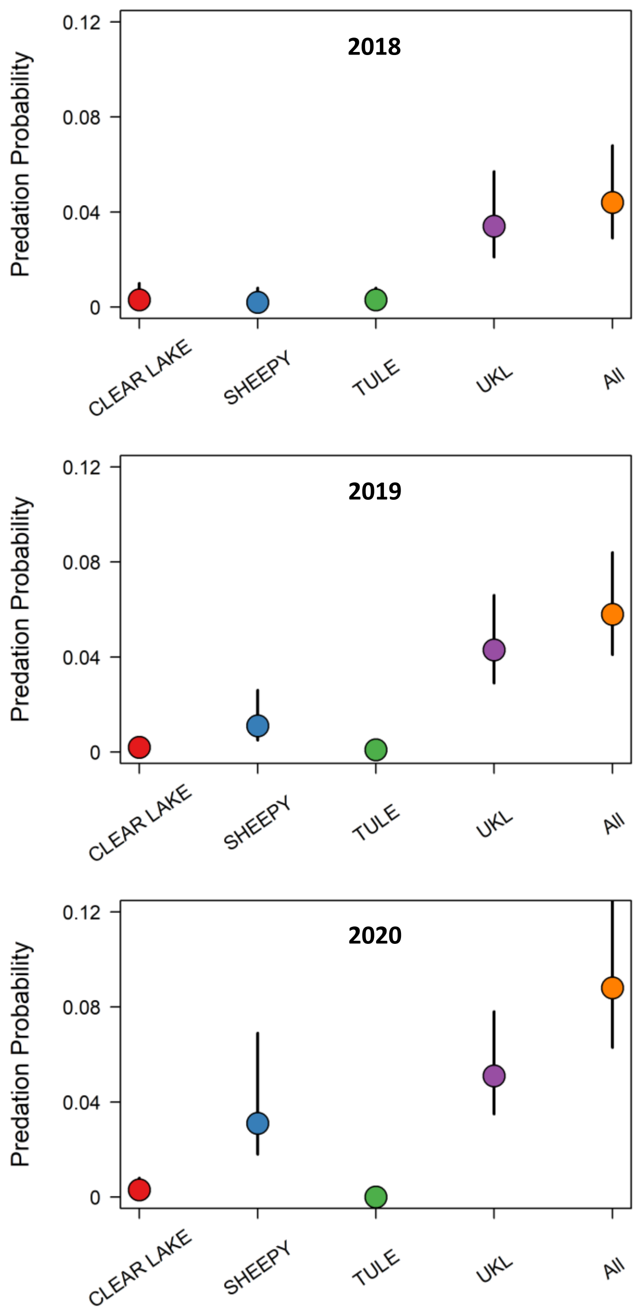


Figure 5. Estimated predation probabilities (proportion consumed; 95% credible intervals) by piscivorous colonial waterbirds nesting in Clear Lake Reservoir, Upper Klamath Lake (UKL), Tule Lake Sump 1B (TULE), and Sheepy Lake on Sucker Assisted Rearing Program (SARP) juvenile suckers during 2018-2020. Predation by all colonies (All) combined is also depicted.

## DISCUSSION

Results of this study provide the first estimates of PIT-tag deposition probabilities from breeding colonies of American White Pelicans. Pelican deposition probabilities, coupled with previously published Double-crested Cormorant and Caspian Tern deposition probabilities and colony-specific detection probabilities, provided the necessary data to generate unbiased estimates of predation on releases of PIT-tagged SARP juvenile suckers during 2018–2020. Estimates of deposition and detection probabilities were also used to retrospectively analyze and update the minimum estimates of predation on PIT-tagged adult suckers and wild juvenile suckers reported by Evans et al. (2016) during 2009–2020. Collectively, results provide a more comprehensive assessment of piscivorous colonial waterbird predation on ESA-listed suckers in the Upper Klamath Basin.

Results of deposition trials indicated that for every 100 PIT tags consumed by nesting pelicans, on average, 47 were deposited on-colony where researchers could potentially recover them following the breeding season. Teuscher et al. (2015) also investigated pelican predation on PIT-tagged fish of conservation concern and fed PIT-tagged fish with known tag codes to pelicans. Estimates of detection probabilities, however, were unavailable, so it was unknown what proportion of consumed tags were lost due to off-colony deposition of tags versus the imperfect detection of tags on bird colonies by researchers following the breeding season. Results of this and other studies indicate that detection probabilities vary by colony, year, and week, necessitating a direct measure of detection efficiency at each colony in each year (Evans et al. 2012, Osterback et al. 2013, Hostetter et al. 2015, Evans et al. 2016, Payton et al. 2019). Similar to the results of the cormorant and tern deposition study conducted by Hostetter et al. (2015), pelican deposition probabilities did not vary significantly by trial or period within the breeding season, or by colony location. Small sample sizes of consumed tagged fish during some trials, however, resulted in imprecise weekly estimates of pelican deposition probabilities and results were limited to a single year (2020). Despite these caveats, due to the lack of intra-annual variation in estimates of deposition and similar estimates of deposition from two different pelican colonies, results suggest that the pelican deposition estimate derived from this study may be applicable or appropriate for use in other American white pelican predation studies utilizing PIT-tagged fish.

Estimates of pelican deposition probabilities (0.47, 95% credible interval [CRI] = 0.36–0.60) were very similar to those of cormorants (0.51, 95% CRI = 0.34–0.70; Hostetter et al. 2015). Deposition probability estimates in pelicans and cormorants were, however, lower than those of terns (0.71, 95% CRI = 0.51–0.89; Hostetter et al. 2015). Several of the nesting areas scanned for sucker PIT tags in the UKB were from mixed-species breeding sites, sites where the depredating predator (pelican, cormorant, or tern) was unknown. Results suggest that the assumption of equal deposition via use of an average pelican and cormorant deposition probability (ca. 0.50, 95% CRI = 0.27–0.69) at breeding sites on Clear Lake Reservoir and Upper Klamath Lake had little influence on estimates of predation probabilities because estimates of pelican and cormorant deposition were so similar. Estimates of average pelican, cormorant, and tern deposition probabilities (ca. 0.56, 95% CRI = 0.25–0.82) at nesting sites in Sheepy Lake, however, could have slightly underestimated predation if most of the tags were deposited by pelicans and cormorants or slightly overestimated predation if most of the tags were deposited by terns. For instance, a predation rate of 5% based on a mixed pelican/cormorant/tern colony deposition probability would be closer to 4% if most of the recovered tags were actually consumed and deposited by terns or, conversely, closer to 6% if most of the tags were actually consumed and deposited by pelicans or cormorants.

Accounting for all nesting colonies, predation by pelicans, cormorants, and terns on SARP juvenile suckers released into the Upper Klamath Lake system accounted for an estimated 4 to 9% of available suckers annually.  Given the ESA status of these fish, impacts may be considered substantial by managers. However, SARP suckers appear to suffer high mortality within the first year of release, which is consistent with the poor survival observed for wild juvenile suckers (Burdick and Martin 2017). Of the SARP suckers released as part of this study, less than 1% were subsequently detected on remote PIT tag antennas in the Upper Klamath Lake system more than five months after their release, through spring of 2021. Continued monitoring for PIT tag detections in the Upper Klamath Lake system may reveal more detections of SARP suckers in future years. Results of a telemetry study conducted on SARP suckers released in the spring of 2018 and 2019 also suggested that substantial mortality occurred, with the majority of suckers presumably dead by the end of the summer each year following release (M. Shaffer, USFWS, personal communication). Detection histories of these radio-tagged SARP suckers showed that they used a variety of habitats around Upper Klamath Lake following release, regardless of release location and year. This finding is consistent with our results showing that the proportion of recovered PIT tags from SARP sucker releases did not vary among release locations. Overall, evidence suggests that pelican, cormorant, and tern predation represented a relatively small component of the apparently high total mortality experienced by SARP suckers during 2018–2020.

There was some evidence that predation impacts on wild juvenile suckers were higher than those on captive-reared SARP juvenile suckers. Small sample sizes of wild suckers, however, resulted in imprecise estimates of predation, so relative differences in predation between wild and SARP suckers should be interpreted cautiously. Comparisons do provide evidence that suckers reared in captivity were not substantially more susceptible to predation than their wild counterparts, as some other studies have demonstrated (Fritts et al. 2007, Hostetter et al. 2012). Slightly higher rates of predation in wild juveniles could be associated with differences in the temporal availability of SARP suckers versus wild suckers, where wild suckers were available as prey throughout the entire nesting season (March to August) while some SARP fish were released into the Upper Klamath Lake system during or following the nesting season. Mortality of SARP suckers associated with factors other than avian predation could also influence the number of SARP fish available to predators compared with naturally-reared suckers. Larger sample sizes of wild PIT-tagged juvenile suckers and comparisons of predation on a known number of wild and SARP juvenile suckers at the same location and time would help to better understand sucker susceptibility to colonial waterbird predation based on rearing history. However, poor first year survival of wild suckers makes it difficult to obtain larger sample sizes of tagged juveniles.

A retrospective analysis of data indicated that predation on adult suckers was consistently lower than that observed on juvenile suckers. The greater susceptibility of juvenile suckers to avian predation is likely due, in part, to the gap width and size of terns, cormorants, and pelicans, with terns capable of consuming fish upward of 280 mm, cormorants upwards of 450 mm, and pelicans upwards of 730 mm (Hatch and Weseloh 1999, Hostetter et al. 2012, Evans et al. 2016). As such, juvenile suckers are subject to predation by all three predators (terns, cormorants, and pelicans) but terns are not capable of consuming adult-sized suckers, and many of the larger-sized adult suckers, particularly LRS, exceed the gap width of cormorants. Pelicans on the other hand can consume all but the largest of LRS (Evans et al. 2016). The smaller size of juvenile suckers may also increase their susceptibility to other piscivorous waterbird species, species that were not investigated as part of this study. For instance, Forster's Terns, herons, Common Mergansers [*Mergus merganser*], and grebes [*Aechmophorus* spp.] may be consuming juvenile suckers but impacts to adult-sized suckers from these species are likely small or non-existent. Furthermore, these species are less numerous compared with pelicans, cormorants, and terns in the UKB (Evans et al. 2016). In the case of gulls (*Larus* spp.), which are not strictly piscivorous but are numerous in the UKB (several thousand breeding adults annually), no (zero) sucker PIT tags have been recovered on colony areas exclusively used by nesting gulls (authors, unpublished data), suggesting gull impacts to both juvenile and adult suckers were small or non-existent. In addition to avian species, the impacts to suckers from piscivorous predators, like Rainbow Trout and non-native Brown Bullhead Catfish (*Ameiurus nebulosus*), are unknown but could also contribute to juvenile sucker mortality. For instance, Rainbow Trout have been confirmed to feed on sucker eggs and juvenile suckers in Upper Klamath Lake in the spring (S. Burdick, USGS, personal communication).

Predation impacts reported herein are on a seasonal or annual basis, but the overall effects of avian predation on sucker populations may be greater than what is implied by annual estimates of predation alone. For instance, annual predation rates of 1–7% on adult suckers over the course of many years with little or no juvenile recruitment will reduce the number of spawning adults. While lack of recruitment continues to be the primary limiting factor to spawning populations in Upper Klamath Lake (Burdick et al. 2018), recent reports suggest that limited or infrequent access to spawning tributaries or an inability to return to Clear Lake Reservoir after spawning are limiting factors for populations of suckers in that system, and these factors appear to correspond with higher susceptibility to avian predation (Burdick et al. 2018, Hewitt et al. 2021, Banet et al. 2021). Predation of suckers in spawning tributaries to Clear Lake Reservoir have also been confirmed (Banet et al. 2021), similar to predation of Bonneville Cutthroat Trout (*O. clarkii utah*), Yellowstone Cutthroat Trout (*O. clarkii bouvieri*), Lahontan Cutthroat Trout (*O. clarkii henshawi*), and Cui-ui (*Chasmistes cujus*) during spawning migrations by pelicans and cormorants in other systems (Scoppettone et al. 2014, Teuscher et al. 2015, Budy et al. 2016). Lower Clear Lake Reservoir water levels that resulted in limited (2013) or no (2015) access to spawning tributaries also corresponded with higher avian predation (Banet et al. 2021, Hewitt et al. 2021). The large number of pelicans nesting at Clear Lake Reservoir in 2020 was similar to the number present in 2013 (Evans et al. 2016), however, predation rates, on average, were lower in 2020 than in 2013. This may have been due to higher water levels in 2020 relative to 2013, which likely reduced pelican access to spawning suckers in 2020. Although avian predation was not the original cause of sucker declines in the UKB, piscivorous colonial waterbirds may now be contributing to the lack of recovery of ESA-listed suckers because avian predators are consuming adult suckers during a time period with little or no juvenile recruitment.

Breeding populations of pelicans, cormorants, and terns, all native piscivorous colonial waterbirds, have historically nested at colonies in the UKB (Shuford 2010). Results of this and other studies indicate that colony sizes in the UKB vary substantially by species, colony, and year (Shuford 2010, Evans et al. 2016, Lawes et al. 2021). This is typical of historical piscivorous waterbird breeding colonies in high desert wetland ecosystems, such as those in the Harney Basin and Warner Valley, OR where suitable nesting habitat varies based on fluctuating water levels due to periodic drought and flooding events (Lawes et al. 2021). Given that habitat conditions can vary on an annual basis and that these piscivorous waterbirds are long-lived species (in excess of 20 years; Suryan et al. 2004, Roby et al. 2021), individuals can nest at multiple colony sites over the course of their lifetime. For instance, banding data from Caspian Terns shows connectivity amongst and between colonies in Columbia River Basin and the UKB (Roby et al. 2021). Despite the relatively large number of terns breeding on Tule Lake Sump 1B and Sheepy Lake during 2018-2020, predation rates on juvenile suckers were low to non-existent and terns are not capable of consuming adult suckers. All SARP fish and most adult suckers, however, are susceptible to predation by cormorants and pelicans. In recent years, the cormorant colonies in the Klamath Basin were larger than those in the Columbia Plateau region but substantially smaller than those in the Columbia River estuary (Roby et al. 2021). Although there is little to no connectivity between colony sites for cormorants located along the coast with those located at interior sites in the Pacific Northwest, some connectivity exists amongst and between interior cormorant colony sites (Courtot et al. 2012, Cramer et al. 2021, Roby et al. 2021). Outside of the UKB, pelican populations have been shown to be increasing in other interior regions, such as Strawberry Reservoir in Utah (Budy et al. 2016) and Badger Island in the Columbia Plateau region (Cramer et al. 2021), and these colonies also show connectivity to the UKB based on PIT tag recoveries of fish on UKB colonies (authors unpublished data). Variable colony sizes of piscivorous waterbird species and colonies in the UKB are likely expected in future years, particularly in a region that continues to experience highly variable hydrologic conditions. This, in part, will impact predation pressure on ESA-listed suckers in the UKB.

Finally, although more accurate estimates of predation by pelicans, cormorants, and terns were generated as part of this study, several uncertainties remain regarding the degree to which predation limits sucker survival in the UKB. More specifically, estimates of the survival of SARP released juvenile suckers are currently lacking but are necessary to determine what proportion of all sources of SARP mortality were due to avian predation. Although beyond the scope of this study, recently developed state-space mark-recapture-recovery models, which incorporate tag detections from both live and dead animals (King 2012, Hostetter et. 2018, Payton et al. 2019), could be used to jointly estimate predation and survival in the same group of tagged fish, providing a better understanding of predation across space and time, and the importance of avian predation relative to other sources of mortality experienced by suckers in the UKB. These models could also begin to evaluate the degree to which environmental conditions experienced by suckers, 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 UKB (Evans et al. 2016, Banet et al. 2021). Similarly, for SARP released suckers, the effects of release size, location, and timing of release (e.g., spring, fall, winter season) on overall mortality and avian predation could be evaluated if releases were designed to provide contrast in these factors. Addressing these remaining uncertainties would help resource managers better understand the impacts of predation by piscivorous waterbirds on the survival of ESA-listed sucker populations in the UKB.

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## APPENDIX

Table A.1. Numbers of PIT-tagged Sucker Assisted Rearing Program (SARP) juvenile suckers released into Upper Klamath Lake or its tributaries that were subsequently recovered on colonial waterbird nesting sites during 2018–2020. See *Figure 1* for a map of release sites. The number of tags recovered was not adjusted to account for detection or deposition probabilities and thus represent minimum numbers of consumed tagged fish.

| Year | Release Site | No. Released | No. Recovered |
|---|---|---|---|
| 2018 | Malone Springs | 100 | 2 |
| | Rocky Point | 933 | 15 |
| | Shoalwater Bay | 563 | 4 |
| | TNC Boat Ramp | 739 | 16 |
| | **Total 2018** | **2,335** | **37** |
| 2019 | Hanks Marsh | 929 | 16 |
| | Odessa Springs | 460 | 7 |
| | Pelican Bay | 1,032 | 27 |
| | TNC Boat Ramp | 590 | 11 |
| | **Total 2019** | **3,011** | **61** |
| 2020 | Malone Springs | 656 | 19 |
| | Odessa Springs | 1,063 | 34 |
| | Pelican Bay Mo. | 140 | 3 |
| | Williamson TNC | 225 | 8 |
| | Williamson Mouth | 1,427 | 49 |
| | **Total 2020** | **3,511** | **113** |

Table A.2. Numbers of PIT-tagged naturally-reared (wild) juvenile suckers, Sucker Assisted Rearing Program (SARP) juvenile suckers, and adult Lost River Suckers (LRS), Shortnose Suckers (SNS), or Shortnose/Klamath Largescale suckers (SNS-KLS) available to piscivorous waterbirds nesting at colonies in the Upper Klamath Basin during 2009–2020. SARP releases were first conducted in Upper Klamath Lake starting in 2018 (see also Table 2). Only suckers tagged with 134 kHz PIT tags and where > 100 tagged suckers were annually released or re-encountered (i.e. previously tagged) are reported.

| Release Location | Sucker Group | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Upper Klamath Lake | Adult LRS | 14,211 | 17,224 | 19,893 | 22,607 | 24,709 | 26,298 | 28,278 | 31,069 | 16,972 | 17,728 | 16,423 | 17,314 |
| | Adult SNS | 4,766 | 6,407 | 5,592 | 5,979 | 5,522 | 5,603 | 6,185 | 6,828 | 4,526 | 4,525 | 4,009 | 4,011 |
| | Juvenile (Wild) | 170 | | 170 | 218 | | | | | | | | |
| | Juvenile (SARP) | | | | | | | | | | 2,335 | 3,011 | 3,512 |
| Clear Lake Reservoir | Adult LRS | 185 | 299 | 469 | 513 | 721 | 674 | 469 | 833 | 1,080 | 889 | 1,354 | 957 |
| | Adult SNS-KLS | 1,010 | 2,445 | 3,363 | 1,220 | 2,070 | 2,375 | 3,153 | 5,415 | 4,249 | 2,887 | 4,140 | 2,034 |
| | Juvenile (Wild) | | | | | | | | | 148 | | 139 | 111 |

Table A.3. Numbers of PIT-tagged adult Lost River Suckers (LRS), Shortnose Suckers (SNS), Klamath Largescale Suckers (KLS), and SNS-KLS Suckers and juvenile suckers (species unknown), including Sucker Assisted Rearing Program (SARP) and naturally-reared (wild) suckers, recovered on avian colonies in the Upper Klamath Basin during 2009−2020. Numbers 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 site. Nesting locations represent mixed-species colonies of American White Pelicans, Double-crested Cormorants, Caspian Terns, and potentially other species breeding on islands within Clear Lake Reservoir, Upper Klamath Lake, Sheepy Lake, and Tule Lake Sump 1B (see Methods and Evans et al. 2016). Not all nesting locations were used during each breeding season in all years. Dashes (–) denote that scanning for PIT tags did not take place that year at that site. Releases of SARP juveniles did not commence until 2018. The number of tags was not adjusted to account for detection or deposition probabilities and thus represent minimum numbers of consumed tagged fish.

| Location [1] | Sucker Group [2] | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 | **Total** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clear Lake Reservoir | Adult LRS | 45 | 18 | 4 | 42 | 45 | 29 | 15 | 7 | 16 | 16 | 6 | 9 | **252** |
| | Adult SNS-KLS | 187 | 57 | 77 | 159 | 162 | 111 | 38 | 111 | 60 | 64 | 41 | 43 | **1110** |
| | Juvenile (Wild) | 0 | 0 | 0 | 4 | 1 | 0 | 1 | 0 | 1 | 1 | 5 | 7 | **20** |
| | Juvenile (SARP) | | | | | | | | | | 1 | 0 | 2 | **3** |
| Upper Klamath Lake | Adult LRS | 38 | 1 | – | 72 | 13 | 29 | 14 | – | 116 | 136 | 8 | 5 | **432** |
| | Adult SNS | 39 | – | – | 68 | 1 | 25 | 18 | – | 99 | 83 | 2 | 2 | **337** |
| | Adult KLS | 15 | 2 | – | 6 | 4 | 2 | 2 | – | 4 | 3 | 1 | 0 | **39** |
| | Juvenile (Wild) | 6 | 0 | – | 8 | 0 | 1 | 2 | – | 1 | 0 | 0 | 0 | **18** |
| | Juvenile (SARP) | | | | | | | | | | 32 | 50 | 87 | **169** |
| Sheepy Lake | Adult LRS | 1 | – | – | 3 | 0 | – | – | 17 | 11 | 4 | 3 | 0 | **39** |
| | Adult SNS | 2 | – | – | 1 | 0 | – | – | 10 | 13 | 6 | 3 | 1 | **36** |
| | Adult SNS-KLS | 0 | – | – | 0 | 0 | – | – | 1 | 0 | 0 | 0 | 0 | **1** |
| | Juvenile (Wild) | 0 | – | – | 0 | 0 | – | – | 2 | 0 | 0 | 0 | 7 | **9** |
| | Juvenile (SARP) | | | | | | | | | | 1 | 12 | 41 | **54** |
| Tule Lake | Adult LRS | – | – | – | – | – | 1 | 0 | 0 | – | 0 | 0 | 0 | **1** |
| | Adult SNS | – | – | – | – | – | 0 | 0 | 0 | – | 0 | 2 | 0 | **2** |
| | Adult SNS-KLS | – | – | – | – | – | 1 | 1 | 3 | – | 0 | 0 | 1 | **6** |
| | Juvenile (Wild) | – | – | – | – | – | 0 | 0 | 0 | – | 6 | 2 | 0 | **8** |
| | Juvenile (SARP) | | | | | | | | | | 4 | 1 | 0 | **5** |
| **ALL** | | **333** | **78** | **81** | **363** | **226** | **199** | **91** | **151** | **321** | **357** | **136** | **205** | **2,541** |

*[1] PIT tags recovered from multiple nesting sites within each waterbody; see Figure 1*

*[2] Unidentified suckers (adults or juveniles of unknown origin) or suckers salvaged from canals or used in net pen experiments were excluded*

Table A.4. Retrospectively analyzed estimates of predation rates (95% credible intervals) on ESA-listed PIT-tagged Lost River Suckers (LRS), Shortnose Suckers (SNS), Shortnose/Klamath Largescale Suckers (SNS-KLS), naturally-reared (wild) juvenile suckers, and SARP juvenile suckers by piscivorous colonial waterbirds nesting at colonies in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake Sump 1B, and Sheepy Lake combined (i.e., cumulative predation effects). Predation estimates are adjusted to account for PIT tag detection and deposition probabilities that were unique to each predator species, colony, and year (see Methods). Dashed line (–) denotes that sample sizes of available tagged fish were fewer than 100 or that PIT tag recovery did not occur at that site in that year. SARP releases commenced in Upper Klamath Lake in 2018. Estimates update the minimum estimates of predation reported by Evans et al. (2016) during 2009–2014.

| | **Upper Klamath Lake Suckers** | | | | **Clear Lake Reservoir Suckers** | | |
|---|---|---|---|---|---|---|---|
| Year | LRS | SNS | Wild Juvenile | SARP | LRS | SNS-KLS | Wild Juveniles |
| 2009 | 0.5% (0.3–1.1) | 1.6% (1.0–2.9) | 13.9% (6.0–27.9) | | 7.1% (2.4–18.7) | 4.6% (2.9–8.8) | – |
| 2010 | – | – | – | | 0.7% (0.2–4.1) | 0.7% (0.2–2.0) | – |
| 2011 | – | – | – | | 0.4% (0.1–2.3) | 3.4% (2.0–6.5) | – |
| 2012 | 1.1% (0.7–1.7) | 3.8% (2.7–6.3) | 14.9% (7.6–29.3) | | 3.0% (1.2–10.2) | 2.5% (1.0–6.2) | – |
| 2013 | – | – | – | | 7.2% (3.9–14.0) | 6.3% (4.3–11.4) | – |
| 2014 | 0.1% (<0.1–0.3) | 0.8% (0.4–1.7) | – | | 2.2% (0.8–5.6) | 1.9% (1.0–4.0) | – |
| 2015 | 0.2% (0.1–0.4) | 0.8% (0.4–1.4) | – | | 2.5% (0.8–6.5) | 1.4% (0.7–3.0) | – |
| 2016 | – | – | – | | 1.7% (0.6–4.0) | 4.2% (2.9–7.0) | – |
| 2017 | 1.1% (0.7–1.7) | 3.7% (2.5–6.1) | – | | 0.4% (0.1–1.5) | 1.9% (1.1–3.6) | 4.7% (1.0–13.9) |
| 2018 | 1.0% (0.7–1.8) | 2.6% (1.7–4.3) | – | 4.4% (2.9–6.8) | 2.4% (1.0–5.3) | 1.0% (0.4–2.2) | – |
| 2019 | 0.3% (0.2–0.5) | 0.9% (0.5–1.5) | – | 5.8% (4.1–8.4) | 0.5% (0.2–1.6) | 1.8% (1.0–3.2) | 6.7% (1.8–18.2) |
| 2020 | 0.1% (<0.1–0.2) | 0.5% (0.2–1.0) | – | 8.8% (6.3–13.3) | 1.2% (0.4–3.4) | 2.1% (1.1–4.7) | 12.7% (4.5–30.0) |