Prepared in cooperation with the Bureau of Reclamation

Status and Trends of Adult Lost River (*Deltistes luxatus*) and Shortnose (*Chasmistes brevirostris*) Sucker Populations in Upper Klamath Lake, Oregon, 2017

Open-File Report 2018–1064

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Conversion Factors

International System of Units to Inch/Pound

Multiply	By	To obtain
	Length	
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as:

°F = (1.8 × °C) + 32.

Acronyms

CJS	Cormack-Jolly-Seber
FL	fork length
LRS	Lost River sucker
PIT	passive integrated transponder
SNS	shortnose sucker
UKL	Upper Klamath Lake

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Executive Summary

Data from a long-term capture-recapture program were used to assess the status and dynamics of populations of two long-lived, federally endangered catostomids in Upper Klamath Lake, Oregon. Lost River suckers (LRS; *Deltistes luxatus*) and shortnose suckers (SNS; *Chasmistes brevirostris*) have been captured and tagged with passive integrated transponder (PIT) tags during their spawning migrations in each year since 1995. In addition, beginning in 2005, individuals that had been previously PIT-tagged were re-encountered on remote underwater antennas deployed throughout sucker spawning areas. Captures and remote encounters during the spawning season in spring 2016 were incorporated into capture-recapture analyses of population dynamics.

Cormack-Jolly-Seber (CJS) open population capture-recapture models were used to estimate annual survival probabilities, and a reverse-time analog of the CJS model was used to estimate recruitment of new individuals into the spawning populations. In addition, data on the size composition of captured fish were examined to provide corroborating evidence of recruitment. Model estimates of survival and recruitment were used to derive estimates of changes in population size over time and to determine the status of the populations through 2015. Separate analyses were done for each species and also for each subpopulation of LRS. Shortnose suckers and one subpopulation of LRS migrate into tributary rivers to spawn, whereas the other LRS subpopulation spawns at groundwater upwelling areas along the eastern shoreline of the lake.

Capture-recapture analyses indicated that with a few exceptions, the survival of males and females in both Lost River sucker subpopulations was high (greater than 0.88) from 1999 to 2015. Survival was notably lower for males from the river in 2000, 2006, and 2012, and for the shoreline areas in 2002. From 2001 to 2015, the abundance of males in the lakeshore spawning subpopulation decreased by at least 64 percent and the abundance of females decreased by at least 56 percent. Capture-recapture models suggested that the abundance of both sexes in the river spawning subpopulation of LRS had increased substantially since 2006; increases were mostly due to large estimated recruitment events in 2006 and 2008. We know that the estimates in 2006 are substantially biased in favor of recruitment because of a sampling issue. We are skeptical of the magnitude of recruitment indicated by the 2008 estimates as well because (1) few small individuals that would indicate the presence of new recruits were captured in that year, and (2) recapture probabilities in recruitment models based on just physical recaptures of fish were lower than desired for robust inferences from capture-recapture models. If we assume instead that little or no recruitment occurred for this subpopulation, the abundance of both sexes in the river spawning subpopulation likely has decreased at rates similar to the rates for the lakeshore spawning subpopulation from 2002 to 2015.

Shortnose suckers experienced lower and more variable annual survival than either LRS subpopulation. Annual survival of both sexes was relatively low in 2003, 2004, 2010, and 2012. In addition, female survival was low in 1999 and 2000 while male survival was low in 2002. Survival estimate precision in early years of the study; however, are poor. Capture-recapture models and size composition data indicate that recruitment of new individuals into the SNS spawning population was trivial from 2001 to 2005. Models indicate that more than 10 percent of the population was new recruits in a number of more recent years. As a result, capture-recapture modeling suggests that the abundance of adult spawning SNS was relatively stable from 2006 to 2010. We are skeptical of the estimated recruitment in 2006 because of the known sampling issue. We also are skeptical of the estimated recruitment in other recent years because few small individuals that would indicate the presence of new recruits were captured in any of those years, and recapture probabilities in recruitment models were low. The best-case scenario for SNS, based on capture-recapture recruitment modeling, indicates that the abundance of males in the spawning population decreased by 78 percent and the abundance of females decreased by 77 percent from 2001 to 2015. Decreases in abundance for both sexes are likely greater than these estimates indicate.

Despite relatively high survival in most years, we conclude that both species have experienced substantial decreases in the abundance of spawning adults because losses from mortality have not been balanced by recruitment of new individuals. Although capture-recapture data indicate substantial recruitment of new individuals into the spawning populations for SNS and river spawning LRS in some years, size data do not corroborate these estimates. As a result, the status of the endangered sucker populations in Upper Klamath Lake remains distressed, especially for SNS. Our monitoring program provides a robust platform for estimating vital population parameters, evaluating the status of the populations, and assessing the effectiveness of conservation and recovery efforts.

Introduction

Lost River suckers (LRS; *Deltistes luxatus*) and shortnose suckers (SNS; *Chasmistes brevirostris*) are long-lived catostomids that are endemic to the Upper Klamath River Basin in southern Oregon and northern California (Scoppettone and Vinyard, 1991). Historical accounts indicate that both species once were extremely abundant throughout the upper basin and were caught in a subsistence fishery by Native Americans and later in a popular recreational snag fishery that was closed in 1987 (Markle and Cooperman, 2002). Decreasing population abundance trends and range reductions were noted for both species as early as the mid-1960s. However, the extent of these declines was not evident until the mid-1980s when recreational catch rates showed substantial decreases that were partly attributed to overfishing (Markle and Cooperman, 2002; National Research Council, 2004). Estimated annual fishery harvest of spawning suckers in the Williamson and Sprague Rivers, tributaries to Upper Klamath Lake in Oregon, decreased from more than 10,000 fish in 1968 to 687 fish in 1985 (Markle and Cooperman, 2002). In addition to decreasing catches, age data from suckers collected during a 1986 fish die-off indicated that the LRS population was composed of old individuals and that no substantial recruitment had occurred during the previous 15 years (Scoppettone and Vinyard, 1991; U.S. Fish and Wildlife Service, 1993). These findings led to the Federal listing of both species under the Endangered Species Act in 1988 (U.S. Fish and Wildlife Service, 1988). Upper Klamath Lake contains the largest remaining population of LRS (National Research Council, 2004) and one of the largest remaining populations of SNS.

Life history and spawning characteristics of suckers in Upper Klamath Lake are reasonably well documented (Scoppettone and Vinyard, 1991; Moyle, 2002; Cooperman and Markle, 2003). Age estimates for LRS have exceeded 50 years, and age estimates for SNS have exceeded 30 years (National Research Council, 2004; Terwilliger and others, 2010). Both species are obligate lake dwellers that make spawning migrations from March to May of each year. Shortnose suckers spawn primarily in the Williamson and Sprague Rivers, but two distinct subpopulations of LRS have been identified in Upper Klamath Lake (National Research Council, 2004). One subpopulation spawns in the Williamson and Sprague Rivers, and the other subpopulation spawns at several groundwater upwelling areas (referred to as springs) along the eastern shoreline of the lake below Modoc Rim (fig. 1). Capture-recapture data show an extremely high degree of spawning site fidelity and little reproductive mixing between the two subpopulations (Janney and others, 2008; Hewitt and others, 2012).

Although fishing mortality was eliminated with the closure of the recreational fishery in 1987, poor survival of adult suckers is still considered a factor that can potentially limit recovery of Upper Klamath Lake populations (Janney and others, 2008). Upper Klamath Lake is a large, shallow system that has progressed to a hypereutrophic state because of increased nutrient loading from wetland drainage, grazing, and timber harvest (Bradbury and others, 2004; Eilers and others, 2004). These conditions lead to massive blooms of the cyanobacterium *Aphanizomenon flos-aquae* from June to October of each year (Wood and others, 2006; Hoilman and others, 2008; Lindenberg and others, 2009; Eldridge and others, 2012). The algal blooms and their subsequent die-offs produce water quality conditions that are harmful to fish health—low concentrations of dissolved oxygen, elevated concentrations of un-ionized ammonia, high pH, and high concentrations of toxic microcystins (Kann and Smith, 1999; Eldridge and others, 2013). Poor water quality conditions are thought to have contributed to a number of substantial fish die-offs in the lake, most recently during the summers of 1986, 1995, 1996, and 1997 (Perkins and others, 2000; National Research Council, 2004), and to a much lesser extent in 2003.

In this report, we analyze capture-recapture data from 1999 to 2016 to evaluate demographic trends in LRS and SNS spawning populations. Annual adult survival and recruitment probabilities were modeled and compared to assess differences attributable to species, LRS subpopulation, sex, and year. We used model-averaged estimates of these probabilities to calculate estimates of population rate of change and to determine status as of spring 2014. In addition to estimating recruitment from capture-recapture data, we assessed relative changes in size composition to provide additional insight into the frequency and magnitude of recruitment into the spawning populations.

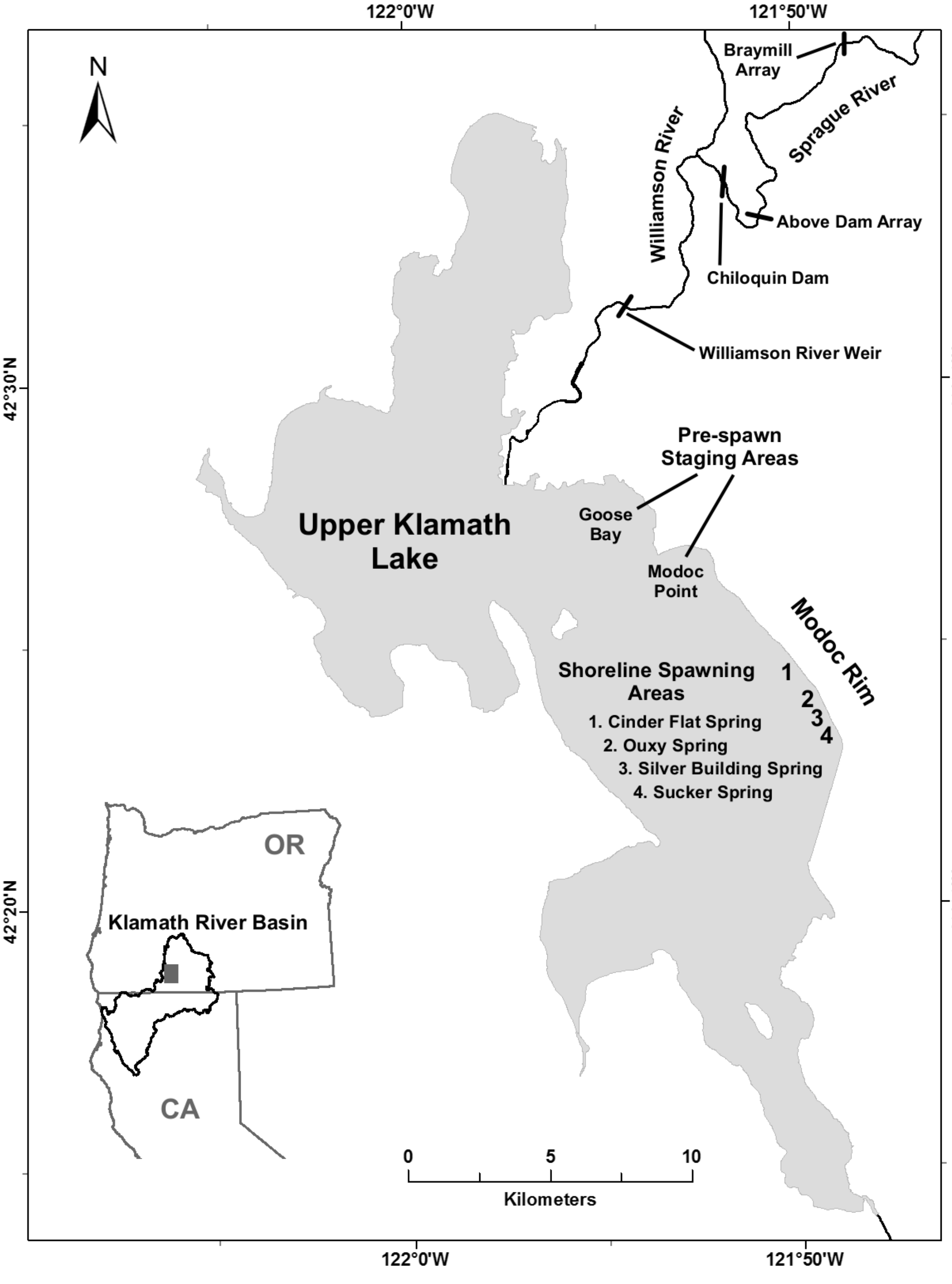

Figure 1. Map showing sampling locations for Lost River suckers and shortnose suckers in Upper Klamath Lake and its tributaries, Oregon. The inset shows the Klamath River Basin and the location of Upper Klamath Lake in south-central Oregon.

Methods

Sampling and Fish Handling

Lost River suckers from the subpopulation that spawns at springs along the eastern shoreline of Upper Klamath Lake were sampled at four locations (fig. 1) using 30-m trammel nets (1.8 m high; two 30-cm mesh outer panels; one 3.8-cm mesh inner panel; foam-core float line; lead-core bottom line). Nets generally were set twice per week at each spawning area from February to May from 1999 to 2015. The only exception to this sampling schedule occurred in 2006, when each spawning area was sampled only once per week. Nets were set starting at the shoreline and extending out in a semicircular fashion, encompassing the area where spawning activity was concentrated.

Lost River and shortnose suckers also were sampled at two locations in tributary rivers. From 2000 to 2008, fish were sampled three times per week at the Chiloquin Dam fish ladder on the Sprague River (fig. 1). Before sampling, a screen was placed over the bottom entrance (outflow) to prevent fish from exiting, and the upstream end (inflow) was blocked by a board to lower the water level in the cells of the fish ladder. A combination of dip nets and short trammel nets were used to collect fish trapped in the ladder. Chiloquin Dam and the associated fish ladder were removed from the river in the late summer and autumn of 2008. Beginning in 2005 and continuing through 2016, a resistance board weir (described in detail by Tobin, 1994) was installed on the Williamson River at river kilometer 10 to improve capture rates of suckers during the spawning migrations (fig. 1). The weir restricted the passage of suckers to two short sections, each fitted with a live trap. An upstream trap was used to capture fish as they migrated upriver, and a downstream trap was left open to allow downriver migrating suckers to pass the weir. High flows in the Williamson River during most of the 2006 spawning season inundated the weir and allowed fish to pass over and around the weir without swimming through the upstream trap. The weir was not installed or operated during the 2017 spawning season due to high flows.

Additional trammel net sampling for pre-spawn adult suckers of both species was conducted from 1995 to 2017 at various staging areas in Upper Klamath Lake. Most of this sampling, especially after 2005, has taken place near Modoc Point and Goose Bay (fig. 1). From 1995 to 2006, pre-spawn suckers were sampled with trammel nets in the lowest 2 km of the Williamson River (Janney and others, 2006).

Suckers captured at all sample locations were identified to species and sex, measured for fork length (FL), and scanned for the presence of a passive integrated transponder (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 PIT tags. All subsequent tagging, beginning with the 2005 sampling season, has used 134.2 kHz full-duplex tags.

Remote Passive Integrated Transponder Tag Detection Systems

In addition to capture sampling, detections of PIT-tagged fish on remote antennas were incorporated into the capture-recapture study design beginning in 2005. Remote antennas were incorporated to improve the probability of re-encountering previously tagged suckers (Hewitt and others, 2010). Suckers detected by these systems were not physically handled, but were confirmed to be alive and thus were considered live re-encounters in survival analyses. Locations of remote PIT tag detection systems are shown in figure 1 and are listed here with the range of years during which they were operational:

- Antennas on the substrate at lakeshore springs in Upper Klamath Lake (limited in 2005, full implementation in 2006–17);
- One antenna in each of the upstream and downstream traps of the Williamson River weir (2005–16);
- A river-wide antenna array on the substrate immediately upstream of the weir (2007–17);
- A river-wide antenna array on the substrate immediately downstream of the Chiloquin Dam site (2008–17);
- Antennas in the entrance, middle, and exit of the Chiloquin Dam fish ladder (2006–08);
- A river-wide antenna array on the substrate about 2.5 river kilometers upstream of the Chiloquin Dam site (2007–17); and
- A river-wide antenna array on the substrate about 12 river kilometers upstream of the Chiloquin Dam site at Braymill (2009–13).

Survival Analysis

We used Cormack-Jolly-Seber (CJS) live-recapture models (Williams and others, 2002; Nichols, 2005) to obtain maximum likelihood estimates of apparent survival (Φ) and re-encounter (p) probabilities. Apparent survival includes permanent emigration when the study area is not geographically closed (Pollock and others, 2007). Emigration from Upper Klamath Lake is possible, but radio telemetry indicated that emigration by adults of either sucker species is rare (Reiser and others, 2001; Banish and others, 2009). Similarly, detections of PIT-tagged suckers on remote antennas in the fish ladder at Link River Dam (southern outlet of the lake), as well as captures of PIT-tagged suckers in Bureau of Reclamation (Reclamation) trammel net sampling in Lake Ewauna (downstream of the Link River), have recorded fewer than 25 suckers emigrating from Upper Klamath Lake by way of the Link River. Therefore, we expect that our estimates of apparent survival are nearly equivalent to true survival. Lost River sucker data were analyzed separately for the two spawning subpopulations—lakeshore spawners and river spawners.

The CJS model makes the following assumptions: (1) tags are not lost or overlooked when individuals are re-encountered; (2) sampling periods are "instantaneous" relative to the interval between sampling periods; and (3) there is no unmodeled individual variability (heterogeneity) in survival or re-encounter probabilities among the tagged individuals. Although double-tagging experiments with Floy and PIT tags showed that PIT tag loss rates were less than 1 percent over 3 or more years (U.S. Geological Survey, unpub. data, 2010), an unknown proportion of the 125 kHz PIT tags released in 2001–03 are not detectable on the remote antennas. For fish that were physically recaptured, we ensured that tags were not missed when present by scanning a test tag prior to scanning each fish, and also scanning a test tag after each fish that was untagged. Regarding assumption 2, sampling in our study occurred over a 3–3.5 month spawning period and was not instantaneous. However, most captures and encounters occurred over a much shorter time period, and individuals were fairly consistent from year to year in the relative times at which they joined the spawning aggregations (Burdick and others, 2015). Thus, on an individual basis, sampling can be considered nearly instantaneous relative to an annual interval used for parameter estimation. In addition, spawning fish almost always appeared to be in excellent condition, and water quality was good during the spring. Thus, we expect that mortality during the sampling period was low and did not bias survival estimates.

We assessed whether our data conformed to the assumptions of the CJS model using goodness-of-fit testing in the program U-CARE (Choquet and others, 2009). Goodness-of-fit tests pooled over time indicated significant departures from frequencies expected under the CJS model for LRS subpopulations and for SNS. Lack of fit can be an indication of model assumption violations, sparse data, or lack of independence. Closer examination of our goodness-of-fit tests for individual time periods revealed no consistent or systematic bias that would suggest tagging effects. We suspect that lack of fit was largely due to lack of independence in the encounter histories of tagged fish. The lack of independence, or overdispersion, probably results from schooling behavior and is relatively common in capture-recapture studies of fish (Pollock and others, 2007). An overdispersion correction factor ($\hat{c}$) was determined from the most general model for each species or subpopulation by use of the median $\hat{c}$ estimation method in program MARK (Cooch and White, 2013). These $\hat{c}$ values were applied to the respective set of candidate models to compensate for overdispersion in model selection statistics and to inflate variances associated with parameter estimates. Applying a variance inflation factor is recommended when heterogeneity is detected in the data and supports a conservative approach to inference based on model selection (Anderson and others, 1994).

Model sets were developed by considering the effects of sex and time (year) on Φ and p, and then including models with and without those factors. We modeled Φ as a function of sex because past analyses have shown that female suckers often have higher survival than males (Janney and others, 2008; Hewitt and others, 2012). Most importantly, we modeled Φ as a function of time to detect changes in annual survival. For p, we expected sex to be important because of differences in reproductive behavior; for example, males stay at spawning areas longer than females, potentially increasing their probability of being encountered (Burdick and others, 2015). We also expected time to be important for p because of annual differences in sampling intensity and environmental effects on the condition of spawning habitats. Past analyses showed that models with some combination of both sex and time effects on p were overwhelmingly supported in model selection, so we only considered models with some combination of both effects (Janney and others, 2009; Hewitt and others, 2012). We included models with both additive and interactive effects for Φ and p. Additive models constrained effects to be the same between groups across time (for example, the difference between male and female survival is the same in each year), whereas interactive models included more parameters and allowed effects to vary through time (for example, separate estimates of survival for each sex in each year). Note that, as in many CJS designs, the last estimates of Φ and p are confounded in the likelihood and cannot be separately estimated. As such, we do not report or discuss estimates of Φ for 2016.

The models used in the analyses were specified and passed to program MARK (White and Burnham, 1999) using the RMark package (Laake, 2011; Laake and Rexstad, 2013) in the R software environment (R Development Core Team, 2011). All model likelihoods were constructed using a logit link function and optimized using the default Newton-Raphson algorithm. We used Akaike's information criterion corrected for small sample bias and adjusted for overdispersion (quasilikelihood AICc, or QAICc) as a statistical criterion to evaluate the competing models (Burnham and Anderson, 2002). Akaike weights (w_i) are reported as a measure of the relative weight among the models, or the likelihood of each model being the best model in the set given the data. Rather than making inferences from only the best model in the set, parameter estimates were model-averaged using the w_i as weights. Model-averaged parameter estimates account for model selection uncertainty in the estimated precision of the parameters and thus produce unconditional estimates of variances and standard errors (Buckland and others, 1997).

Recruitment and Population Rate of Change

A primary requirement for recovering the endangered sucker populations is knowledge of changes in population size over time (U.S. Fish and Wildlife Service, 2012). In addition to survival, recruitment can be estimated from open population capture-recapture data (Pradel, 1996; Franklin, 2001; Nichols, 2005). Specifically, the reverse-time analog of survival can be estimated; this parameter is termed seniority and denoted γ. Seniority is defined as the probability that an animal present in the sampled population at period i also was present in period i-1 (that is, no recruitment when seniority is 1.0). Given estimates of Φ and γ, population rate of change ($\lambda_i = N_{i+1}/N_i$) can be estimated without estimating N using the equation:

$$\lambda_i = \frac{\Phi_i}{\gamma_{i+1}}. \tag{1}$$

Pradel (1996) introduced a likelihood that models the entire encounter history and is based on the temporal symmetry of capture-recapture data (Nichols and Hines, 2002). This approach combines probabilities describing forward time (survival) and reverse-time (seniority) processes, allowing the direct estimation and modeling of λ. The assumptions of the temporal symmetry model are similar to assumptions of the Cormack-Jolly-Seber model, but temporal symmetry further assumes that the study area is well defined and does not expand over time and that there is no permanent trap response in encounter probability. The incorporation of remote PIT tag detection systems into our study design in 2005 created a situation in which previously tagged fish have a much greater probability of being re-encountered than untagged fish have of being captured in trammel nets. In essence, the remote antenna systems create a dramatic "trap-happy" response in encounter probability (Otis and others, 1978). This difference in encounter probabilities does not cause bias in survival estimates from CJS models, but it does cause substantial bias in estimates of seniority and population rate of change from temporal symmetry models (Franklin, 2001; Hines and Nichols, 2002; Pradel and others, 2010). To avoid such bias, we obtained estimates of survival and seniority from separate model sets and then used the estimates to derive λ using equation 1. Early estimates of γ are not reported because of poor precision owing to sparse data and because simulations have shown that the initial two γ estimates are likely to be substantially more biased than subsequent estimates (Hines and Nichols, 2002).

Encounter histories used to model survival included physical captures and remote detections, but seniority models included only physical captures. Model sets for the seniority analyses were developed and evaluated in a way similar to the survival analyses; however, effects of tag type on p were not included in models for seniority because remote detections were not included.

Standard errors for the derived estimates of λ were calculated using the Delta method. Ideally, estimates of survival and seniority would be generated from a single likelihood using a temporal symmetry model (Pradel, 1996), and the standard error for λ estimates would be corrected for the covariance between these two parameters. Our calculation of the standard error of λ by the Delta method ignores any covariance between survival and seniority. The effect of this approach on the estimated standard errors is expected to be small, but the presented standard errors for λ may be too precise. Derived estimates of λ are not reported for years in which both survival and seniority were estimated on the boundary at 1.0. For years in which either survival or seniority was estimated on the boundary (but not both), λ was calculated by assuming that the parameter that was estimated on the boundary was equal to 1.0, and the standard error for λ was assumed to be equal to the estimated standard error for the parameter that was not estimated on the boundary.

Annual estimates of λ provide insight into the variability in abundance of adult spawning populations by showing whether the population decreased ($\lambda < 1$), remained stable ($\lambda = 1$), or increased ($\lambda > 1$). We summarize the long-term dynamics of the populations using a quantity known as Δ_t, which is simply the cumulative product of the λ estimates over a time period of interest (Anthony and others, 2006). This quantity describes the percentage change in population size from the beginning of the period to the end. Values of Δ_t greater than 1.0 (100 percent) indicate increases in population size, and values less than 1.0 indicate decreases in population size. For purposes of calculating Δ_t, λ was assumed to be 1.0 in years when both survival and seniority were estimated on the boundary. We emphasize that estimates of λ and Δ_t values apply only to the adult spawning populations and are not necessarily representative of changes in the whole populations. Increases in juvenile abundance are not incorporated until those individuals join the spawning aggregations and are fully vulnerable to our sampling. Size composition of the catches in the most recent year may provide an earlier indication of potential recruitment.

Size Composition Analysis

Fork lengths of captured suckers were used to assess changes in the size structure of the LRS subpopulations and the SNS population over time. This assessment provides additional evidence about recruitment that can be compared with capture-recapture seniority estimates, and also illustrates trends in growth. Length data were grouped separately for each sex in each population or subpopulation. Data from 1999 to 2017 were included for the lakeshore spawning LRS, and data from 2000 to 2017 were included for river spawning LRS and for SNS.

For the lakeshore spawning LRS and for SNS, size composition analyses and capture-recapture analyses are focused on the same statistical populations. In contrast, for the river spawning LRS the two analyses are focused on different statistical populations. To focus only on spawning adults, the capture-recapture analysis is restricted to fish that were encountered in either the Williamson River or the Sprague River during at least one spawning season and that were never encountered at the lakeshore springs. Many LRS are captured during sampling in Upper Klamath Lake outside the spawning areas, and these individuals do not enter our capture-recapture analyses until they are encountered at a spawning area (lakeshore springs or one of the rivers). In contrast, the size composition analysis for the river spawning subpopulation includes all LRS that were never encountered at the lakeshore springs, including fish captured in Upper Klamath Lake that were never encountered at a spawning area. As a result, the size composition analysis may include data for small LRS that are not yet mature but are staging with the spawners in the lake prior to the spawning migration. This is done intentionally to provide an early indication of recruitment to the spawning subpopulation, if and when recruitment occurs.

Results

Lost River Suckers

Upper Klamath Lake Lakeshore Spawning Subpopulation

Thirty-five CJS models were fitted to the encounter histories of fish in this subpopulation to estimate apparent annual survival and re-encounter probabilities. The top model in the set accounted for almost all of the weight in the model set ($w_i = 0.99$; table 1). This model included separate Φ parameters for each sex in each year, and sex, year, and additive tag type effects for p. Model-averaged estimates of Φ varied across years and female survival was consistently, albeit only slightly, higher than male survival (table 2). With the exception of males in 2002, survival estimates showed relatively little inter-annual variation and fell within the range expected for animals with a lifespan similar to that of LRS (table 2).

The encounter histories for the recruitment analysis included the same individuals as the survival analysis, but only included physical recaptures of those individuals. As a result, the density of the encounter histories and the size of the model set were much reduced. Model selection statistics were adjusted with a small overdispersion correction factor ($\hat{c}$) of 1.10 and indicated almost no model selection uncertainty. The best model accounted for all of the weight in the model set ($w_i = 1.00$) and included separate γ parameters for each sex but did not include a year effect. This model included both a sex and year effect on p (table 3). Model-averaged estimates of p were low and mostly similar to estimates from the survival analysis for the years prior to implementation of the remote PIT tag detection systems. Recapture probability estimates for females ranged from 0.01 to 0.08. Estimates for males ranged from 0.06 to 0.15, except for the most recent 5 years when estimates were 0.21–0.29. Model-averaged γ estimates indicated consistently low levels of recruitment of new male spawners and almost no recruitment of new females into the subpopulation (table 2). In every year from 2002 to 2015, point estimates of seniority were slightly higher than estimates of apparent survival such that derived annual estimates of population rate of change (λ) were less than 1.0 (table 2). Compounding the 15 estimates of λ indicates that the abundance of female LRS in this subpopulation decreased by 56 percent ($\Delta_t = 0.44$) and the abundance of male LRS decreased by 64 percent ($\Delta_t = 0.36$) through 2015 (fig. 2).

Similar to seniority estimates obtained from the capture-recapture analysis, the fork length data collected over the past 19 years at the lakeshore spawning sites suggest that this subpopulation consists almost entirely of similarly sized individuals growing through time, with little evidence of recruitment (fig. 3). The time series of fork length data presented in Janney and others (2008) included data back to 1987 and showed that this subpopulation “turned over” during the early to mid-1990s. Prior to 1990, the subpopulation was rather homogeneous and was composed of relatively old, large individuals (males about 650 mm FL; females about 725 mm FL). Recruitment in the late 1980s to early 1990s, coupled with substantial losses of adults in large fish die-offs in 1995, 1996, and 1997, resulted in relatively young and small populations in the late 1990s and early 2000s. This subpopulation apparently is now composed of a subset of the same individuals that were present in the early 2000s.

Table 1. Model selection results for the Cormack-Jolly-Seber capture-recapture models fitted to the data for adult Lost River sucker and shortnose sucker populations in Upper Klamath Lake, Oregon.

[Akaike's Information Criterion corrected for small sample size and overdispersion (quasilikelihood AICc [QAICc]) was used to compare the candidate models of survival (Φ) and re-encounter (*p*) probabilities. The overdispersion correction factor, ĉ, is given for each model set. Thirty-five models were fitted to the data from each population, but only plausible models (ΔQAICc less than 20) are shown. In the model names, a × symbol indicates fully interactive effects and the + symbol indicates additive effects. The *tagtype* effect on *p* in the model name refers to the difference between 125 kHz and 134.2 kHz PIT tags, which is only included for 2006 through 2017. The *tagtype* effect is either constrained to be the same across years (*tagtype* alone) or allowed to vary by year (*tagtype*×*time*). Both structures were combined additively (+ precedes *tagtype*) and interactively (× precedes *tagtype*) with the other effects in the models. The best model in each set is presented first, and ΔQAICc values are the difference between the QAICc value of a given model and that of the best model. Akaike weights (w_i) provide a measure of the relative weight of each model or the likelihood of it being the best model in the set given the data. Number of parameters (*K*) is the total number that is theoretically estimable in the model; $-2Log_eL$ is the value of the maximized log likelihood function]

Model	*K*	QAICc	ΔQAICc	w_i	$-2Log_eL$
Lakeshore Spawning Lost River Suckers, 1999–2016 (ĉ = 1.54)					
Φ(sex × time) *p*(sex × time + [tagtype × time])	82	59,471.5	0.0	0.99	91,036.7
Φ(sex + time) *p*(sex × time + [tagtype × time])	66	59,482.6	11.1	0.00	91,103.0
Φ(sex × time) *p*(sex × time × tagtype)	94	59,484.8	13.4	0.00	91,020.3
Φ(sex × time) *p*(sex + time + [tagtype × time])	65	59,487.8	16.4	0.00	91,114.1
River Spawning Lost River Suckers, 2000–16 (ĉ = 1.31)					
Φ(sex × time) *p*(sex × time × tagtype)	90	176,345.3	0.0	1.00	231,481.1
Shortnose Suckers, 1999–2016 (ĉ = 1.18)					
Φ(sex × time) *p*(sex × time + [tagtype × time])	82	103,160.2	0.0	0.99	121,535.3
Φ(sex × time) *p*(sex × time × tagtype)	94	103,171.2	11.0	0.00	121,519.9
Φ(sex × time) *p*(sex + time + [tagtype × time])	65	103,173.2	13.0	0.00	121,590.8

Table 2. Demographic parameter estimates for Lost River suckers from the lakeshore spawning subpopulation, Upper Klamath Lake, Oregon.

[Model-averaged estimates of annual apparent survival probabilities (Φ) and seniority probabilities (γ), the derived estimates of annual population rate of change (λ), and the estimated standard errors (SE) and 95 percent confidence intervals (CI) for all estimates. Confounded parameters (C) and estimates on the boundary at 1.0 (B) are shaded gray]

Sex	Year	Φ Est	Φ SE	Φ CI	γ Est	γ SE	γ CI	λ Est	λ SE	λ CI
Female	1999	0.91	0.086	0.57-0.99	C	NA	NA	NA	NA	NA
Female	2000	0.92	0.050	0.75-0.97	NA	NA	NA	NA	NA	NA
Female	2001	B	NA	NA	0.99	0.005	0.97-0.99	1.01	0.005	1.00-1.02
Female	2002	0.88	0.031	0.81-0.93	0.99	0.005	0.97-0.99	0.89	0.032	0.83-0.95
Female	2003	0.90	0.027	0.83-0.94	0.99	0.005	0.97-0.99	0.91	0.027	0.86-0.97
Female	2004	0.95	0.021	0.89-0.98	0.99	0.005	0.97-0.99	0.97	0.022	0.92-1.01
Female	2005	0.94	0.012	0.91-0.96	0.99	0.005	0.97-0.99	0.95	0.013	0.93-0.98
Female	2006	0.96	0.006	0.95-0.97	0.99	0.005	0.97-0.99	0.97	0.007	0.96-0.99
Female	2007	0.96	0.005	0.95-0.97	0.99	0.005	0.97-0.99	0.97	0.007	0.96-0.98
Female	2008	0.95	0.006	0.93-0.96	0.99	0.005	0.97-0.99	0.96	0.007	0.95-0.97
Female	2009	0.95	0.006	0.94-0.96	0.99	0.005	0.97-0.99	0.97	0.007	0.95-0.98
Female	2010	0.93	0.006	0.92-0.94	0.99	0.005	0.97-0.99	0.94	0.008	0.93-0.96
Female	2011	0.93	0.006	0.91-0.94	0.99	0.005	0.97-0.99	0.94	0.007	0.92-0.95
Female	2012	0.91	0.006	0.90-0.92	0.99	0.005	0.97-0.99	0.92	0.008	0.91-0.94
Female	2013	0.91	0.006	0.90-0.92	0.99	0.005	0.97-0.99	0.92	0.008	0.91-0.94
Female	2014	0.93	0.006	0.92-0.94	0.99	0.005	0.97-0.99	0.95	0.007	0.93-0.96
Female	2015	0.92	0.006	0.90-0.93	0.99	0.005	0.97-0.99	0.93	0.008	0.91-0.94
Female	2016	C	NA	NA	0.99	0.005	0.97-0.99	NA	NA	NA
Male	1999	0.90	0.040	0.79-0.95	C	NA	NA	NA	NA	NA
Male	2000	0.98	0.037	0.60-1.00	NA	NA	NA	NA	NA	NA
Male	2001	B	NA	NA	0.96	0.002	0.96-0.97	1.03	0.041	1.03-1.04
Male	2002	0.80	0.029	0.73-0.85	0.96	0.002	0.96-0.97	0.83	0.030	0.77-0.89
Male	2003	0.86	0.022	0.82-0.90	0.96	0.002	0.96-0.97	0.90	0.023	0.85-0.94
Male	2004	0.93	0.018	0.89-0.96	0.96	0.002	0.96-0.97	0.96	0.019	0.93-1.00
Male	2005	0.91	0.011	0.89-0.93	0.96	0.002	0.96-0.97	0.94	0.012	0.92-0.97
Male	2006	0.89	0.007	0.88-0.90	0.96	0.002	0.96-0.97	0.92	0.008	0.91-0.94
Male	2007	0.93	0.006	0.92-0.94	0.96	0.002	0.96-0.97	0.96	0.006	0.95-0.98
Male	2008	0.91	0.007	0.90-0.92	0.96	0.002	0.96-0.97	0.95	0.007	0.93-0.96
Male	2009	0.92	0.007	0.91-0.93	0.96	0.002	0.96-0.97	0.95	0.007	0.94-0.97
Male	2010	0.90	0.007	0.88-0.91	0.96	0.002	0.96-0.97	0.93	0.008	0.91-0.94
Male	2011	0.89	0.007	0.87-0.90	0.96	0.002	0.96-0.97	0.92	0.007	0.90-0.93
Male	2012	0.90	0.007	0.88-0.91	0.96	0.002	0.96-0.97	0.93	0.007	0.91-0.94
Male	2013	0.90	0.007	0.88-0.91	0.96	0.002	0.96-0.97	0.93	0.007	0.92-0.95
Male	2014	0.91	0.007	0.89-0.92	0.96	0.002	0.96-0.97	0.94	0.007	0.93-0.96
Male	2015	0.90	0.007	0.88-0.91	0.96	0.002	0.96-0.97	0.93	0.008	0.92-0.95
Male	2016	C	NA	NA	0.96	0.002	0.96-0.97	NA	NA	NA

Table 3. Model selection results for the reverse time Cormack-Jolly-Seber (seniority) capture-recapture models fitted to the data for adult sucker populations in Upper Klamath Lake, Oregon.

[Akaike's Information Criterion corrected for small sample size and overdispersion (quasilikelihood AICc [QAICc]) was used to compare the candidate models of seniority (γ) and re-encounter (*p*) probabilities. The overdispersion correction factor, ĉ, is given for each model set. Twenty-five models were fitted to the data from each population, but only plausible models (ΔQAICc less than 20) are shown. In the model names, a × symbol indicates fully interactive effects and the + symbol indicates additive effects. The best model in each set is presented first, and ΔQAICc values are the difference between the QAICc value of a given model and that of the best model. Akaike weights (w_i) provide a measure of the relative weight of each model or the likelihood of it being the best model in the set given the data. Number of parameters (*K*) is the total number that is theoretically estimable in the model; $-2Log_eL$ is the value of the maximized log likelihood function]

Model	*K*	QAICc	ΔQAICc	w_i	$-2Log_eL$
Lakeshore Spawning Lost River Suckers, 1999–2014 (ĉ = 1.10)					
γ(sex) *p*(sex × time)	38	63,699.9	0.0	1.00	70,367.9
γ(sex + time) *p*(sex × time)	54	63,716.5	16.6	0.00	70,350.8
γ(.) *p*(sex × time)	37	63,718.5	18.6	0.00	70,390.7
River Spawning Lost River Suckers, 2000–14 (ĉ=1.27)					
γ(sex + time) *p*(sex × time)	51	66,750.9	0.0	0.78	84,644.0
γ(time) *p*(sex × time)	50	66,753.6	2.6	0.21	84,649.9
γ(sex + time) *p*(time)	34	66,759.3	8.3	0.02	84,697.9
γ(sex + time) *p*(sex + time)	35	66,762.3	11.4	0.00	76,493.7
γ(sex × time) *p*(sex × time)	66	66,769.6	18.7	0.00	84,629.6
Shortnose Suckers, 1999–2014 (ĉ = 1.11)					
γ(sex + time) *p*(sex × time)	54	57,816.0	0.0	0.98	63,882.5
γ(sex) *p*(sex × time)	38	57,824.2	8.3	0.02	63,927.2
γ(time) *p*(sex × time)	53	57,829.7	13.7	0.00	63,899.9
γ(sex + time) *p*(time)	36	57,830.6	14.6	0.00	63,938.7
γ(time) *p*(sex + time)	30	57,831.2	15.2	0.00	63,952.6
γ(sex + time) *p*(sex + time)	37	57,832.3	16.3	0.00	63,938.3
γ(.) *p*(sex × time)	37	57,833.0	17.1	0.00	63,939.1
γ(sex × time) *p*(sex × time)	70	57,833.8	17.8	0.00	63,866.6

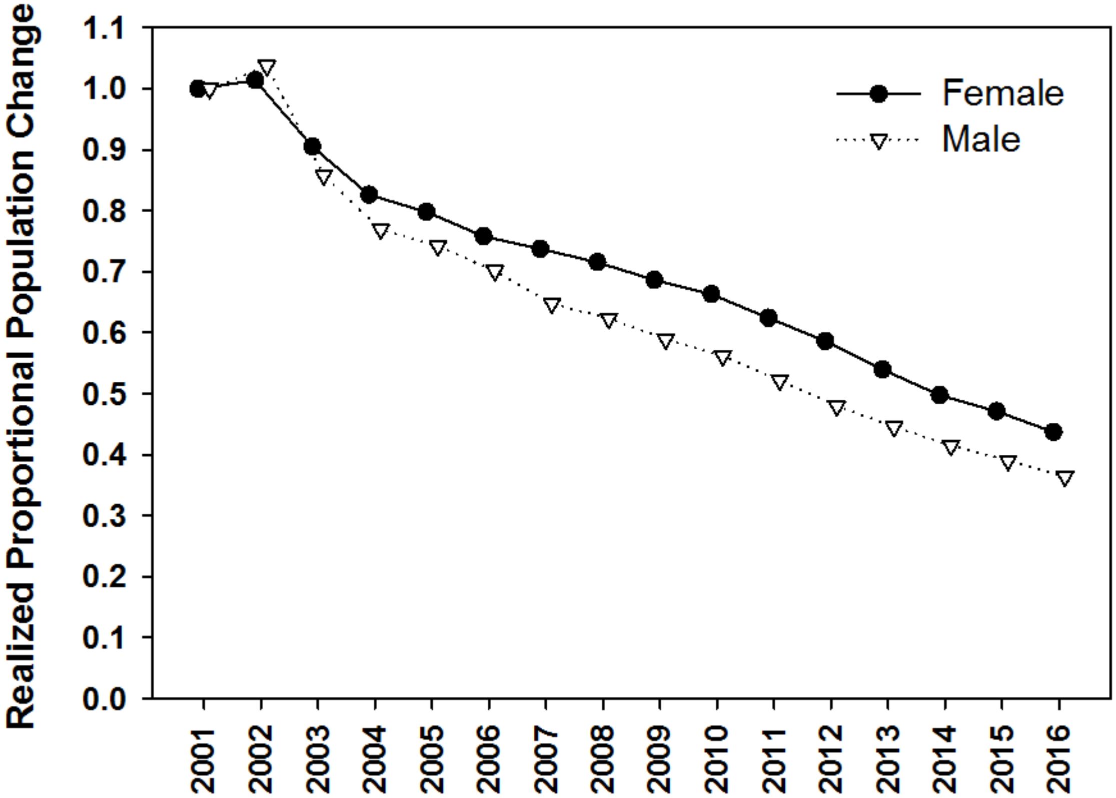

Figure 2. Graph showing realized proportional change in the size of the lakeshore spawning subpopulation of Lost River suckers from 2001 to 2016. Annual changes are based on λ estimates derived from separate models of annual apparent survival (Cormack-Jolly-Seber [CJS] likelihood) and seniority (reverse time CJS likelihood) probabilities, using both physical and remote encounters for survival estimates and physical captures only for seniority estimates.

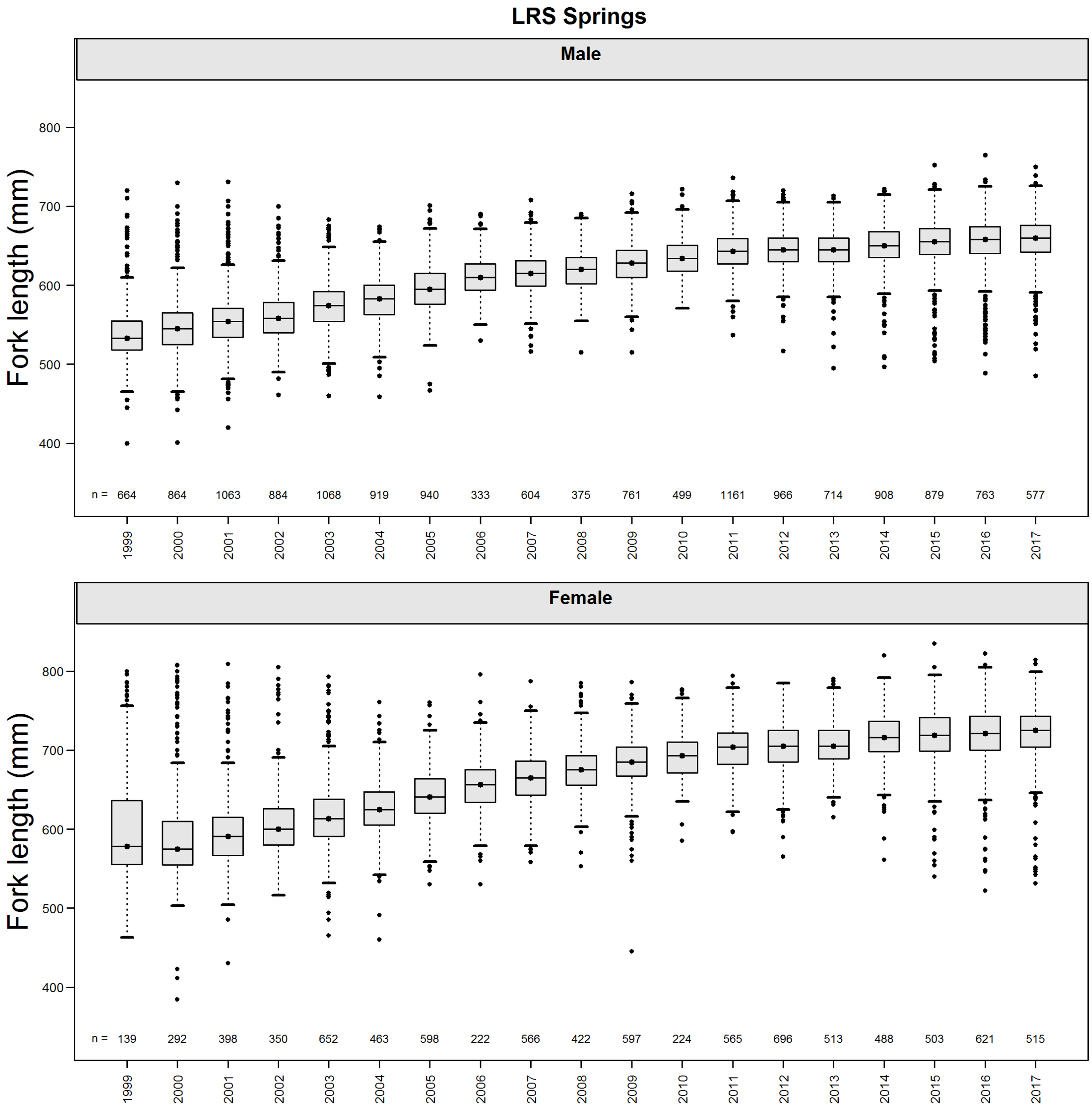

Figure 3. Boxplots showing fork lengths of male and female Lost River suckers captured in trammel nets at lakeshore springs, 1999–2017. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The numbers of fish included in the boxplots for each year are given near the *x*-axis in each panel.

Williamson River and Sprague River Spawning Subpopulations

Model selection statistics for the 35 CJS models fitted to the encounter histories for this subpopulation indicated that the most parameterized model (that is, the global model) received all the support (w_i = 1.00; table 1). This model included separate survival (Φ) parameters for each sex in each year, separate re-encounter probabilities (*p*) for each sex in each year, and separate tag type effects on *p* for each sex in each year since 2006. Because of the unequivocal support for the top model in model selection, model-averaged parameter estimates were the same as those from the top model. The estimates of Φ for males in 2005 and both sexes in 2001 and 2004 were on the boundary at 1.0, indicating estimability problems (table 4). Survival of females generally was consistently high (greater than 0.90) except for 2000 (table 4). In contrast, males showed greater variation in annual survival and experienced several years of relatively poor survival (2000, 2006, and 2012; table 4). During 2001–04, prior to use of the remote PIT tag detection systems, estimates of *p* for males and females were similar and ranged from 0.02 to 0.07. Beginning in 2005, the remote antennas in the traps at the Williamson River weir and additional river-wide arrays in subsequent years dramatically increased recapture probabilities for the river spawning subpopulation. The improvement in recapture probabilities has led to extremely precise survival estimates from 2005 to 2015.

The encounter histories for the recruitment analysis were handled in the same way as for the lakeshore spawning subpopulation. Model selection statistics were adjusted with a ĉ value of 1.27. The best model, which accounted for over three quarters of the weight in the model set (w_i = 0.78), included an additive effect of sex and year for the seniority estimates (table 3). This model included separate *p* parameters for each sex in each year. The second best model (w_i = 0.21) included the same parameter structure for *p* but no sex effect on seniority. Model-averaged estimates of *p* were low and similar between males and females, ranging from 0.02 to 0.12 with an average of 0.04.

All models in the set that received support included effects that showed temporal variation in seniority. Model averaged γ estimates for 11 of the 15 years (2002, 2004, 2005, 2007, 2010, 2011, 2012, 2013, 2014, 2015, and 2016) were on the boundary at 1.0. The model-averaged estimates of seniority indicated that in 2003, 2006, 2008, and 2009, the percentage of individuals of each sex in this subpopulation that were newly recruited to the spawning population ranged from 13 to 65 percent (table 4). In contrast to these estimates, the fork length data collected over the past 18 years show that few individuals small enough to be considered new recruits were captured in any of those years (fig. 4). An issue with sampling in the Chiloquin Dam fish ladder during the high flows of 2006 is responsible for the biased seniority estimates in that year (Hewitt and others, 2011). The low estimates of seniority in the other years are likely biased by a combination of factors related to the difficulty in monitoring this subpopulation by capture-recapture. We return to this issue in section, “Discussion,” but note here that we view these low seniority estimates with considerable skepticism. Although the estimates of γ for more than one-half of the years in the study were on the boundary at 1.0, which to some extent indicates problems with estimation, the length data suggest that it is reasonable that there was little recruitment of new individuals in those years. Furthermore, even if some new recruits entered the spawning population in some years, the small γ estimates that indicate large recruitment events in 2006 and 2008 contrast sharply with the length data. Therefore, we regard the estimates of λ for those years and the increasing trend in abundance that they imply as highly improbable (increases of more than 230 percent for both sexes since 2002; table 4).

Table 4. Demographic parameter estimates for Lost River suckers from the river spawning subpopulation, Upper Klamath Lake, Oregon.

[Model-averaged estimates of annual apparent survival probabilities (Φ) and seniority probabilities (γ), the derived estimates of annual population rate of change (λ), and the estimated standard errors (SE) and 95 percent confidence intervals (CI) for all estimates. Confounded parameters (C) and estimates on the boundary at 1.0 (B) are shaded gray]

Sex	Year	Φ Est	Φ SE	Φ CI	γ Est	γ SE	γ CI	λ Est	λ SE	λ CI
Female	2000	0.88	0.036	0.79-0.94	C	NA	NA	NA	NA	NA
Female	2001	B	NA	NA	NA	NA	NA	NA	NA	NA
Female	2002	0.92	0.022	0.86-0.95	B	NA	NA	0.92	0.022	0.86-0.93
Female	2003	0.90	0.016	0.87-0.93	0.83	0.065	0.66-0.93	1.08	0.087	0.91-1.25
Female	2004	B	NA	NA	B	NA	NA	NA	NA	NA
Female	2005	0.96	0.009	0.93-0.97	B	NA	NA	0.96	0.009	0.93-0.97
Female	2006	0.93	0.007	0.91-0.94	0.38	0.022	0.34-0.43	2.42	0.140	2.15-2.70
Female	2007	0.95	0.004	0.94-0.96	B	NA	NA	0.95	0.004	0.94-0.96
Female	2008	0.93	0.004	0.92-0.94	0.58	0.040	0.50-0.66	1.61	0.111	1.39-1.83
Female	2009	0.95	0.003	0.95-0.96	0.87	0.054	0.72-0.95	1.09	0.068	0.96-1.23
Female	2010	0.93	0.003	0.92-0.93	B	NA	NA	0.93	0.003	0.92-0.93
Female	2011	0.92	0.003	0.92-0.93	B	NA	NA	0.92	0.003	0.92-0.93
Female	2012	0.91	0.003	0.91-0.92	B	NA	NA	0.91	0.003	0.91-0.92
Female	2013	0.91	0.003	0.91-0.92	B	NA	NA	0.91	0.003	0.91-0.92
Female	2014	0.94	0.002	0.93-0.94	B	NA	NA	0.94	0.003	0.93-0.94
Female	2015	0.90	0.003	0.90-0.91	B	NA	NA	0.90	0.003	0.90-0.91
Female	2016	C	NA	NA	B	NA	NA	NA	NA	NA
Male	2000	0.70	0.042	0.62-0.78	C	NA	NA	NA	NA	NA
Male	2001	B	NA	NA	NA	NA	NA	NA	NA	NA
Male	2002	0.93	0.028	0.85-0.97	B	NA	NA	0.93	0.028	0.85-0.97
Male	2003	0.89	0.021	0.84-0.93	0.81	0.074	0.61-0.90	1.10	0.101	0.90-1.30
Male	2004	B	NA	NA	B	NA	NA	NA	NA	NA
Male	2005	B	NA	NA	B	NA	NA	NA	NA	NA
Male	2006	0.81	0.009	0.79-0.83	0.35	0.023	0.30-0.39	2.31	0.155	2.00-2.61
Male	2007	0.96	0.005	0.95-0.97	B	NA	NA	0.96	0.005	0.95-0.97
Male	2008	0.93	0.006	0.92-0.94	0.55	0.042	0.46-0.62	1.69	0.129	1.44-1.95
Male	2009	0.90	0.005	0.89-0.91	0.85	0.060	0.71-0.96	1.06	0.076	0.91-1.21
Male	2010	0.92	0.004	0.91-0.93	B	NA	NA	0.92	0.004	0.91-0.93
Male	2011	0.92	0.004	0.91-0.93	B	NA	NA	0.92	0.004	0.91-0.93
Male	2012	0.86	0.005	0.85-0.87	B	NA	NA	0.86	0.005	0.85-0.87
Male	2013	0.91	0.004	0.90-0.91	B	NA	NA	0.91	0.004	0.90-0.91
Male	2014	0.94	0.003	0.94-0.95	B	NA	NA	0.94	0.003	0.94-0.95
Male	2015	0.92	0.004	0.92-0.93	B	NA	NA	0.92	0.004	0.92-0.93
Male	2016	C	NA	NA	B	NA	NA	NA	NA	NA

The time series of fork length data provided in Janney and others (2008) showed that river spawning LRS went through a demographic transition similar to that experienced by lakeshore spawning LRS. In the mid-1980s, this subpopulation was rather homogeneous and was composed of relatively old, large individuals (males about 620 mm FL; females about 675 mm FL), although somewhat smaller than individuals in the lakeshore spawning subpopulation. As a result of recruitment in the late 1980s to early 1990s, and losses of adults in fish die-offs in 1995, 1996, and 1997, the subpopulation was composed of relatively young and small individuals by the late 1990s. A subset of those individuals apparently now makes up most of the current spawning population. Individuals of both sexes show relatively little variability in size, and although some small fish collected at pre-spawn staging areas are evident in some years, these smaller fish never make up a large part of the sample.

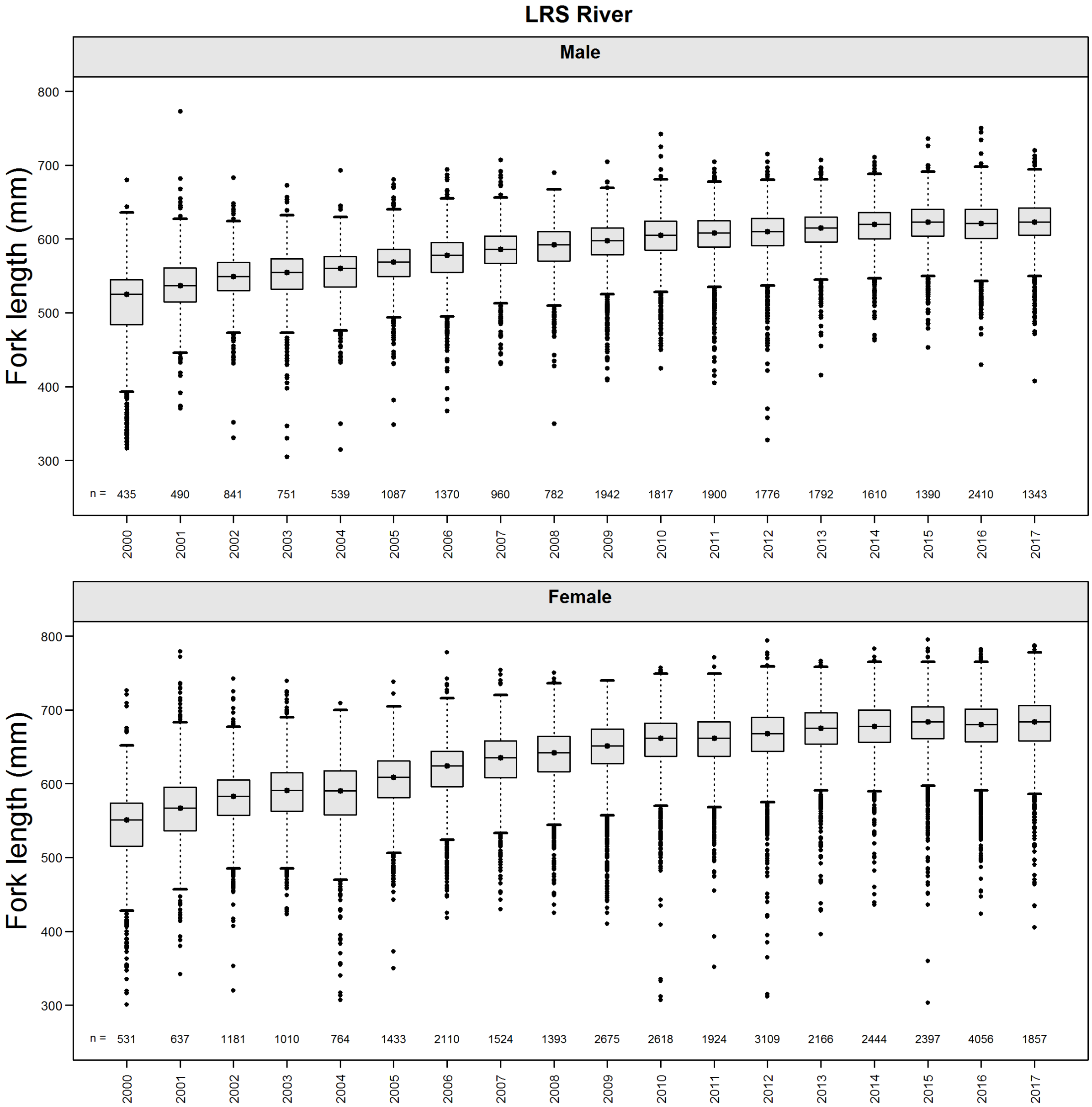

Figure 4. Boxplots of fork lengths of male and female Lost River suckers captured at pre-spawn staging areas in Upper Klamath Lake and in the Williamson and Sprague Rivers, 2000–2017. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The numbers of fish included in the boxplots for each year are given near the *x*-axis in each panel.

Shortnose Suckers

Survival, Recruitment, and Size Composition

Thirty-five CJS models were fitted to the encounter histories of fish in this subpopulation to estimate apparent annual survival and re-encounter probabilities. The top model in the set accounted for nearly all of the weight in the model set (w_i = 0.99; table 3). This model included separate Φ parameters for each sex in each year, and sex, year, and additive tag type effects for *p*. Because of the unequivocal support for the top model in model selection, model-averaged parameter estimates were the same as those from the top model. On average, annual survival was lower and varied more for SNS than for either subpopulation of LRS (table 5). Mean annual survival probability from 1999 to 2015 was 0.84 for males and 0.85 for female SNS. Survival for both sexes was relatively low during 2004, and 2010–2012. Survival was particularly low for females in 1999 and 2000 although estimate precision was poor for those years. Similar to both LRS subpopulations, survival estimate precision improved dramatically in 2005 due to improved sampling efficacy associated with remote underwater PIT tag antennas.

The encounter histories and modeling for the recruitment analysis were handled in the same way as for LRS. Model selection statistics were adjusted with a ĉ value of 1.11. The best model, which accounted for the vast majority of the weight in the model set (w_i = 0.98), included an additive effect of sex and year for the γ estimates (table 3). Model-averaged estimates of *p* were low and similar between males and females, ranging from 0.02 to 0.16 and generally increasing over the course of the study. Similar to river spawning LRS, the model that received the vast majority of support included temporal variation in seniority. However, 6 of the 16 seniority estimates (2001–05 and 2007) were estimated on the boundary at 1.0.

The model-averaged estimates of seniority indicated that no substantial recruitment occurred in most of the early years of the study (2001–05, 2007). In the other years of the study, the estimated percentage of individuals that were newly recruited to the spawning population was 2–16 percent for females and 5–21 percent for males (table 5). As with river spawning LRS, the low estimates of seniority in 2006 likely are biased low by an issue with sampling in the Chiloquin Dam fish ladder (Hewitt and others, 2011). Derived estimates of λ for 2008 and 2009 were imprecise and the confidence intervals broadly overlapped 1.0, but the point estimates indicated slight increases in the size of the spawning population (table 5; fig. 5). However, the size of the spawning population declined substantially in 2010 and the overall trend from 2001 to 2016 is negative. Compounding the 13 estimates of λ indicates that the abundance of female SNS decreased by 77 percent (Δ_t = 0.23), and the abundance of male SNS decreased by 78 percent (Δ_t = 0.22) through 2015 (fig. 5).

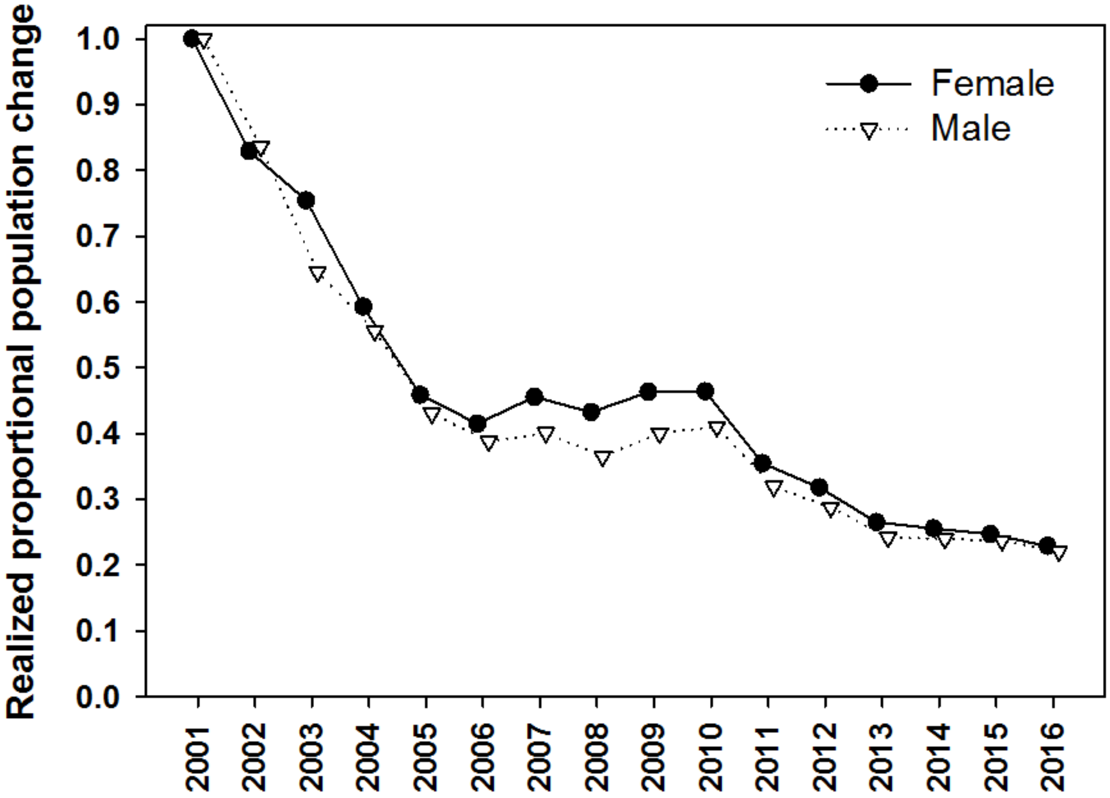

Figure 5. Graph showing realized proportional change in the size of the shortnose sucker spawning population from 2001 to 2016. Annual changes are based on λ estimates derived from separate models of annual apparent survival (Cormack-Jolly-Seber [CJS] likelihood) and seniority (reverse time CJS likelihood) probabilities, using both physical and remote encounters for survival estimates and physical captures only for seniority estimates.

Table 5. Demographic parameter estimates for the shortnose sucker spawning population, Upper Klamath Lake, Oregon.

[Model-averaged estimates of annual apparent survival probabilities (Φ) and seniority probabilities (γ), the derived estimates of annual population rate of change (λ), and the estimated standard errors (SE) and 95 percent confidence intervals (CI) for all estimates. Confounded parameters (C) and estimates on the boundary at 1.0 (B) are shaded gray]

Sex	Year	Φ Est	Φ SE	Φ CI	γ Est	γ SE	γ CI	λ Est	λ SE	λ CI
Female	1999	0.69	0.259	0.17-0.96	C	NA	NA	NA	NA	NA
Female	2000	0.68	0.059	0.55-0.78	NA	NA	NA	NA	NA	NA
Female	2001	0.83	0.044	0.73-0.90	B	NA	NA	0.83	0.044	0.73-0.90
Female	2002	0.91	0.048	0.76-0.97	B	NA	NA	0.91	0.048	0.76-0.97
Female	2003	0.78	0.035	0.71-0.85	B	NA	NA	0.78	0.035	0.71-0.85
Female	2004	0.77	0.020	0.73-0.81	B	NA	NA	0.77	0.020	0.73-0.81
Female	2005	0.90	0.012	0.88-0.93	B	NA	NA	0.90	0.012	0.88-0.93
Female	2006	0.92	0.009	0.91-0.94	0.84	0.041	0.74-0.91	1.10	0.055	0.99-1.21
Female	2007	0.95	0.006	0.94-0.96	B	NA	NA	0.95	0.006	0.94-0.96
Female	2008	0.92	0.006	0.90-0.93	0.86	0.046	0.74-0.92	1.07	0.058	0.96-1.19
Female	2009	0.90	0.007	0.89-0.92	0.90	0.043	0.78-0.96	1.00	0.048	0.91-1.10
Female	2010	0.74	0.008	0.72-0.75	0.96	0.041	0.73-1.00	0.76	0.034	0.70-0.83
Female	2011	0.82	0.007	0.81-0.83	0.92	0.038	0.80-0.97	0.90	0.038	0.83-0.97
Female	2012	0.79	0.007	0.78-0.81	0.95	0.039	0.79-0.93	0.83	0.035	0.77-0.90
Female	2013	0.86	0.006	0.85-0.87	0.98	0.040	0.79-0.95	0.96	0.044	0.88-1.05
Female	2014	0.89	0.006	0.88-0.90	0.92	0.036	0.82-0.97	0.97	0.038	0.89-1.04
Female	2015	0.82	0.007	0.80-0.83	0.88	0.026	0.82-0.93	0.93	0.029	0.87-0.98
Female	2016	C	NA	NA	0.94	0.027	0.86-0.98	NA	NA	NA
Male	1999	B	NA	NA	NA	NA	NA	NA	NA	NA
Male	2000	0.90	0.087	0.58-0.98	NA	NA	NA	NA	NA	NA
Male	2001	0.83	0.066	0.66-0.93	B	NA	NA	0.83	0.066	0.66-0.90
Male	2002	0.77	0.061	0.63-0.87	B	NA	NA	0.77	0.061	0.63-0.87
Male	2003	0.86	0.057	0.71-0.94	B	NA	NA	0.86	0.057	0.71-0.94
Male	2004	0.77	0.035	0.70-0.83	B	NA	NA	0.77	0.035	0.70-0.83
Male	2005	0.90	0.022	0.85-0.94	B	NA	NA	0.90	0.022	0.85-0.94
Male	2006	0.82	0.016	0.79-0.85	0.79	0.051	0.68-0.88	1.03	0.071	0.90-1.17
Male	2007	0.91	0.010	0.89-0.93	B	NA	NA	0.91	0.010	0.89-0.93
Male	2008	0.89	0.011	0.87-0.91	0.81	0.058	0.67-0.90	1.10	0.084	0.94-1.25
Male	2009	0.89	0.010	0.87-0.91	0.87	0.055	0.72-0.95	1.03	0.070	0.90-1.16
Male	2010	0.74	0.011	0.72-0.76	0.95	0.055	0.66-0.99	0.78	0.049	0.69-0.87
Male	2011	0.80	0.011	0.78-0.82	0.89	0.050	0.75-0.95	0.90	0.056	0.80-1.00
Male	2012	0.79	0.010	0.76-0.81	0.93	0.052	0.73-0.99	0.84	0.050	0.75-0.94
Male	2013	0.85	0.009	0.83-0.87	0.86	0.051	0.73-0.93	0.99	0.063	0.87-1.11
Male	2014	0.89	0.009	0.87-0.91	0.90	0.047	0.76-0.96	0.99	0.056	0.89-1.09
Male	2015	0.79	0.010	0.77-0.81	0.85	0.034	0.77-0.90	0.93	0.039	0.85-1.01
Male	2016	C	NA	NA	0.92	0.035	0.82-0.97	NA	NA	NA

Fork length data collected over the past 19 years for SNS suggests that the population consists almost entirely of similarly sized individuals, with evidence of only sparse recruitment (fig. 6). This evidence contrasts with the recent seniority estimates (2006, 2008, 2009, 2011, 2013, and 2015) that indicate substantial recruitment of new individuals into the spawning population. Recruitment analyses for SNS share some of the difficulties with capture-recapture monitoring that was seen for river spawning LRS, although to a lesser degree. Again, we defer a full account of these issues to section, "Discussion," but these issues lead us to caution that the overall trend in spawning population size could be more negative than indicated by the derived λ estimates.

The time series of fork length data provided in Janney and others (2008) included data back to 1984 and showed that the SNS population in Upper Klamath Lake went through a demographic transition similar to that for LRS. In the mid-1980s, the SNS population was rather homogeneous and was composed of relatively old and large individuals (males about 425 mm FL; females about 450 mm FL). The population then "turned over" as a result of recruitment in the late 1980s to early 1990s and losses of adults in fish die-offs in 1995, 1996, and 1997. The current population is mostly a subset of the individuals that were present in the late 1990s. Both male and female SNS have grown little since 2009 (Hewitt and others, 2012; fig. 6), and the median fork length of each sex is now similar to what it was in the mid-1980s.

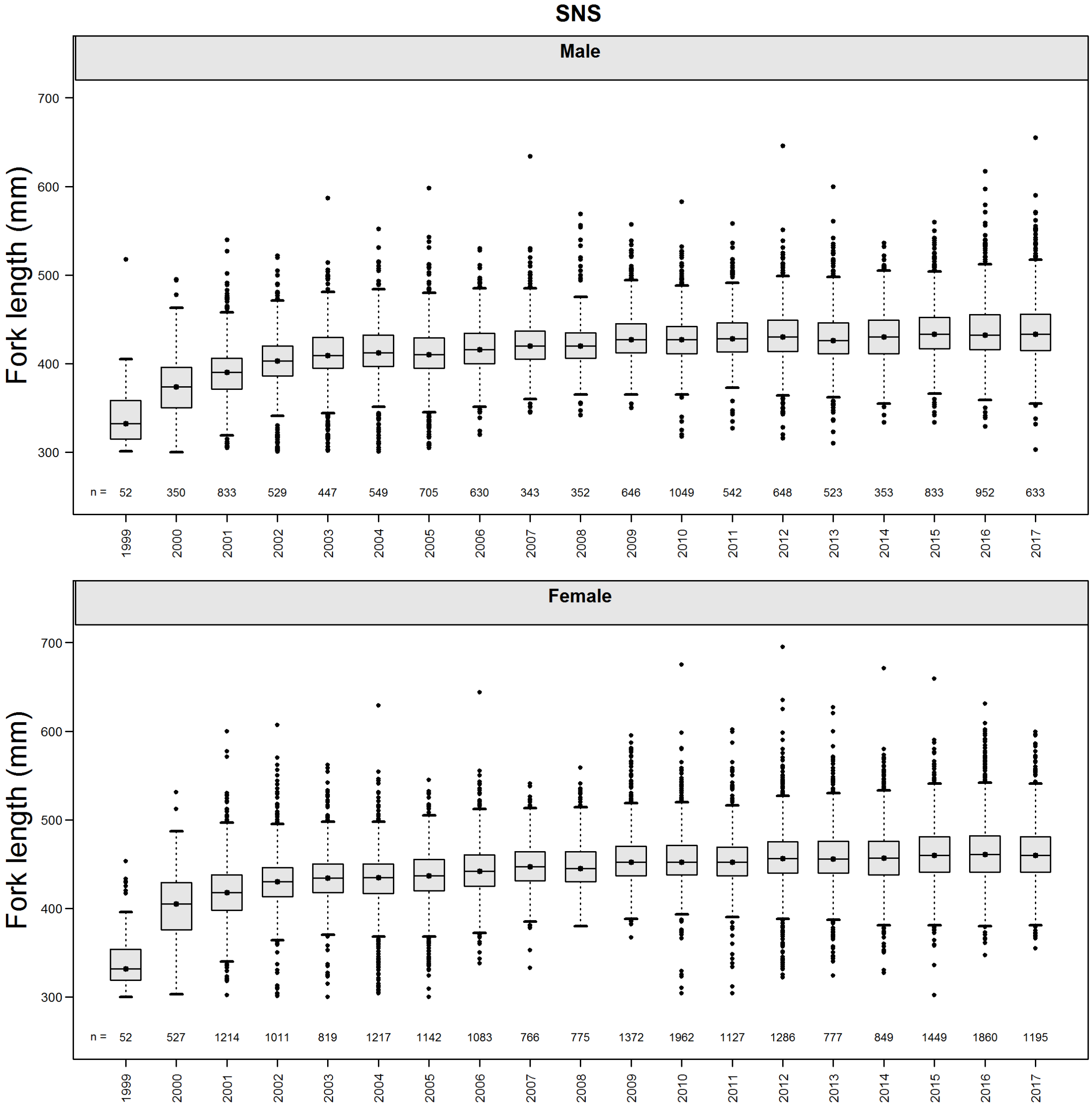

Figure 6. Boxplots showing fork lengths of male and female shortnose suckers captured in Upper Klamath Lake and the Williamson and Sprague Rivers, Oregon, 1995–2017. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The number of fish included in the boxplots for each year are given near the *x*-axis in each panel.

Discussion

Serious concern is warranted for the spawning populations of LRS and SNS in Upper Klamath Lake, and the current situation is most dire for SNS. Capture-recapture results and size composition data show that the abundance of both species has decreased since the early 2000s, continuing trends documented previously (Hewitt and others, 2011, 2012, 2014, 2017). The SNS population has decreased more than either subpopulation of LRS, but the abundances of both species probably have decreased by more than 40 percent since the early 2000s. These decreases primarily indicate a lack of recruitment of new individuals into the spawning populations, but capture-recapture estimates show that both species have experienced some years with relatively poor survival as well. The decrease in abundance for SNS was estimated to be more than 75 percent since 2001, and SNS have experienced more years with poor survival than either subpopulation of LRS.

Most of the suckers in the lake were spawned in the early 1990s, meaning that most of the individuals of both species, but especially SNS, have been mature for many years and are now beyond the average expected lifespan for the species. Classical theory suggests that some senescence should be occurring through reduced fecundity, increased mortality, or both (Hamilton, 1966). However, more recent research shows that it is possible for senescence to be negligible or even “negative” for animals such as fish, with so-called indeterminate growth, or growth beyond reproductive maturity (Vaupel and others, 2004; Williams and others, 2006; Finch, 2009; McNamara and others, 2009; Baudisch, 2011; Jones and others, 2014; Wensink and others, 2014). Continued capture-recapture monitoring of survival for the endangered suckers in Upper Klamath Lake will provide evidence about whether senescence occurs through mortality for these populations (for example, Peron and others, 2010).

Despite the distressed status of the populations, our monitoring shows that the abundance of both species of endangered suckers in Upper Klamath Lake is still at an order of magnitude that affords some protection from widespread mortality events, such as die-offs in the summer and autumn caused by poor water quality (for example, Perkins and others, 2000).

Formal estimation of abundance through capture-recapture requires strict attention to modeling variability and heterogeneity in encounter probabilities to avoid biased estimates (Link, 2003; Holzmann and others, 2006; Morgan and Ridout, 2009; Cubaynes and others, 2010; Pledger and others, 2010). Modeling of encounter probabilities typically is the Achilles heel of abundance estimation for large fish populations (Pine and others, 2003; Hewitt and others, 2010). Instead of providing estimates of abundance that are likely to be biased to an unknown degree, our monitoring program focuses on estimating survival and seniority parameters that can track relative changes in abundance through time. Such methods are more robust to issues associated with encounter probabilities than methods for abundance estimation (Lebreton and others, 1992; Marescot and others, 2011). Survival estimates from our program are expected to be particularly robust to heterogeneity in encounter probabilities (Fletcher and Efford, 2009; Fletcher and others, 2012; Abadi and others, 2013). Modeling and estimation of seniority and population rate of change with capture-recapture data is an active area of research (Pradel and others, 2010; Marescot and others, 2011), and estimates of these parameters are more likely to be biased when heterogeneity is present than are estimates of survival (Nichols and others, 2000; Fletcher and others, 2012).

Heterogeneity in encounter probabilities is difficult to detect and account for when encounter probabilities are low because the encounter histories are less informative. Recapture probabilities often are low in studies of large fish populations (Pine and others, 2003), such as those of LRS and SNS in Upper Klamath Lake. Partly as a result of this challenge, most applications of this type of modeling in fisheries research have involved smaller populations of relatively long-lived species (Zehfuss and others, 1999; Pine and others, 2001; Dieterman and others, 2010). Difficulties with estimation in our program arise primarily because the detections from the remote PIT tag antennas cannot be used in estimating seniority parameters, and recapture probabilities based on weir and trammel net sampling alone are smaller than typically is desired for robust capture-recapture inferences. Despite considerable sampling effort each year, recapture probabilities almost always were less than 0.15 and usually were less than 0.10; a good rule of thumb is that recapture probabilities should be greater than 0.20 (Hightower and Gilbert, 1984; Pollock and others, 1990; Hewitt and others, 2010).

Modeling of seniority has been most successful for lakeshore spawning LRS because recruitment has been trivial since our monitoring began and because the nature of those spawning aggregations makes it possible to sample a large proportion of the subpopulation. More than 70 percent of the subpopulation is now PIT-tagged, and goodness-of-fit tests for the models used in the seniority analysis indicated little heterogeneity in recapture probabilities. In contrast, heterogeneity was more apparent in goodness-of-fit tests for models in the seniority analysis for river spawning LRS. Heterogeneity also is indicated by the difference in the percentage of recaptures between the trammel net sampling at the pre-spawn staging areas and captures in the weir trap. The recapture percentage at staging areas always has been greater than at the weir, and has been greater by 10 percent or more every year since 2011. If these sampling efforts target the same statistical population, differences of this magnitude would be unlikely. Some of the observed differences are caused by variability in capture probabilities at the weir. Although we typically capture thousands of river spawning LRS each year, this number represents a relatively small proportion of the total spawning population. Another possibility is that some river spawning LRS do not aggregate at staging areas prior to spawning, or aggregate somewhere else that we do not sample, but nonetheless join the spawning migration and are available for capture at the weir. Finally, some heterogeneity probably derives from fish not being fully independent and instead associating in groups during the spawning season, thus either avoiding capture or being captured together. Indeed, we see this happen at the weir on some days, when numerous LRS are captured but few of them have PIT tags.

As a result of the heterogeneity in recapture probabilities, estimation and interpretation of seniority and population rate of change are more complicated for the river spawning subpopulation of LRS than for the lakeshore spawning subpopulation of LRS. Some of the seniority estimates are likely biased. Although some recruitment of new spawners is likely, the magnitude of recruitment suggested by the low estimate of seniority in 2008 contrasts with size composition data. The same issues apply to the SNS population, but to a lesser extent, because (1) the SNS population is much smaller than the river spawning subpopulation of LRS, (2) we have captured and tagged a larger proportion of the SNS population, and (3) modeling and estimation indicate a smaller amount of heterogeneity for SNS. Although the seniority estimates for SNS in some recent years are also likely biased low, the derived estimates of λ have large confidence intervals that appropriately reflect their lack of precision. Furthermore, the overall trend in abundance is not affected by these estimates nearly as much as for river spawning LRS.

For river spawning LRS, the size composition data are less likely to be misleading about recruitment of new spawners than the seniority estimates for a few reasons. First, as discussed above, the recapture probabilities in the seniority analysis are low, which can lead to estimability problems in capture-recapture models. We suspect that the fish interpreted as new recruits to the spawning population in the models are rather just individuals, or groups of individuals, that previously have avoided capture by the monitoring program. Second, the addition of a substantial number of new recruits to the spawning population should cause a reduction in the percentage of fish captured in a given year that were previously captured and tagged. The percentage of river spawning LRS that are recaptures has rarely declined from one year to the next, so any additions of new recruits must be relatively small. Finally, most fish in the populations are large adults and new recruits should be evident as a smaller mode in the size composition data. Smaller fish that could be considered new recruits have not made up a substantial part of the catch in any year in the last decade. Sampling with the same trammel nets in the past in Upper Klamath Lake (Janney and others, 2008), as well as in Clear Lake Reservoir, California, where recruitment of new spawners has occurred (Hewitt and Hayes, 2013), showed that the nets captured fish as small as 300 mm FL. Thus, trammel net selectivity cannot explain the lack of smaller fish in the recent catches in Upper Klamath Lake. If new recruits were contributing to the catches but were similar in size to the other, older adults, this would imply substantial changes in growth or maturity dynamics, or both (for example, reproduction shifted to an older age or larger body size). The most commonly observed response in stressed populations of fishes, including populations that have been substantially reduced in abundance, is a shift in maturity to smaller size and younger age (Trippel, 1995; Olsen and others, 2005). However, most such evidence comes from studies of populations that have been affected by fishing, circumstances that are not directly applicable to imperiled suckers in Upper Klamath Lake. Furthermore, other responses in terms of growth or maturity have been predicted and documented (Stearns and Koella, 1986; Trippel and Harvey, 1989; Reznick, 1990; Reznick and others, 1990). Without more direct evidence, we cannot be conclusive about the role of changing growth or maturity dynamics in our assessment of recruitment for river spawning LRS, but the role of any such change must still be reconciled with the other concerns discussed above. Overall, the weight of evidence currently favors little recruitment of new spawners and thus seniority estimates from capture-recapture models that are negatively biased in some years.

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