Prepared in cooperation with the Bureau of Reclamation

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Conversion Factors

Inch/Pound to SI

Multiply	By	To obtain
	Flow rate	
cubic foot per second (ft^3/s)	0.02832	cubic meter per second (m^3/s)

SI 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 follows:
°F=(1.8×°C)+32.

Abbreviations and 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 (*Deltistes luxatus*) and shortnose suckers (*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 spring 2012 were used to describe the spawning migrations in that year and also 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 in 2011. Separate analyses were conducted for each species and also for each subpopulation of Lost River suckers (LRS). Shortnose suckers (SNS) 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.

In 2012, we captured, tagged, and released 749 LRS at four lakeshore spawning areas and recaptured an additional 969 individuals that had been tagged in previous years. Across all four areas, the remote antennas detected 6,578 individual LRS during the spawning season. Spawning activity peaked in April and most individuals were encountered at Cinder Flats and Sucker Springs. In the Williamson River, we captured, tagged, and released 3,376 LRS and 299 SNS, and recaptured 551 LRS and 125 SNS that had been tagged in previous years. Remote PIT tag antennas in the traps at the weir on the Williamson River and remote antenna systems that spanned the river at four different locations on the Williamson and Sprague Rivers detected a total of 19,321 LRS and 6,124 SNS. Most LRS passed upstream between late April and mid-May when water temperatures were increasing and greater than 10 °C. In contrast, most upstream passage for SNS occurred in early and mid-May when water temperatures were increasing and near or greater than 12 °C. Finally, an additional 1,188 LRS and 1,665 SNS were captured in trammel net sampling at pre-spawn staging areas in the northeastern part of the lake. Of these, 291 of the LRS and 653 of the SNS had been PIT-tagged in previous years. For LRS

captured at the staging areas that had encounter histories that were informative about their spawning location, over 90 percent of the fish were members of the subpopulation that spawns in the rivers.

Capture-recapture analyses for the LRS subpopulation that spawns at the shoreline areas included encounter histories for more than 12,150 individuals, and analyses for the subpopulation that spawns in the rivers included more than 29,500 encounter histories. With a few exceptions, the survival of males and females in both subpopulations was high (greater than 0.9) between 1999 and 2010. Notably lower survival occurred for both sexes from the rivers in 2000, for both sexes from the shoreline areas in 2002, and for males from the rivers in 2006. Between 2001 and 2011, the abundance of males in the lakeshore spawning subpopulation decreased by 53–65 percent and the abundance of females decreased by 36–48 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 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 were lower than desired for robust inferences from capture-recapture models. If we assume that little or no recruitment occurred in 2006 or 2008, the abundance of both sexes in the river spawning subpopulation likely has decreased at rates similar to the rates for the lakeshore spawning subpopulation between 2002 and 2011.

Capture-recapture analyses for SNS included encounter histories for more than 17,700 individuals. Most annual survival estimates between 2001 and 2010 were high (greater than 0.8), but SNS experienced more years of low survival than either LRS subpopulation. Annual survival of both sexes was particularly low in 2001, 2004, and 2010. In addition, male survival was somewhat low in 2002. Capture-recapture models and size composition data indicate that recruitment of new individuals into the SNS spawning population was trivial between 2001 and 2005. Models indicate substantial recruitment of new individuals into the SNS spawning population in 2006, 2008, and 2009. As a result, capture-recapture modeling suggests that the abundance of adult spawning SNS was relatively stable between 2006 and 2010. We are skeptical of the estimated recruitment in 2006, 2008, and 2009 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 71 percent and the abundance of females decreased by 69 percent between 2001 and 2011. The worst-case scenario, which assumes no recruitment and seems more likely, suggests an 86 percent decrease for males and an 81 percent decrease for females.

Despite relatively high survival in most years, we conclude that both species have experienced substantial declines in the abundance of spawning fish 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 adult spawning populations for SNS and river spawning LRS in some years, size data do not corroborate these estimates. In fact, fork length data indicate that all populations are largely comprised of fish that were present in the late 1990s and early 2000s. As a result, the status of the endangered sucker populations in Upper Klamath Lake remains worrisome, and the situation is especially dire for shortnose suckers. Future investigations should explore the connections between sucker recruitment and survival and various environmental factors, such as water quality and disease. 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 (*Deltistes luxatus*) and shortnose suckers (*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). Declining 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 exhibited remarkable 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 Lost River sucker (LRS) population was composed of old individuals and that no substantial recruitment had occurred during the previous 15 years (Scoppettone and Vinyard, 1991; USFWS, 1993). These findings led to the federal listing of both species under the Endangered Species Act in 1988 (USFWS, 1988). Upper Klamath Lake contains the largest remaining population of Lost River suckers (National Research Council, 2004) and one of the largest remaining populations of shortnose suckers.

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 Lost River suckers have exceeded 50 years and age estimates for shortnose suckers (SNS) have exceeded 30 years (National Research Council, 2004; Terwilliger and others, 2010). Both species are obligate lake dwellers that make spawning migrations between March and May of each year. Shortnose suckers spawn primarily in the Williamson and Sprague Rivers, but two distinct subpopulations of Lost River suckers 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* between June and 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 ammonia, high pH, and harmful 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 (U.S. Geological Survey, unpub. data, 2003).

In this report, we summarize data collected in 2012 on the timing and magnitude of adult sucker spawning migrations and analyze capture-recapture data from 1999 to 2012 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 2011. In addition to estimating recruitment from capture-recapture data, we assessed relative changes in size composition to provide additional insight into the relative frequency and magnitude of recruitment into the spawning populations.

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 between February and May from 1999 to 2012. 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. Between 2000 and 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 2012, a resistance board weir (described in detail by Tobin [1994]) was deployed 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 used 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 trap.

Additional trammel net sampling for pre-spawn adult suckers of both species was conducted from 1995 to 2012 at various staging areas in Upper Klamath Lake. The overwhelming majority of this type of sampling in recent years has taken place near Modoc Point and Goose Bay (fig. 1). In addition, between 1995 and 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 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 2006–2012);
- one antenna in each of the upstream and downstream traps of the Williamson River weir (2005–2012);
- a river-wide antenna array on the substrate immediately upstream of the weir (2007–2012);
- a river-wide antenna array on the substrate immediately downstream of the Chiloquin Dam site (2008–2012);
- antennas in the entrance, middle, and exit of the Chiloquin Dam fish ladder (2006–2008);
- a river-wide antenna array on the substrate about 2.5 river kilometers upstream of the Chiloquin Dam site (2007–2012); and
- a river-wide antenna array on the substrate about 12 river kilometers upstream of the Chiloquin Dam site at Braymill (2009–2012).

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 within the fish ladder at Link River Dam (the southern outlet of the lake), as well as captures of PIT-tagged suckers in Bureau of Reclamation trammel net sampling in Lake Ewauna (downstream of the Link River), have recorded fewer than 10 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 samples; 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 2001–2003 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 found to be 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 (U.S. Geological Survey, unpub. data, 2013). 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 appear to be in excellent condition and water quality is good during the spring. Thus, we expect that mortality during the sampling period is low and that it does 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 Lost River sucker subpopulations and for shortnose suckers. 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, U.S. Geological Survey, written commun., 2014). 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 2011 or p for 2012.

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) within 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 (USFWS, 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 was also present in period i-1 (in other words, 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 the 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. Past seniority analyses for SNS and both subpopulations of LRS have yielded a large number of seniority parameter estimates from time-dependent models on a boundary of 1.0 (Hewitt and others, 2011; Hewitt and others, 2012). In an attempt to obtain seniority estimates and standard errors that could be used to derive an estimate of λ in those years, and to help determine whether estimability issues were the result of sparse recapture data or simply the lack of any measurable recruitment, we developed models that constrained γ to be the same in years in which γ was estimated on a boundary in time-dependent models. As a result, all of the data for those years contributed to estimation of a single parameter in the model. Models with this type of constraint were considered in model selection along with the other models.

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 survival was estimated on a boundary or both survival and seniority were estimated on a boundary. For years in which seniority was estimated on a boundary but survival was not, λ and its standard error were assumed to be equivalent to estimates for survival.

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 survival or both survival and seniority were estimated on a 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 within each population or subpopulation. Data from 1999 to 2012 were included for the lakeshore spawning LRS, and data from 2000 to 2012 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 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 of 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

Catch Summary and Run Timing for 2012

We captured 1,718 LRS in trammel nets at the lakeshore springs, 969 (56 percent) of which had been tagged prior to the 2012 sampling season (table 1). The percentage of LRS captured at the springs that were previously tagged increased rather steadily between 2003 and 2011, but was the same in 2012 as it was in 2011. Trammel net catches at the springs in 2012 began in mid-March and continued through the third week of May (fig. 2). Most individuals were first captured at Sucker Springs or Cinder Flats (37 and 29 percent), followed by Silver Building Springs (23 percent) and Ouxy Springs (11 percent). In addition to the fish physically captured in trammel nets, 6,578 PIT-tagged LRS were detected swimming over remote antennas at the lakeshore springs. One male detected on the remote antennas was originally tagged in 1995 and has been encountered at the springs every year from 2006 to 2012. Two females were detected for the first time in 2012 since they were originally captured and tagged in 2001. Antennas at Cinder Flats detected more individuals than antennas at any other spring, but antennas at Sucker Springs detected nearly as many (table 2). Lost River suckers were detected beginning in the second week of March and continued to be detected through the end of May (fig. 3). Most individuals joined the spawning aggregations in April. At the lakeshore springs, only 24 percent of the LRS detected on the remote antennas also were physically captured in trammel nets, whereas 90 percent of the PIT-tagged LRS that were physically captured also were detected on the remote antennas.

Trammel net sampling at pre-spawn staging areas captured 1,188 individual LRS (table 1). Of these, 291 (25 percent) had been tagged prior to the 2012 sampling season. The percentage of LRS captured at the staging areas that were previously tagged has increased steadily over the last 10 years. Of the PIT-tagged LRS captured at the staging areas, 76 percent were subsequently captured or detected somewhere in the Williamson or Sprague Rivers, whereas only 7 percent were later captured or detected at the lakeshore springs. One individual was subsequently captured or detected at both spawning areas.

A total of 3,927 LRS were captured in the upstream trap of the Williamson River weir (table 1). Only 551 (14 percent) had been tagged prior to 2012, continuing the long-term trend of a smaller recapture percentage for LRS in the weir compared to the trammel net sampling at the staging areas. Most individuals were captured in the weir between the fourth week of April and the middle of May (fig. 4). The combination of remote PIT tag antennas at the weir (upstream and downstream traps and the river-wide array) detected a total of 19,230 individuals (table 2). The antenna on the upstream trap showed that most detections occurred from late April to mid-May when water temperatures were 10–15 °C (fig. 5). A total of 41 individuals that had not been encountered since they were captured and tagged in 2001 or before were detected on the remote antennas in the rivers. Two of these individuals were males tagged on the same day in the Williamson River in 1996, and they were detected on the same weir antenna within 3 days of each other in 2012.

Upstream of the Williamson River weir, the river-wide antenna array in the Sprague River just downstream of the Chiloquin Dam site detected 4,907 individual LRS (table 2). Most individuals were detected between late April and mid-May when water temperatures were greater than 10 °C (fig. 6). The next upstream antenna array, located upstream of the Chiloquin Dam site, detected 737 LRS between March 25 and May 31. The farthest upstream array on the Sprague River, located at Braymill, detected 23 individual LRS between April 7 and May 30.

Survival, Recruitment, and Size Composition

Upper Klamath Lake Lakeshore Spawning Subpopulation

From 1999 to 2011, we captured, tagged, and released 4,469 female and 6,361 male Lost River suckers at the lakeshore springs. Excluding re-encounters in the year of tagging, we subsequently recaptured or remotely detected 3,830 (86 percent) of the females and 4,842 (76 percent) of the males on at least one occasion through 2012. An additional 266 females and 303 males from this subpopulation that were captured and tagged previously or elsewhere and then re-encountered at the springs between 1999 and 2012 also were included in the survival analysis. Fish that were first captured and tagged in 2012 do not contribute to parameter estimation in survival models. However, the subset of those fish that are included in this subpopulation do contribute information to models used in the recruitment analysis (469 females and 321 males).

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 the vast majority of the weight in the model set ($w_i = 0.89$; table 3). This model included an additive effect of sex and year for Φ, and sex, year, and tag type effects for p. The second best model ($w_i = 0.10$) included separate Φ parameters for each sex in each year (a fully interactive model) and the same structure for p as in the best model. Model-averaged estimates of Φ varied across years and female survival was consistently, albeit only slightly, higher than male survival (fig. 7). With the exception of 2002, survival estimates were within the range expected for animals with a lifespan similar to that of Lost River suckers. Prior to full implementation of the remote PIT tag detection systems, which began in 2006, model-averaged estimates of p for males were always lower than 0.2 and were double the estimates for females, which were never higher than 0.1. Estimates of p were much higher for both sexes in 2006–2011, although estimates for males remained slightly higher than estimates for females. Except for 2010, estimates were about 0.93 for males with 125 kHz tags and about 0.985 for males with 134 kHz tags. Similarly, estimates were about 0.90 for females with 125 kHz tags and about 0.975 for females with 134 kHz tags. In 2010, estimates for both sexes and both tag types were the lowest values since full implementation of the remote detection systems. Estimates of p for males decreased by about 0.09 for both tag types and estimates for females decreased by about 0.15 for both tag types.

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 1.16, and indicated a fair amount of model selection uncertainty. The best model accounted for half of the weight in the model set ($w_i = 0.50$) and included the constraint that all annual γ estimates that were on a boundary of 1.0 in the time-varying model were set to be equal through a single parameter. This model included an additive effect of sex and year for the other γ estimates. The second best model ($w_i = 0.37$) only differed from the top model in that there was a year effect and no sex effect on γ for the years in which it was not constrained to be equal. The other two models with some support ($w_i \approx 0.06$) included either a simple sex effect on seniority or a single, time- and sex-constant parameter for seniority. All models with any support included separate p parameters for each sex in each year. Model-averaged estimates of p were low and similar to estimates from the survival analysis for the years prior to implementation of the remote PIT tag detection systems (males: range = 0.06–0.15, average = 0.11; females: range = 0.01–0.06, average = 0.04). For years in which seniority was constrained to be equal through a single parameter (2004, 2006, 2007, and 2010), the model-averaged γ estimate was still on a boundary at 1.0, indicating essentially no recruitment of new individuals into the spawning population in those years. In the other years, model-averaged γ estimates indicated low levels of recruitment of new spawners and upper confidence bounds almost always approached the boundary of 1.0. In every year from 2002 to 2010, except for 2008, point estimates of seniority were higher than estimates of apparent survival such that derived annual estimates of population rate of change (λ) were less than 1.0 (fig. 7). Derived estimates of λ for both sexes in 2008 were relatively imprecise and confidence intervals broadly overlapped 1.0. Compounding the nine λ estimates indicates that the abundance of female LRS in this subpopulation decreased by 36 percent ($\Delta_t = 0.64$) and the abundance of male LRS decreased by 53 percent ($\Delta_t = 0.47$) through 2011 (fig. 8).

The fork length data collected over the last 14 years at the lakeshore spawning sites suggest that this subpopulation consists almost entirely of similarly sized individuals growing through time, with virtually no evidence of recruitment. Therefore, we consider the overall estimates of population decline based on derived λ estimates to be lower bounds; that is, the declines may be more substantial than these estimates indicate. Indeed, the length data show that few individuals of either sex collected since 1999 could be considered new recruits to the spawning population (fig. 9). A difference of a few percent in estimates of γ seems trivial, but such differences can be important in terms of the overall Δ_t when compounded across 9 years. Therefore, we calculated what we consider to be upper bounds (worst-case scenario) on the overall declines by assuming γ to be 1.0 in all years (no recruitment; $\lambda = \Phi$). These calculations indicate that the decline for females could be as much as 48 percent ($\Delta_t = 0.52$) and the decline for males could be as much as 65 percent ($\Delta_t = 0.35$; fig. 8).

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. It appears that this subpopulation is now composed of a subset of the same individuals that were present in the early 2000s. In 2012, the median fork length of males was 645 mm and the median fork length of females was 705 mm, and individuals of both sexes showed relatively little variability in size.

Williamson and Sprague River Spawning Subpopulation

From 2000 to 2011, we captured, tagged, and released 11,066 female and 7,827 male Lost River suckers in the Williamson River or the Sprague River. Excluding re-encounters in the year of tagging, we subsequently recaptured or remotely detected 9,572 (86.5 percent) of the females and 6,474 (83 percent) of the males on at least one occasion through 2012. An additional 3,702 females and 2,892 males from this subpopulation that were captured and tagged previously or elsewhere and then re-encountered in one of the rivers between 2000 and 2012 also were included in the survival analysis. Almost all of these additional individuals were fish originally captured, tagged, and released at pre-spawn staging areas in the lake. Models in the recruitment analysis for this subpopulation included additional data from 2,546 females and 1,492 males that were first captured and tagged in 2012.

Model selection statistics for the 35 CJS models fitted to the encounter histories for this subpopulation indicated that the most parameterized model received all of the support ($w_i = 1.00$; table 4). 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. Survival of both sexes in 2000 was low, with female survival (0.83) higher than that for males (0.69) (fig. 10). The estimates for males in 2005 and both sexes in 2001 and 2004 were on the boundary at 1.0, indicating estimability problems. Survival for both sexes was high and similar to each other in 2002, 2003, and 2007–2010. Survival of females in 2006 was similar to the other years, but male survival was substantially lower in that year. With the exceptions of the year 2000 and males in 2006, survival of LRS spawning in the rivers was similar to estimates from the lakeshore spawning subpopulation. In 2001–2004, prior to use of the remote PIT tag detection systems, estimates of p for males and females were similar and varied between 0.02 and 0.07. In 2005, the remote antennas in the traps at the Williamson River weir raised the estimate for females to 0.47 and the estimate for males to 0.43. Estimates of p for both tag types were lower in 2006 (0.17–0.35) because high flows compromised the detection efficiency of the antennas in the traps. Estimates of p in 2007–2011 for fish tagged with 125 kHz PIT tags were similar to 2005 and 2006 estimates depending on the year, and were slightly higher for females (0.26–0.47) than for males (0.20–0.49) in all but one year. Finally, estimates of p for males and females tagged with 134 kHz tags were similar in 2007–2011, ranging between 0.78 and 0.95. Re-encounter probabilities for fish tagged with 134 kHz tags were less variable because more of the remote detection systems in the rivers could detect those tags, particularly the river-wide array just upstream of the weir that was first installed in 2007. In contrast, the only systems that could detect the 125 kHz tags were the antennas in the weir and the fish ladder at Chiloquin Dam. The antennas in the weir provided all detections for 125 kHz tags following the removal of the dam in late summer and autumn of 2008.

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 $\hat{c}$ value of 1.51. The best model, which accounted for more than half of the weight in the model set ($w_i = 0.68$), constrained seniority estimates to be the same for the years in which seniority was estimated on a boundary (1.0) from the time varying model and included an additive effect of sex and year for the other estimates. This model included a year effect, but no sex effect, on recapture probability (p). The only other model with any support ($w_i = 0.32$) included the same parameter structure for seniority but an additive effect of sex and year for p. Model-averaged estimates of p were low and similar between males and females, ranging between 0.02 and 0.13 with an average of 0.05.

Both models in the set that received support included effects that showed temporal variation in seniority. In both models, the γ estimate for 5 of the 10 years (2002, 2004, 2005, 2007, and 2011) was on the boundary at 1.0 even though these years were constrained to a single parameter. The model-averaged estimates of seniority indicated that in 2003, 2006, and 2008, the percentage of individuals of each sex in this subpopulation that were newly recruited to the spawning population ranged from 21 to 67 percent. Between 3 and 11 percent of the individuals were estimated to be newly recruited in 2009 and 2010. In contrast to these estimates, the fork length data collected over the last 13 years show that few individuals small enough to be considered new recruits were captured in any of those years (fig. 11). An issue with sampling in the Chiloquin Dam fish ladder during the high flows of 2006 is responsible for the erroneous 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 the section, “Discussion,” but note here that we view these low seniority estimates with considerable skepticism. Although the estimates of γ for half of the years were on the boundary at 1.0, which to some extent indicates problems with estimation, the length data suggest that it is entirely reasonable that there was very 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 350 percent for females and 430 percent for males since 2002). Rather, the overall trend in abundance probably is better characterized (if somewhat pessimistically) by assuming that no recruitment occurred in any year between 2002 and 2010 ($\gamma = 1.0$, $\lambda = \Phi$). Calculated in this way, the abundance of females in this subpopulation may have decreased by as much as 45 percent ($\Delta_t = 0.55$) and the abundance of males may have decreased by as much as 52 percent ($\Delta_t = 0.48$) through 2011 (fig. 12).

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. In 2012, the median fork length of males was 610 mm and the median fork length of females was 668 mm. 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 (for example, females in 2004 and 2010), these smaller fish never make up a large proportion of the sample.

Shortnose Suckers

Catch Summary and Run Timing for 2012

Trammel net sampling at the lakeshore springs captured only one shortnose sucker, a female captured and tagged at Sucker Springs in May (table 1). This individual was detected on the remote PIT tag antenna in the upstream trap of the Williamson River weir the day after it was tagged and released at the springs. In total, the remote PIT tag antennas at the lakeshore springs detected 36 individual SNS during the spawning season (table 2). Of the 36 individuals detected, 23 (64 percent) also were detected in the Williamson River or Sprague River in 2012, and a total of 31 (86 percent) have been captured or detected in one of the rivers at some point in their history.

We captured 1,665 shortnose suckers in trammel nets at pre-spawn staging areas, and 653 (39 percent) of these individuals had been tagged prior to the 2012 sampling season (table 1). The capture of one male was the first re-encounter since the individual was captured and tagged in 1997, and the capture of one female was the first re-encounter since it was tagged in 1998. The percentage of SNS captured at the staging areas that were previously tagged has increased steadily over the last 10 years. Of the PIT-tagged SNS captured at the staging areas, 70 percent were subsequently captured or detected somewhere in the Williamson River or Sprague River. Ten individuals also were captured or detected at the lakeshore springs and 70 percent (seven) of those individuals also were detected in the Williamson River.

A total of 424 SNS were captured in the upstream trap of the Williamson River weir, the largest catch in a season since the weir was first installed in 2005 (table 1). Of the 424 captured, 125 (29 percent) had been tagged prior to the 2012 sampling season. The percentage of SNS captured in the weir that were previously tagged had increased steadily from 2005 to 2011, but dropped a few percent in 2012. The recapture percentage in the weir continued to be smaller than the recapture percentage at the staging areas. Most individuals were captured between late April and mid-May. The remote PIT tag antennas at the weir combined to detect a total of 6,067 individual SNS through the end of June (table 2). Detections at the weir for one male and one female were the first re-encounters since the fish were captured and tagged in 1997, and the detections of two other males were the first re-encounters since those fish were tagged in 1998. The first peak in SNS detections coincided with the primary peak of LRS detections in mid- to late April, but most SNS detections occurred as a second peak in early to mid-May. As in past years, SNS detections mostly occurred when water temperatures were approaching or exceeding 12 °C (fig. 13).

The PIT tag antenna array in the Sprague River downstream of the Chiloquin Dam site detected 732 individual SNS between mid-April and mid-June (table 2). The timing of detections was similar to the pattern in the detections at the weir (fig. 14). The antenna array upstream of the Chiloquin Dam site detected 379 SNS, and the antenna array at Braymill detected 5 SNS.

Survival, Recruitment, and Size Composition

From 1999 to 2011, we captured, tagged, and released 10,431 female and 5,649 male shortnose suckers. Excluding re-encounters in the year of tagging, we subsequently recaptured or remotely detected 6,968 (67 percent) of the females and 3,503 (62 percent) of the males on at least one occasion through 2012. An additional 214 females and 162 males that were captured and tagged previously and then re-encountered between 1999 and 2012 also were included in the survival analysis. Models in the recruitment analysis included additional data from 821 females and 439 males that were first captured and tagged in 2012.

Thirty-five CJS models were fitted to the SNS encounter histories to estimate apparent annual survival and re-encounter probabilities. The top model in the set had virtually all of the support ($w_i = 0.92$; table 5). This model included separate Φ parameters for each sex in each year, and sex, year, and tag type effects for p. Estimates of Φ showed that survival was similar between the sexes in most years, but female survival was substantially higher than male survival in 2002 and 2006 (fig. 15). Survival for both sexes was especially low in 2001, 2004, and 2010. With the exception of those 3 years, survival estimates were rather similar to estimates for Lost River suckers and were within the range expected for animals with a lifespan similar to that of shortnose suckers. In 2000–2004, prior to use of the remote PIT tag detection systems, estimates of p for males and females ranged between 0.025 and 0.05, with estimates for females slightly but consistently higher than estimates for males. In 2005, the remote antennas in the traps at the Williamson River weir raised the estimates for both sexes to about 0.37. Estimates of p for males and females tagged with 125 kHz PIT tags decreased to about 0.19 in 2006 because of the reduced efficiency of the antennas caused by the high flows in the river. For males and females tagged with 125 kHz PIT tags, estimates of p from 2007 to 2010 ranged between 0.20 and 0.37 (average = 0.27), with another low in 2008 due to the loss of detection capabilities at the downstream weir trap caused by debris, as well as relatively high flows. Finally, estimates of p for males and females tagged with 134 kHz tags were about 0.4 in 2006 and then increased substantially between 2007 and 2010 (range = 0.88–0.94). For both sexes and both tag types, estimates of p declined by 0.07 in 2011. Re-encounter probabilities for fish tagged with 134 kHz tags were less variable for the same reasons given for the river spawning subpopulation of LRS.

The encounter histories and modeling for the recruitment analysis were handled in the same way as for Lost River suckers. Model selection statistics were adjusted with a $\hat{c}$ value of 1.21. The best model, which accounted for nearly all of the weight in the model set ($w_i = 0.98$), constrained seniority estimates to be the same for the years in which γ was estimated on a boundary (1.0) from the time varying model, and included an additive effect of sex and year for the other γ estimates. The other model with some support ($w_i = 0.02$) included the same constraints for boundary γ estimates, but allowed the other γ estimates to vary by sex and year. Both of the models with any support included separate p parameters for each sex in each year. Model-averaged estimates of p were low and similar between males and females, ranging between 0.02 and 0.14 with an average of 0.06. Similar to river spawning LRS, all of the models in the set that received any support included effects that showed some temporal variation in seniority. However, 6 of the 10 individual γ estimates (2001–2005 and 2007) in these models were estimated on the boundary at 1.0, even in models in which they were constrained to a single parameter.

The model-averaged estimates of seniority indicated that in 2006, 2008, and 2009, the percentage of individuals that were newly recruited to the spawning population ranged between 11 and 17 percent for females and between 15 and 24 percent for males. Estimates indicated that about 6 percent of the individuals of each sex were newly recruited in 2010. As with river spawning LRS, the low estimates of seniority in 2006 likely are biased by an issue with sampling in the Chiloquin Dam fish ladder (Hewitt and others, 2011). Derived estimates of lambda for 2008 and 2009 were imprecise and the confidence intervals broadly overlapped 1.0, but the point estimates indicated an increase in the size of the spawning population (fig. 15). However, the size of the spawning population declined substantially in 2010 and the overall trend is negative. Compounding the 10 λ estimates indicates that the abundance of female SNS decreased by 69 percent ($\Delta_t = 0.31$) and the abundance of male SNS decreased by 71 percent ($\Delta_t = 0.29$) through 2011 (fig. 16).

Similar to lakeshore spawning LRS, the fork length data collected over the last 13 years for SNS suggests that the population is comprised almost entirely of similarly sized individuals, with little evidence of recruitment (fig. 17). This evidence contrasts with the recent seniority estimates that indicate recruitment of new spawners. 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 the section, “Discussion,” but these issues lead us to conclude that the overall trend in spawning population size probably is more negative than indicated by the derived λ estimates. As we have done for the LRS subpopulations, we calculated what we consider to be worst-case scenarios for the overall declines by assuming γ to be 1.0 in all years ($\lambda = \Phi$). The decline for females could be as much as 81 percent ($\Delta_t = 0.19$) and the decline for males could be as much as 86 percent ($\Delta_t = 0.14$; fig. 16).

The time series of fork length data provided in Janney and others (2008) included data back to 1984 and showed that the shortnose sucker population in Upper Klamath Lake went through a demographic transition similar to that for Lost River suckers. 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 appear to have grown little since 2009 (Hewitt and others, 2012; fig. 17), and the median fork length of each sex is now similar to what it was in the mid-1980s (males about 430 mm; females about 457 mm).

Discussion

A number of factors lead us to conclude that serious concern is warranted for the spawning populations of Lost River suckers and shortnose suckers in Upper Klamath Lake, and that the current situation is most dire for shortnose suckers. Capture-recapture results and size composition data show that the abundance of both species has declined steadily since the early 2000s, continuing trends documented previously (Hewitt and others, 2011; 2012). The SNS population has declined more than either subpopulation of LRS, but the abundances of both species probably have declined by more than 40 percent since the early 2000s. These declines primarily reflect 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 decline in abundance for SNS could be more than 80 percent since 2001, and SNS have had 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 close to or beyond the average expected lifespan. Furthermore, growth in length has essentially stopped for SNS. Classical theory suggests that some senescence should be occurring through reduced fecundity, increased mortality, or both (Hamilton, 1966). For SNS, the low estimates of survival in 2010 may be an indication that senescence in terms of increased mortality is indeed occurring. 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 could reveal whether senescence occurs through mortality for these populations (for example, Peron and others, 2010).

Despite the worrisome status of the populations, our monitoring shows that the abundance of both endangered suckers in Upper Klamath Lake is still at an order of magnitude that affords some protection from catastrophic mortality events, such as die-offs in the summer and autumn caused by poor water quality (for example, Perkins and others, 2000). Over the course of a spawning season, total counts of PIT-tagged individuals that are either captured in trammel net sampling or detected by the remote PIT tag detection systems provide absolute minimum abundances for the two species. In 2012, we encountered more than 6,500 lakeshore spawning LRS, more than 19,000 river spawning LRS, and more than 6,500 SNS. We know that these numbers are not accurate minimum abundances because the recapture percentages from weir and trammel net sampling show that a large proportion of fish in each population is not PIT-tagged. We can use the recapture percentages to adjust upwards the number of PIT-tagged fish that were encountered during a season (removing encounters of individuals that were first PIT-tagged in that season). As of the start of the 2012 sampling season, these calculations give revised minimum abundances of about 10,000 lakeshore spawning LRS, about 95,000 river spawning LRS, and about 14,000 SNS. These numbers provide a general sense of how many fish are in the spawning populations, but they are not estimates in any formal sense. They cannot be used to track changes in population size and should be used cautiously in any context for at least two major reasons. First, encounter probabilities are high because of the remote detection systems, but they are less than 1.0, are variable through time, and vary among populations and between sexes and PIT tag types (125 versus 134 kHz). Second, the recapture percentages from the weir and trammel net sampling may not apply to the entire spawning populations in Upper Klamath Lake because of the heterogeneity in encounter probabilities and the fact that we do not sample the spawning populations in a randomized design.

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 mainly 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 always were less than 0.16 and often 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 50 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 was greater by about 10 percent in 2011 and 2012. 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, which is due at least partly to the fact that the weir was installed in 2005 and has operated as a method of capture for river spawning LRS for only 7 years (the weir was ineffective during the high flows in 2006). Although we typically capture thousands of individuals 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 appear to be biased. Although some recruitment of new spawners is possible, the magnitude of recruitment suggested by the low estimates of seniority in 2003 and 2008 contrasts strongly 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 2008 and 2009 also appear to be biased low, the derived estimates of lambda 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. We expect that such issues with interpretation will resolve over time as more of the population is captured and PIT-tagged, although this could take many more years. Second, the addition 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 never declined from one year to the next, so any additions of new recruits must be 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 or no recruitment of new spawners and thus seniority estimates from capture-recapture models that are negatively biased in some years.

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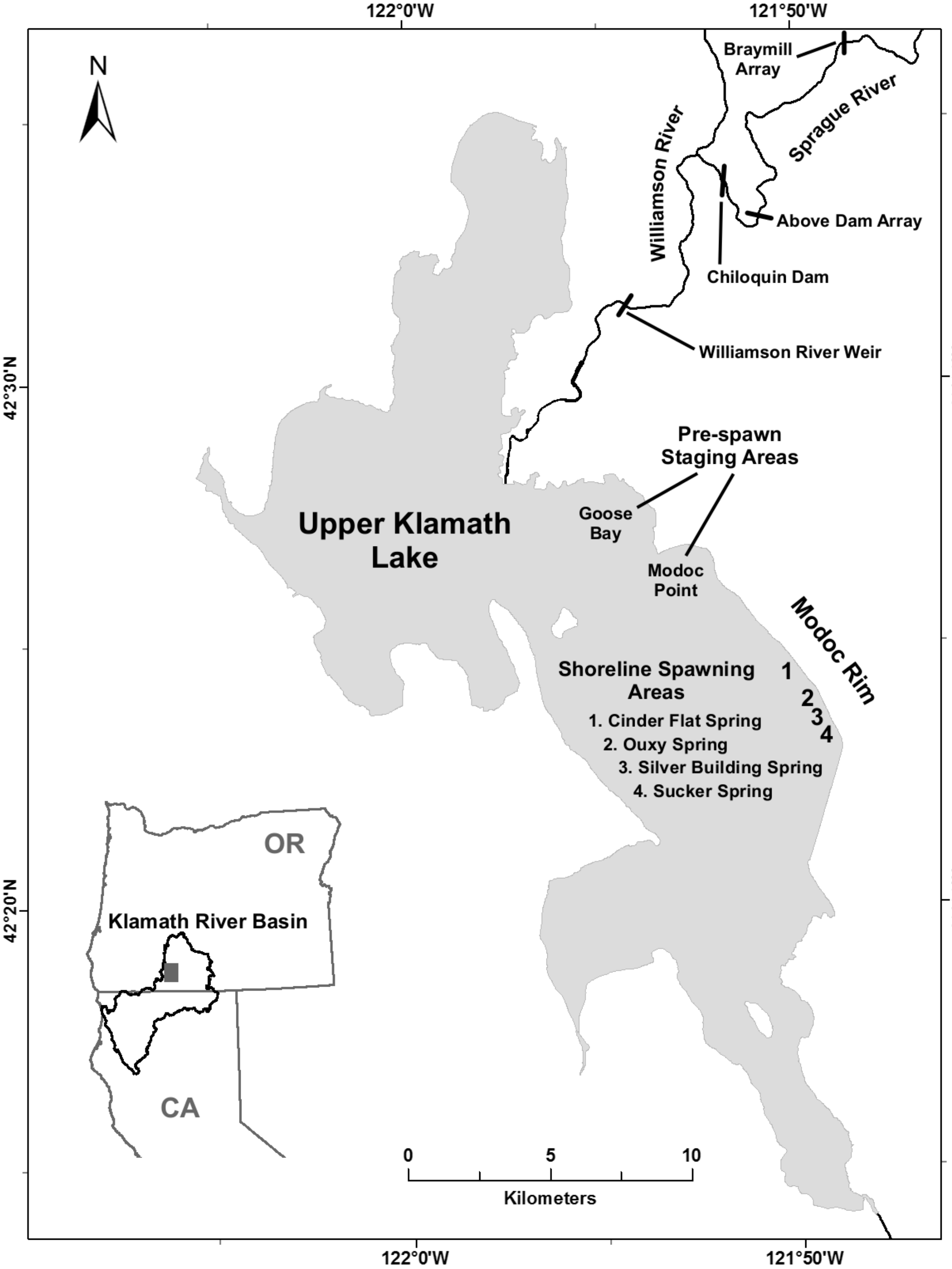

Figure 1. Map showing sampling locations for Lost River suckers and shortnose suckers in Upper Klamath Lake and its tributaries, Oregon, 2012. The inset shows the Klamath River Basin and the location of Upper Klamath Lake in south-central Oregon.

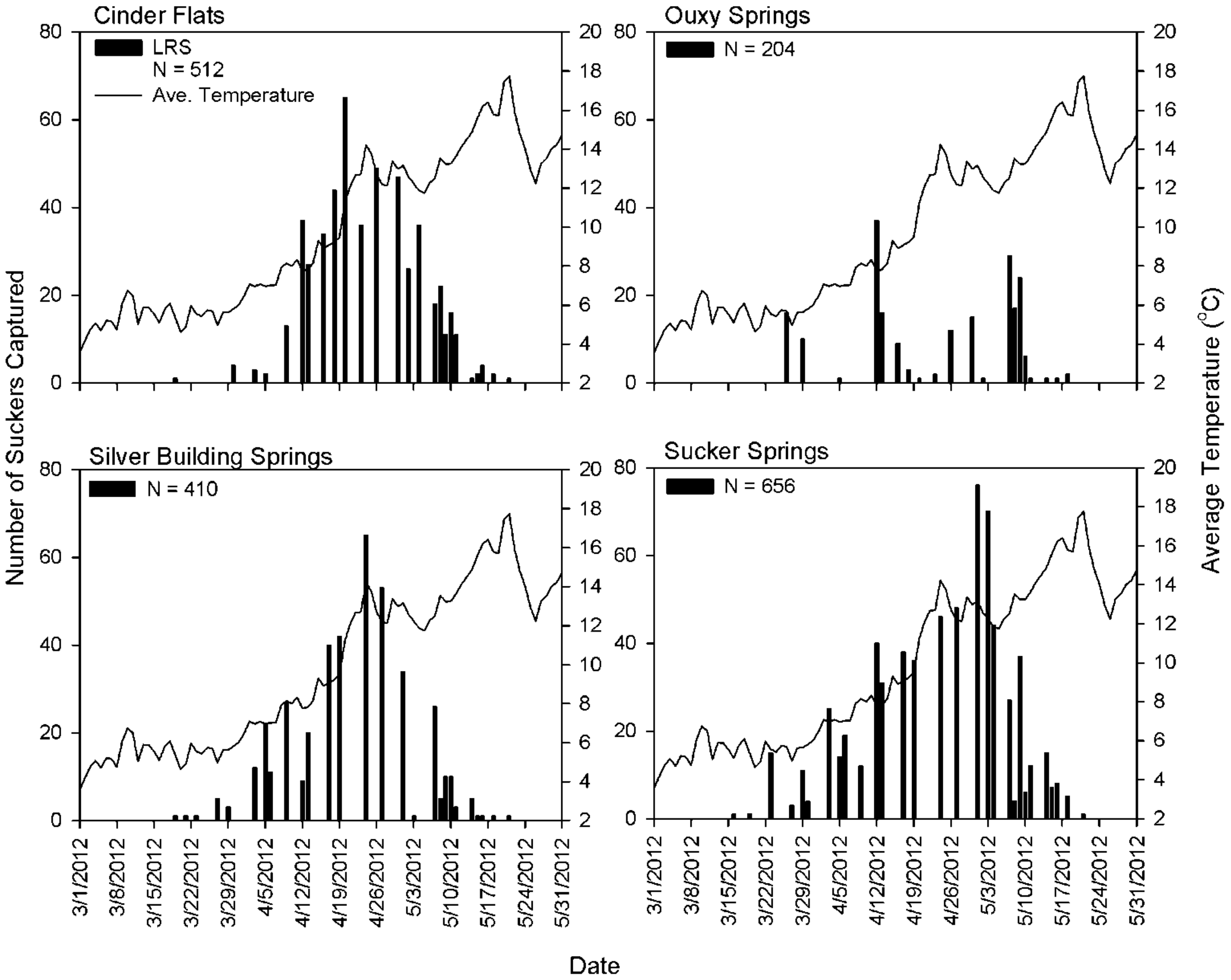

Figure 2. Seasonality of trammel net captures of Lost River suckers at lakeshore springs in Upper Klamath Lake, Oregon, 2012. Average daily water temperature (°C) is reported from a temperature logger that was placed just offshore away from spring influence near Cinder Flats. If fish were captured more than once at a given spring, only the first capture is included. Some fish were captured at multiple springs and thus are included in more than one graph.

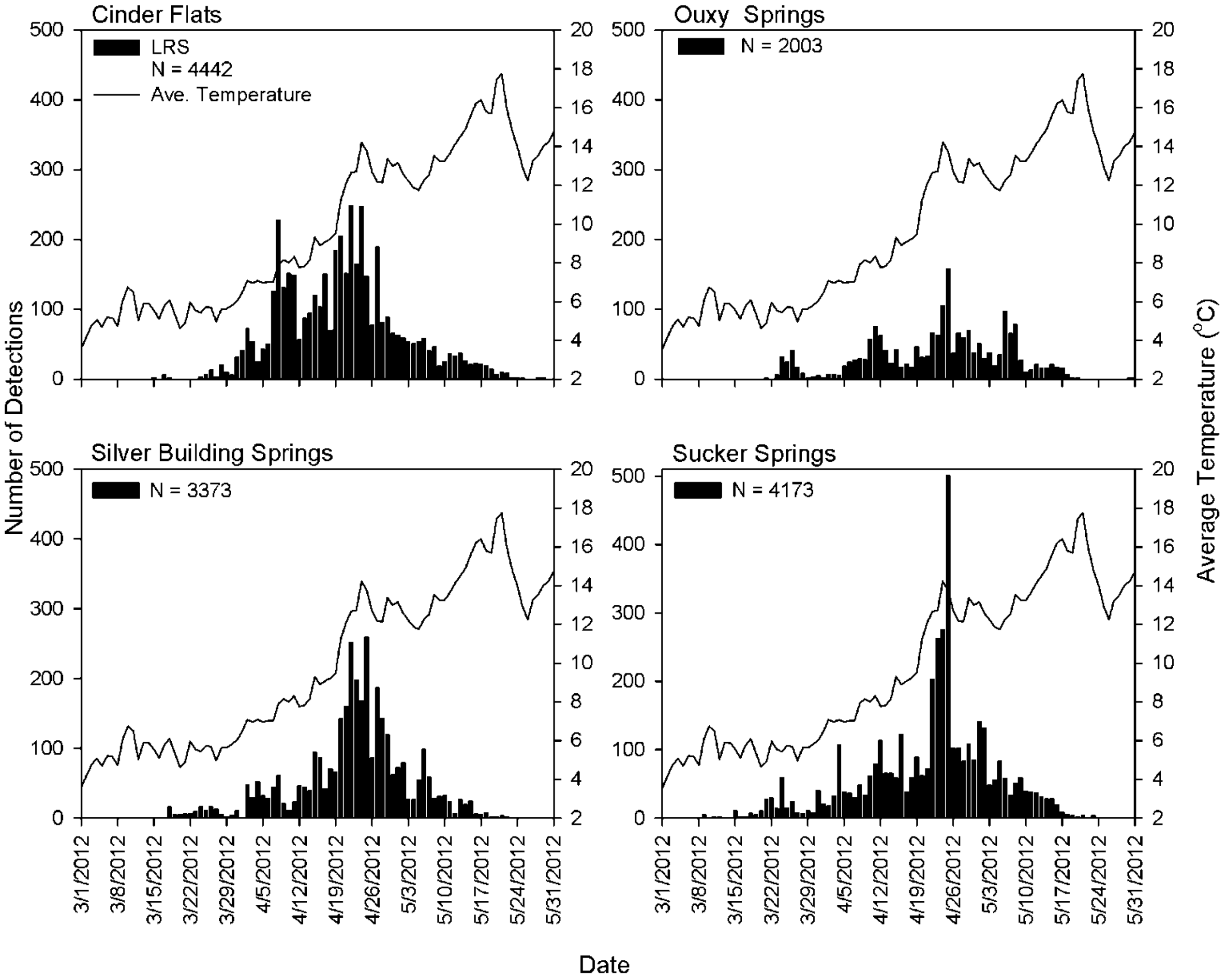

Figure 3. Seasonality of detections of Lost River suckers on remote passive integrated transponder (PIT) tag antennas at lakeshore springs in Upper Klamath Lake, Oregon, 2012. Average daily water temperature (°C) is reported from a temperature logger that was placed just offshore away from spring influence near Cinder Flats. If fish were detected more than once at a given spring, only the first detection is included. Some fish were detected at multiple springs and thus are included in more than one graph.

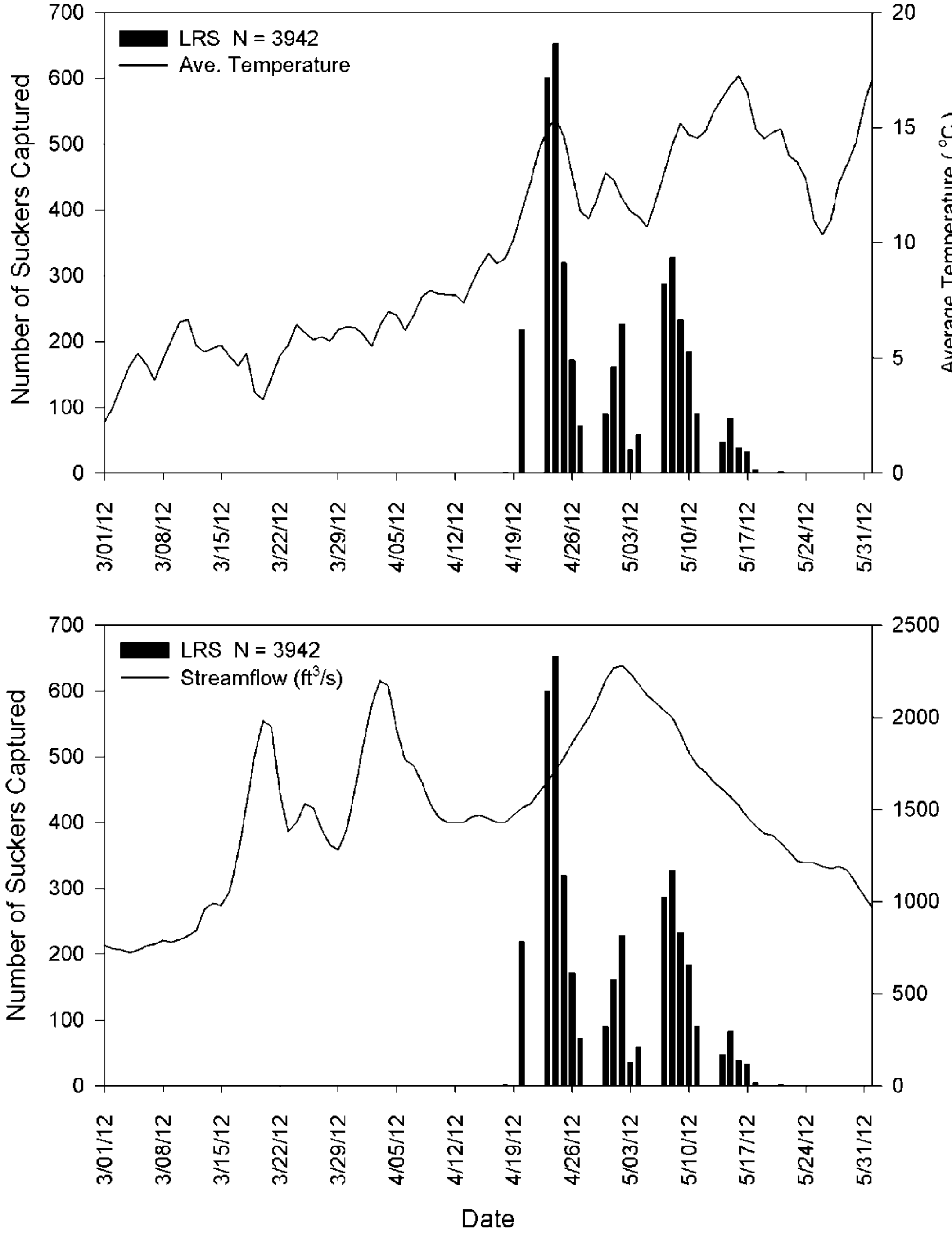

Figure 4. Seasonality of captures of Lost River suckers in the upstream trap of the Williamson River weir, Oregon, 2012. If fish were captured more than once, only the first capture is included. Average daily water temperature (°C) and streamflow (in cubic feet per second [ft^3/s]) are reported from the U.S. Geological Survey streamgage on the Williamson River downstream of the confluence with the Sprague River near Chiloquin, Oregon (11502500).

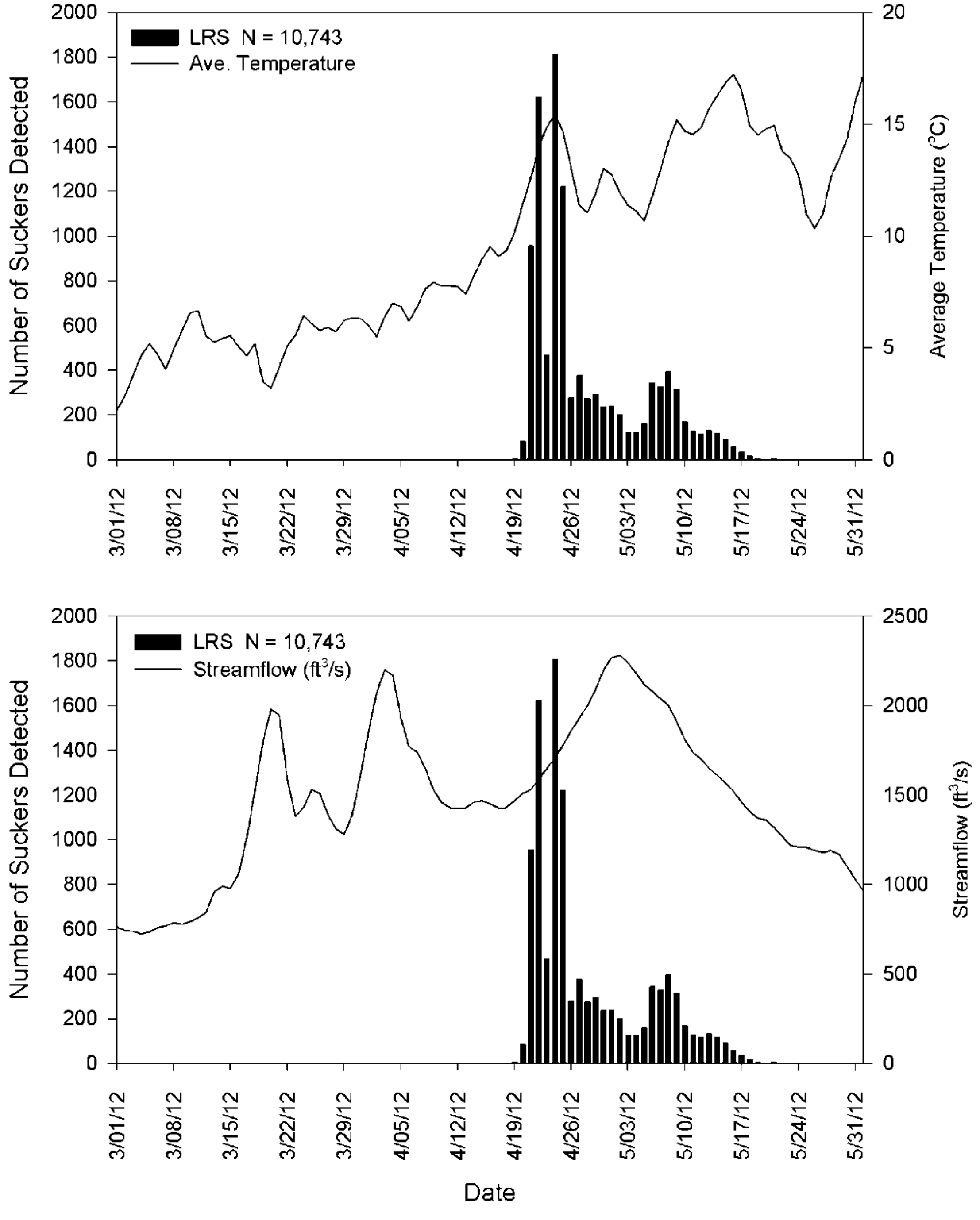

Figure 5. Seasonality of detections of Lost River suckers on the remote passive integrated transponder (PIT) tag antenna at the upstream trap of the Williamson River weir, Oregon, 2012. If fish were detected more than once, only the first detection is included. Average daily water temperature (°C) and streamflow (in cubic feet per second [ft^3/s]) are reported from the U.S. Geological Survey streamgage on the Williamson River downstream of the confluence with the Sprague River near Chiloquin, Oregon (11502500).

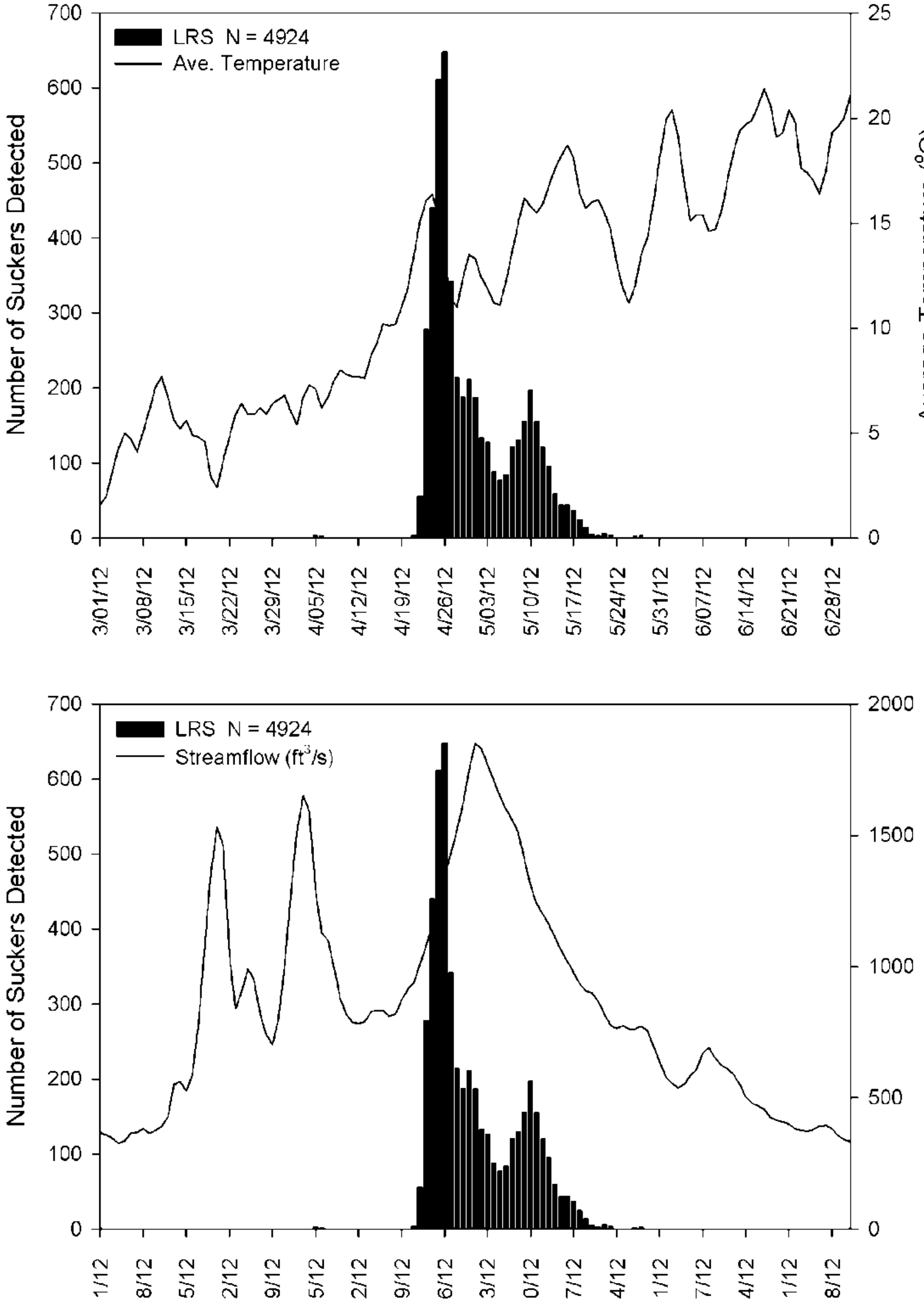

Figure 6. Seasonality of detections of Lost River suckers on the remote passive integrated transponder (PIT) tag antenna array across the Sprague River just downstream of the Chiloquin Dam site, Oregon, 2012. If fish were detected more than once, only the first detection is included. Average daily water temperature (°C) and streamflow (in cubic feet per second [ft³/s]) are reported from the U.S. Geological Survey streamgage on the Sprague River upstream of the confluence with the Williamson River, upstream of Chiloquin, Oregon (11501000).

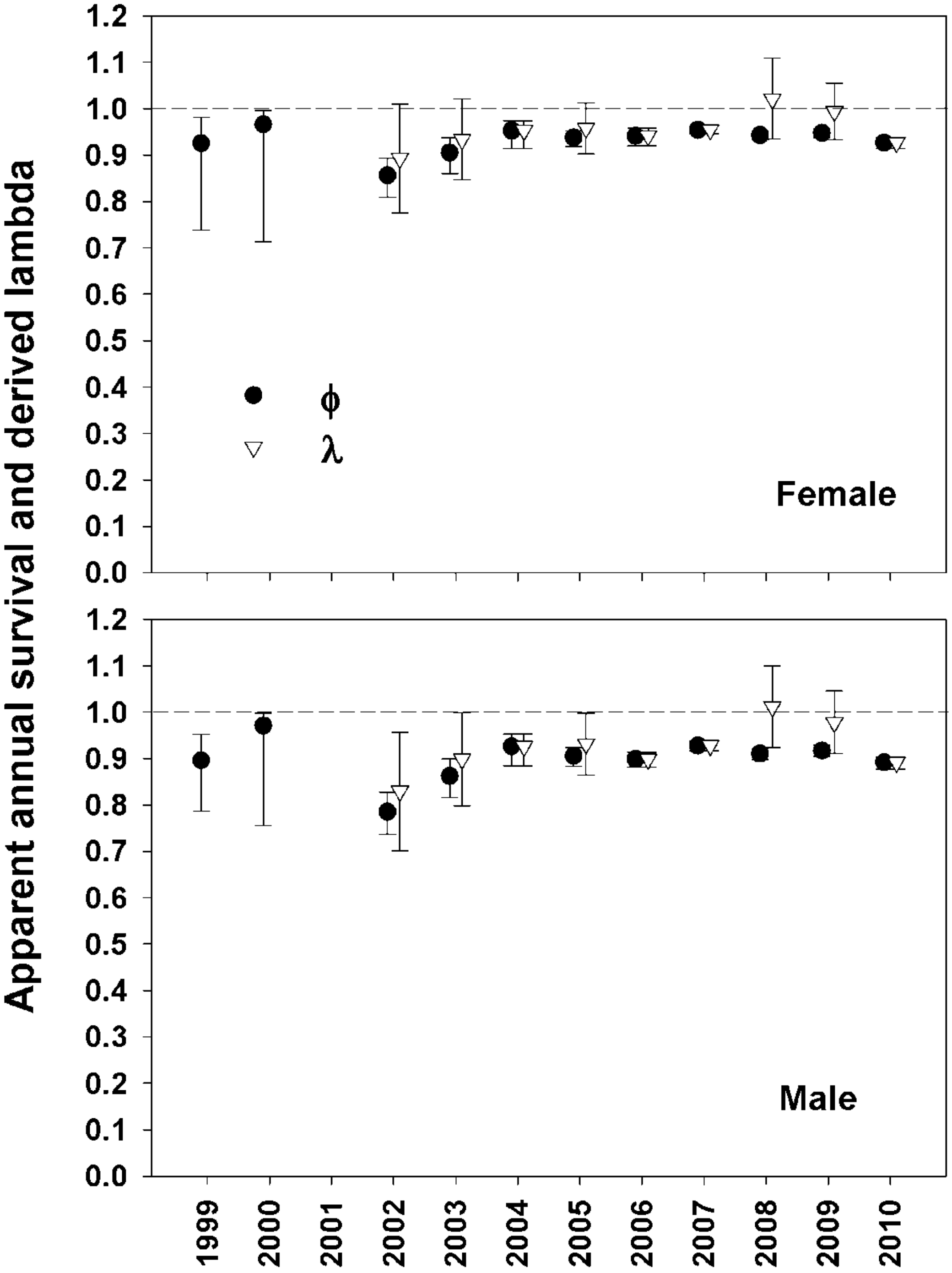

Figure 7. Model-averaged estimates of apparent annual survival probability (Φ) and derived population rate of change (λ) with 95-percent confidence intervals for Lost River suckers from the lakeshore spawning subpopulation, Upper Klamath Lake, Oregon, 1999–2010. The 2001 estimates of Φ were on the boundary at 1.0 and are not shown, as they indicate estimability problems.

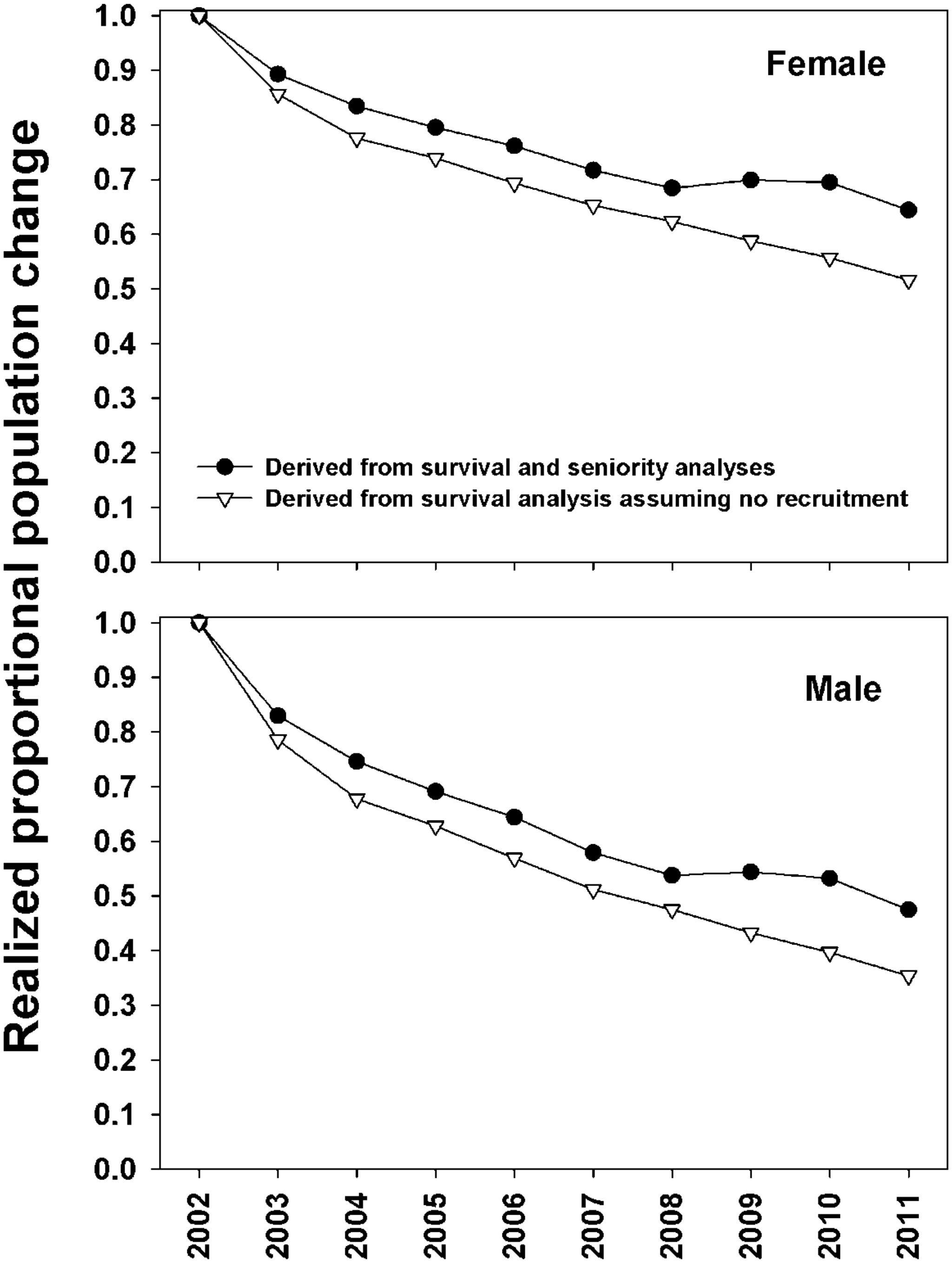

Figure 8. Realized proportional change in the size of the lakeshore spawning subpopulation of Lost River suckers, Upper Klamath Lake, Oregon, between 2002 and 2011. The filled circles show annual changes based on lambda estimates derived from separate models of apparent annual survival (Cormack-Jolly-Seber [CJS] likelihood) and seniority (reverse time CJS likelihood), using all encounters for survival estimates and physical captures only for seniority estimates. The open triangles show annual changes assuming no recruitment, a worst-case scenario but one that is plausible based on evidence from size composition data.

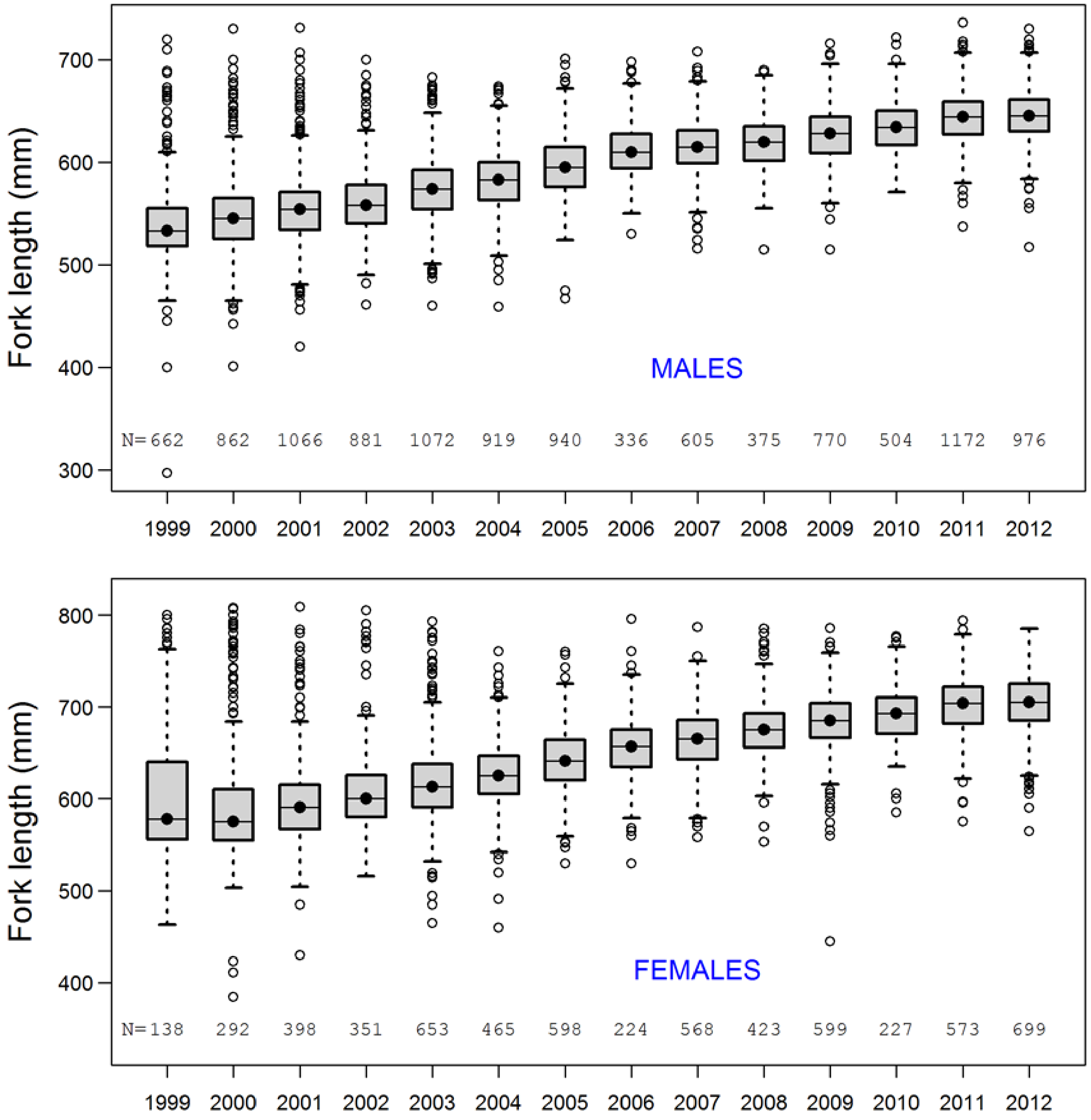

Figure 9. Boxplots of fork lengths (in millimeters [mm]) of male and female Lost River suckers captured in trammel nets at lakeshore springs, Upper Klamath Lake, Oregon, 1999–2012. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The number of fish included in the boxplots for each year are given near the *x*-axis in each panel.

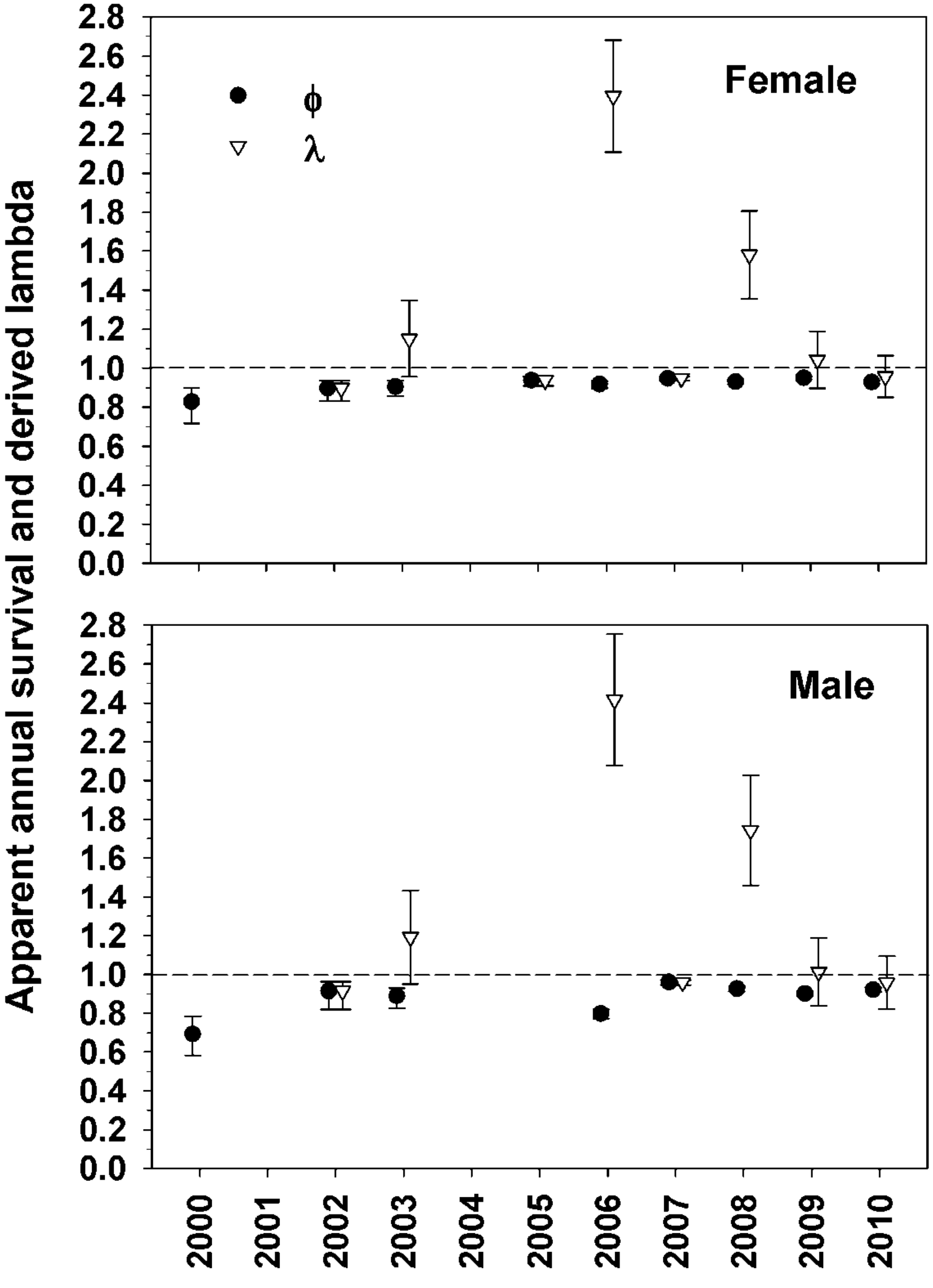

Figure 10. Model-averaged estimates of apparent annual survival probability (Φ) and derived population rate of change (λ) with 95-percent confidence intervals for Lost River suckers from the river spawning subpopulation, Upper Klamath Lake and its tributaries, Oregon, 2000–2010. Estimates of Φ were either on the boundary at 1.0 or were so imprecise that they were not useful for both sexes in 2001 and 2004, and for males in 2005. Estimates of γ for both sexes were on the boundary at 1.0 in 2002, 2004, 2005, and 2007.

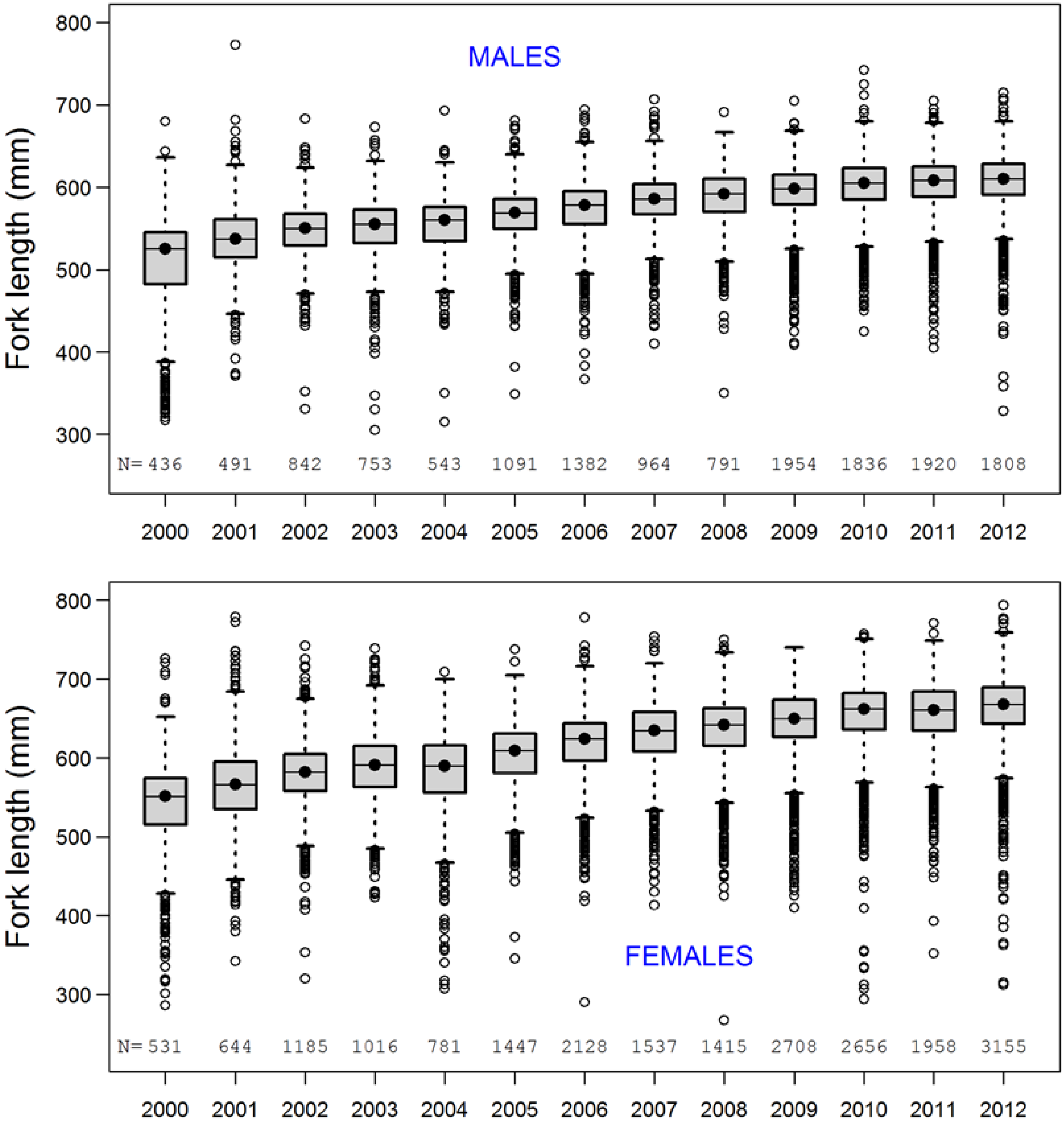

Figure 11. Boxplots of fork lengths (in millimeters [mm]) of male and female Lost River suckers captured at pre-spawn staging areas in Upper Klamath Lake and in the Williamson and Sprague Rivers, Oregon, 2000–2012. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The number of fish included in the boxplots for each year are given near the *x*-axis in each panel.

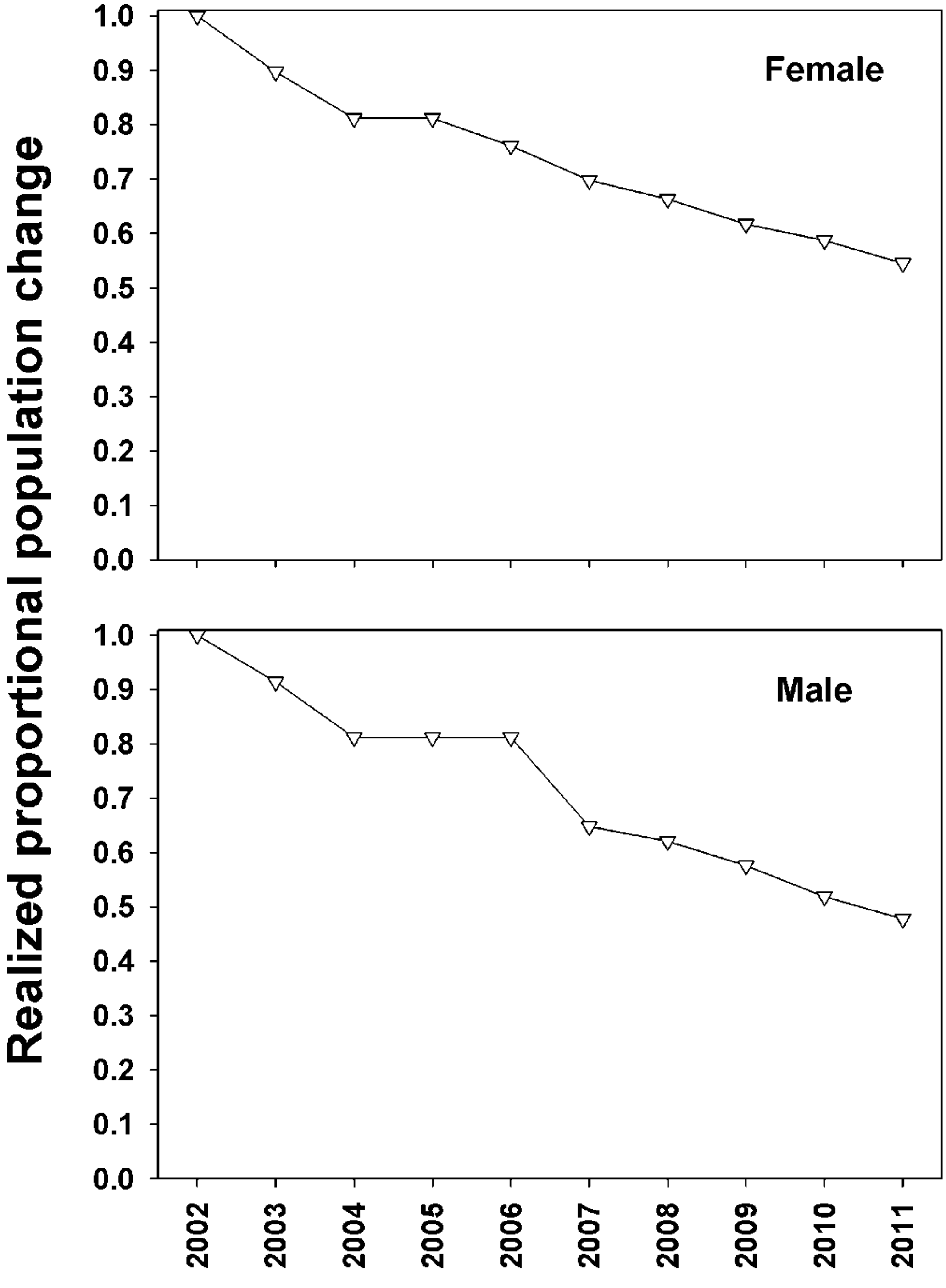

Figure 12. Realized proportional change in the size of the river spawning subpopulation of Lost River suckers, Upper Klamath Lake and its tributaries, Oregon, between 2002 and 2011. Annual changes are based on apparent annual survival estimates from Cormack-Jolly-Seber (CJS) models, assuming no recruitment. The assumption of no recruitment is a worst-case scenario, but is plausible based on evidence from size composition data. Annual changes that include seniority estimates from reverse-time CJS likelihood models are described in the text but are not plotted because they are so improbable in light of the size composition data.

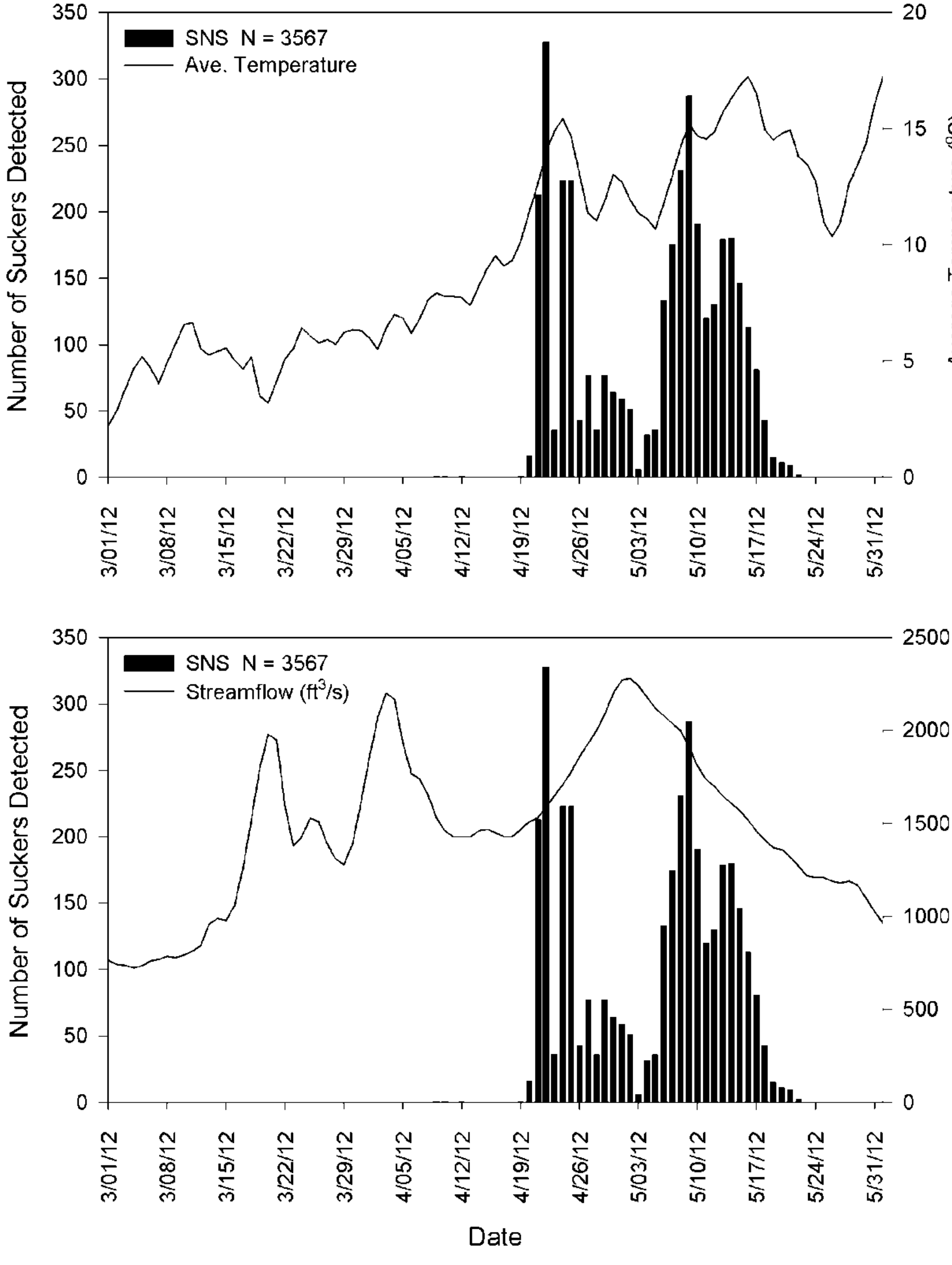

Figure 13. Seasonality of detections of shortnose suckers on the remote passive integrated transponder (PIT) tag antenna at the upstream trap of the Williamson River weir, Oregon, 2012. If fish were detected more than once, only the first detection is included. Average daily water temperature (°C) and streamflow (in cubic feet per second [ft^3/s]) are reported from the U.S. Geological Survey streamgage on the Williamson River downstream of the confluence with the Sprague River near Chiloquin, Oregon (11502500).

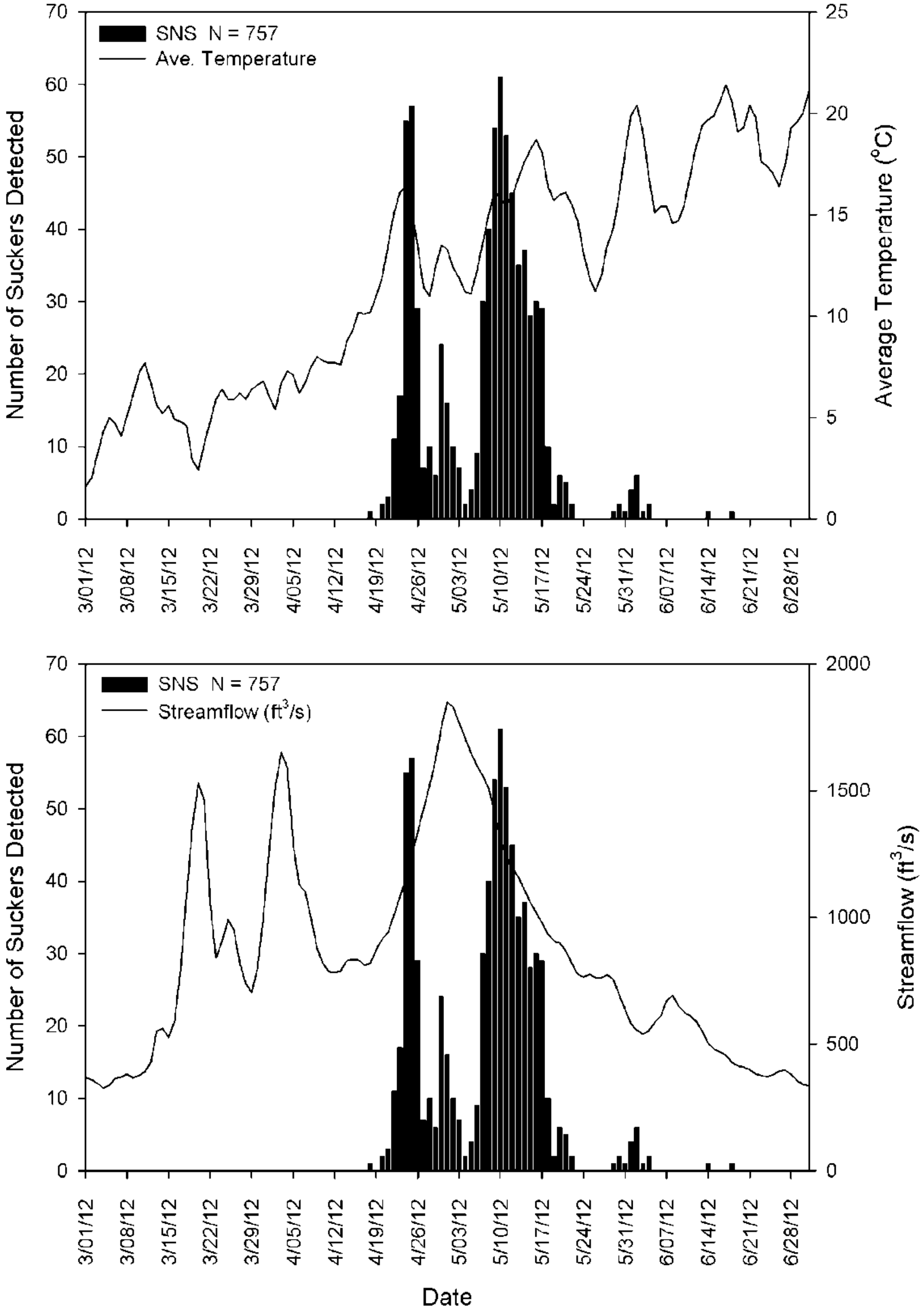

Figure 14. Seasonality of detections of shortnose suckers on the remote passive integrated transponder (PIT) tag antenna array across the Sprague River just downstream of the Chiloquin Dam site, Oregon, 2012. If fish were detected more than once, only the first detection is included. Average daily water temperature (°C) and streamflow (in cubic feet per second [ft^3/s]) are reported from the U.S. Geological Survey streamgage on the Sprague River upstream of the confluence with the Williamson River, upstream of Chiloquin, Oregon (11501000).

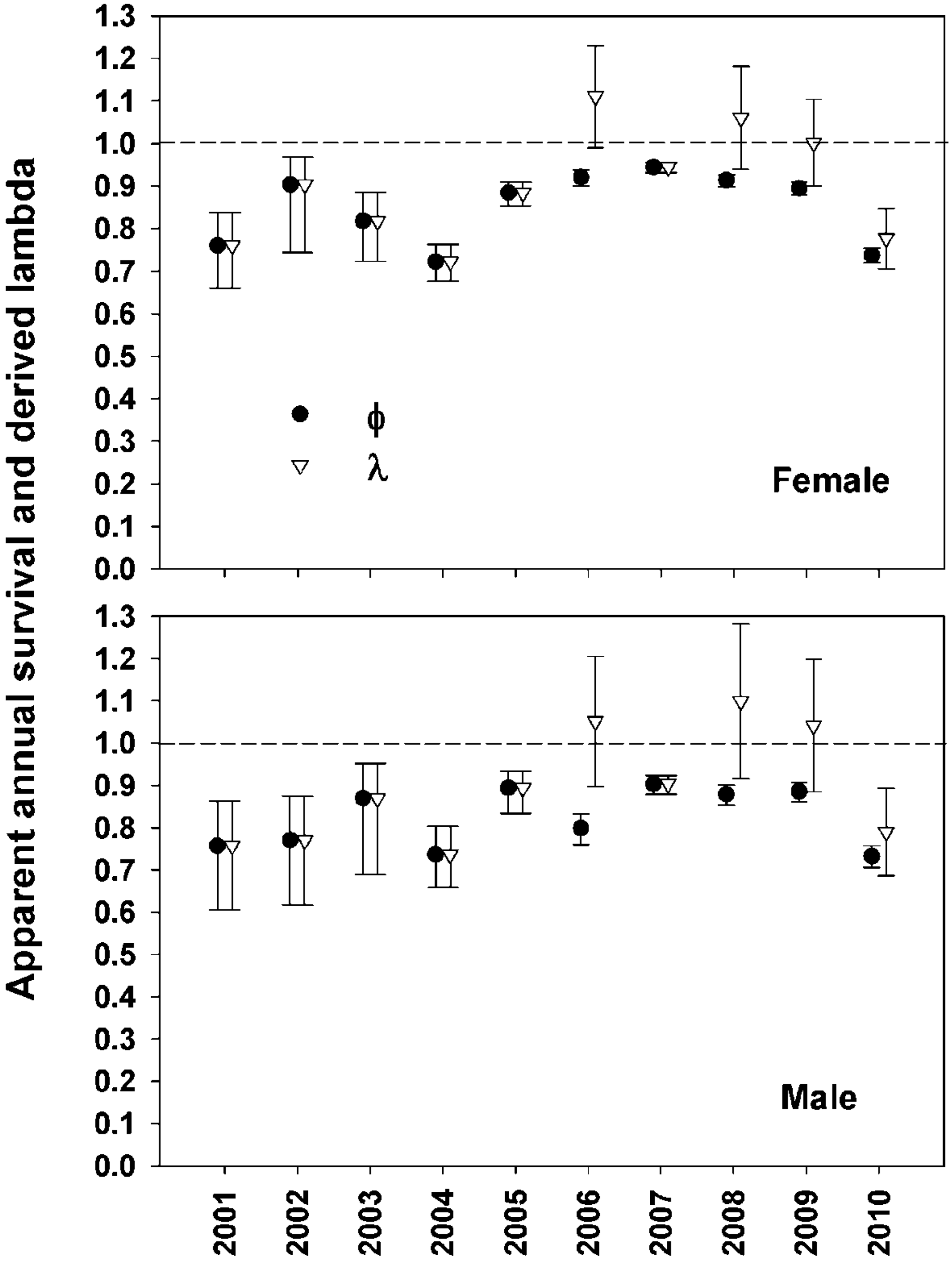

Figure 15. Model-averaged estimates of apparent annual survival probability (Φ) and derived population rate of change (λ) with 95-percent confidence intervals for shortnose suckers, Upper Klamath Lake and its tributaries, Oregon, 2001–2010. The estimates of Φ in 1999 and 2000 were either on the boundary at 1.0 or were so imprecise that they were not useful, so they are not shown.

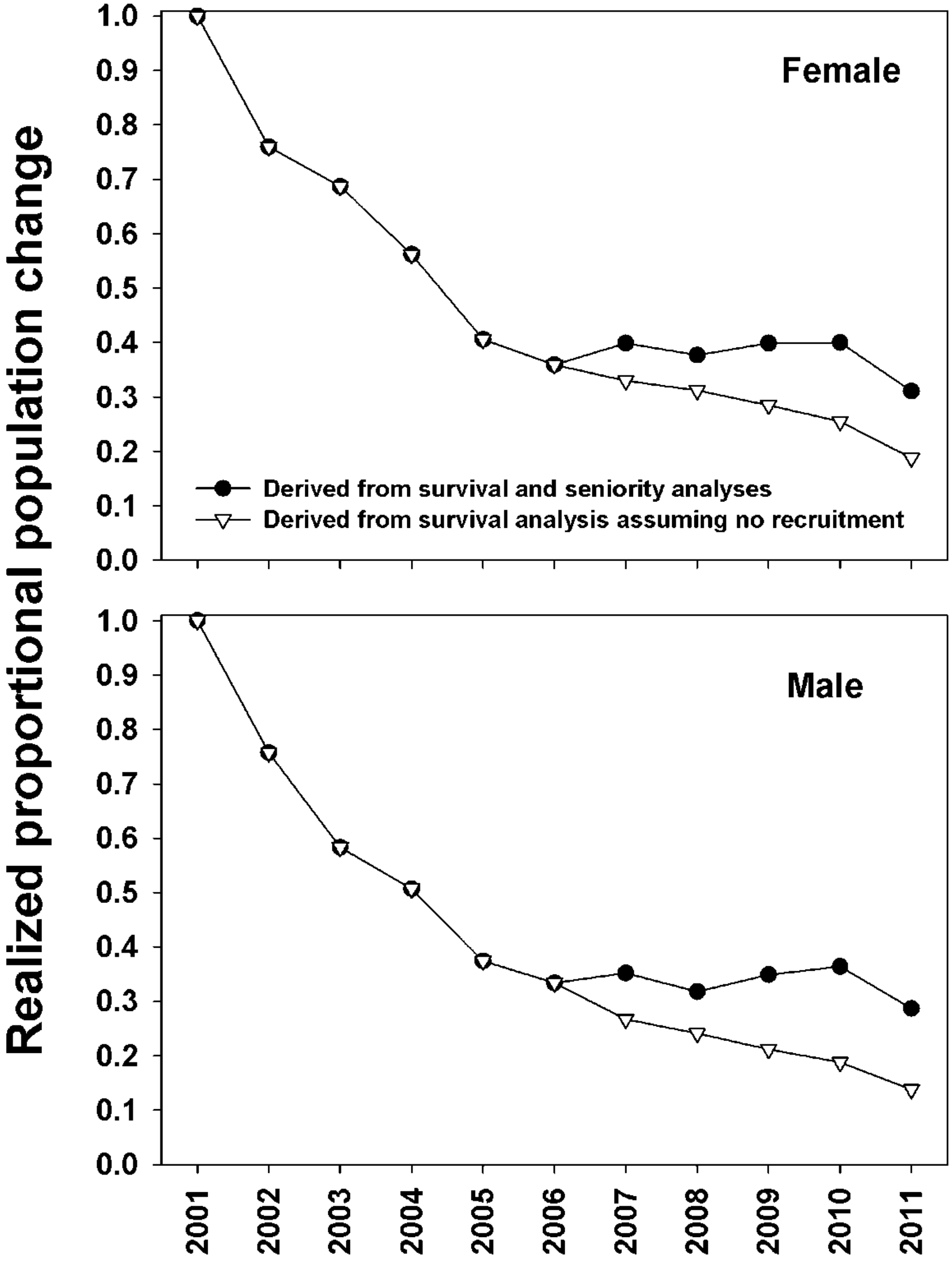

Figure 16. Realized proportional change in the size of the spawning population of shortnose suckers, Upper Klamath Lake and its tributaries, Oregon, between 2001 and 2011. The filled circles show annual changes based on lambda estimates derived from separate models of apparent annual survival (Cormack-Jolly-Seber [CJS] likelihood) and seniority (reverse time CJS likelihood), using all encounters for survival estimates and physical captures only for seniority estimates. The open triangles show annual changes assuming no recruitment, a worst-case scenario but one that is plausible based on evidence from size composition data.

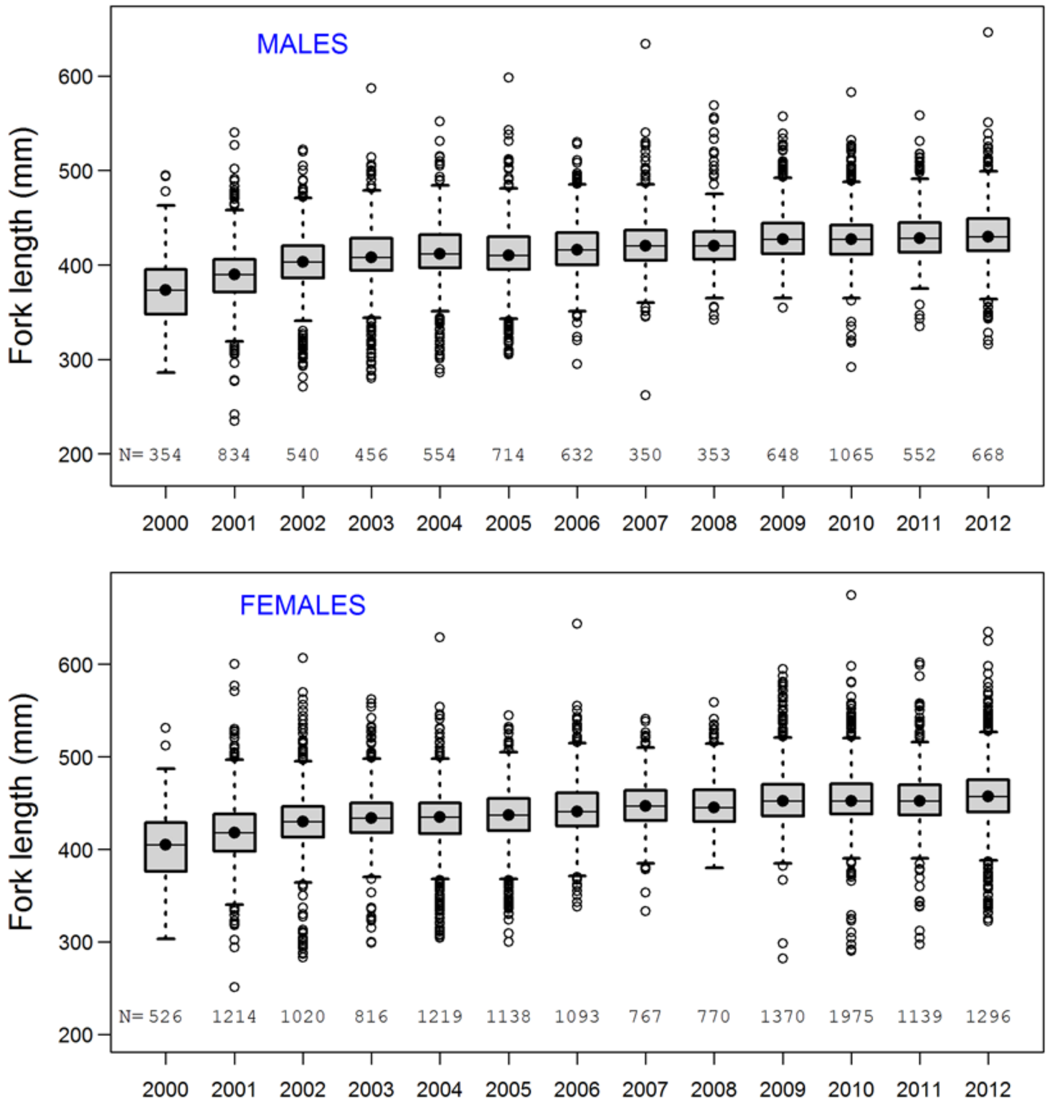

Figure 17. Boxplots of fork lengths (in millimeters [mm]) of male and female shortnose suckers captured in Upper Klamath Lake and the Williamson and Sprague Rivers, Oregon, 2000–2012. Dots in the boxes represent the medians and the boxes cover the central 75 percent of the data. The number of fish included in the boxplots for each year are given near the *x*-axis in each panel.

Table 1. Numbers of Lost River suckers and shortnose suckers captured in Upper Klamath Lake (UKL) and the Williamson River, Oregon, 2003–2012.

[Totals include only the first capture of an individual at a given location, but individuals may have been captured at more than one location in a year. Recaptures are the percentage of individuals captured in a given year that were implanted with a passive integrated transponder (PIT) tag in a previous year. High flows in the Williamson River in 2006 inundated the weir and allowed fish to pass over and around the weir without swimming through the trap]

Capture location	Year	Lost River suckers	Recaptures (percent)	Shortnose suckers	Recaptures (percent)
UKL Pre-spawn Staging Areas	2012	1,188	25	1,665	39
	2011	870	22	1,600	36
	2010	1,523	17	2,951	28
	2009	1,535	13	1,763	25
	2008	461	12	663	19
	2007	336	8	801	21
	2006	432	8	870	16
	2005	471	7	387	12
	2004	929	6	1,413	11
	2003	403	4	586	9
Williamson River Weir	2012	3,927	14	424	29
	2011	3,126	12	181	32
	2010	3,085	9	214	24
	2009	3,276	8	368	22
	2008	1,314	7	283	22
	2007	2,055	6	235	14
	2006	–	–	–	–
	2005	816	2	203	13
UKL Lakeshore Springs	2012	1,718	56	1	0
	2011	1,812	56	3	33
	2010	756	50	10	60
	2009	1,419	45	7	57
	2008	833	44	3	100
	2007	1,212	42	13	69
	2006	579	36	6	83
	2005	1,604	34	18	50
	2004	1,423	30	29	31
	2003	1,762	23	30	37

Table 2. Numbers of Lost River suckers and shortnose suckers detected by remote antennas in Upper Klamath Lake (UKL) and its tributaries, Oregon, 2012.

[Totals include only the first detection of an individual at a given location, but individuals may have been detected at more than one location]

Location of remote antennas	Lost River suckers	Shortnose suckers	Total
Williamson and Sprague Rivers			
Williamson River Weir	19,230	6,067	25,297
Chiloquin Dam Array	4,907	732	5,639
Above Dam Array	737	379	1,116
Braymill Array	23	5	28
UKL Lakeshore Springs			
Cinder Flats	4,440	11	4,451
Ouxy Springs	2,001	4	2,005
Silver Building Springs	3,372	11	3,383
Sucker Springs	4,171	18	4,189

Table 3. Model selection results for the top eight capture-recapture models fitted to the data for the lakeshore spawning subpopulation of Lost River suckers, 1999–2012.

[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 (overdispersion correction factor [ĉ] = 1.59). Twenty-seven other models were considered, but all had ΔQAICc > 55 and are not 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 2012. 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 is presented first, and ΔQAICc values represent 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]

Model	*K*	QAICc	ΔQAICc	w_i	$-2Log_eL$
ϕ(sex + time) *p*(sex × time + [tagtype × time])	50	36,993.7	0.0	0.89	58,660.7
ϕ(sex × time) *p*(sex × time + [tagtype × time])	62	36,998.0	4.3	0.10	58,629.4
ϕ(sex + time) *p*(sex × time × tagtype)	58	37,002.5	8.8	0.01	58,649.2
ϕ(sex × time) *p*(sex × time × tagtype)	70	37,006.7	13.1	0.00	58,617.8
ϕ(sex + time) *p*(sex + time + [tagtype × time])	37	37,017.0	23.3	0.00	58,739.2
ϕ(sex × time) *p*(sex + time + [tagtype × time])	49	37018.7	25.0	0.00	58,703.7
ϕ(sex + time) *p*(sex × time + tagtype)	43	37,023.9	30.2	0.00	58,731.1
ϕ(sex × time) *p*(sex × time + tagtype)	55	37,028.1	34.4	0.00	58,699.6

Table 4. Model selection results for the top three capture-recapture models fitted to the data for the river spawning subpopulation of Lost River suckers, 2000–2012.

[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 (overdispersion correction factor [ĉ] = 1.86). Thirty-two other models were considered, but all had ΔQAICc > 75 and are not shown. See the headnote in table 3 for a complete description of table contents]

Model	*K*	QAICc	ΔQAICc	w_i	$-2Log_eL$
ϕ(sex × time) *p*(sex × time × tagtype)	60	56,557.9	0.00	1.00	105,200.2
ϕ(sex × time) *p*(sex × time + [tagtype × time])	53	56,593.0	35.07	0.00	105,291.7
ϕ(sex + time) *p*(sex × time × tagtype)	50	56,599.0	41.04	0.00	105,314.0

Table 5. Model selection results for the top six capture-recapture models fitted to the data for the shortnose sucker population, 1999–2012.

[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 (overdispersion correction factor [ĉ] = 1.39). Twenty-nine other models were considered, but all had ΔQAICc > 53 and are not shown. See the headnote in table 3 for a complete description of table contents]

Model	*K*	QAICc	ΔQAICc	w_i	$-2Log_eL$
ϕ(sex × time) *p*(sex + time + [tagtype × time])	46	51,495.9	0.0	0.92	71,245.7
ϕ(sex × time) *p*(sex × time + [tagtype × time])	57	51,501.0	5.1	0.07	71,222.2
ϕ(sex × time) *p*(sex × time × tagtype)	64	51,506.4	10.5	0.01	71,210.2
ϕ(sex + time) *p*(sex × time + [tagtype × time])	47	51,529.5	33.6	0.00	71,289.5
ϕ(sex + time) *p*(sex + time + [tagtype × time])	34	51,532.1	36.2	0.00	71,329.2
ϕ(sex + time) *p*(sex × time × tagtype)	53	51,534.6	38.7	0.00	71,279.8

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