Prepared in cooperation with the Bureau of Reclamation

Inter-Annual Variability in Apparent Relative Production, Survival, and Growth of Juvenile Lost River and Shortnose Suckers in Upper Klamath Lake, Oregon, 2001–15

Open-File Report 2017–1069

U.S. Department of the Interior
U.S. Geological Survey

Cover: Photograph showing unidentified juvenile sucker from Upper Klamath Lake, Oregon. Photograph by Summer Burdick, U.S. Geological Survey, May 27, 2009.

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RYAN K. ZINKE, Secretary

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
	Length	
millimeter (mm)	0.03937	inch (in.)
centimeter (cm)	0.3937	inch (in.)
meter (m)	3.281	foot (ft)
meter (m)	1.094	yard (yd)
	Area	
hectare (ha)	2.471	acre
hectare (ha)	0.003861	square mile (mi^2)
	Volume	
liter (L)	33.81	ounce, fluid (fl. oz)
	Mass	
milligram (mg)	3.5274×10^{-5}	ounce, avoirdupois (oz)
kilogram (kg)	2.205	pound avoirdupois (lb)

Concentrations of chemical constituents in water are given either in milligrams per liter (mg/L).

Datum

Horizontal coordinate information is referenced to North American Datum of 1983 (NAD 83).

Abbreviations and Acronyms

AIC	Akaike's information criterion
AICc	Akaike's information criterion adjusted for sample size
CPUE	Catch per unit effort
df	degrees of freedom
FL	fork length
Prob [LRS]	Genetic probability of being a Lost River sucker rather than another Klamath Basin sucker
R^2	coefficient of determination
SD	standard deviation
SE	standard error
SL	standard length
Prob[LRS]	Probability that a sucker was a Lost River sucker
USGS	U.S. Geological Survey

Inter-Annual Variability in Apparent Relative Production, Survival, and Growth of Juvenile Lost River and Shortnose Suckers in Upper Klamath Lake, Oregon, 2001–15

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Executive Summary

Populations of the once abundant Lost River (*Deltistes luxatus*) and shortnose suckers (*Chasmistes brevirostris*) of the Upper Klamath Basin, decreased so substantially throughout the 20th century that they were listed under the Endangered Species Act in 1988. Major landscape alterations, deterioration of water quality, and competition with and predation by exotic species are listed as primary causes of the decreases in populations. Upper Klamath Lake populations are decreasing because fish lost due to adult mortality, which is relatively low for adult Lost River suckers and variable for adult shortnose suckers, are not replaced by new young adult suckers recruiting into known adult spawning aggregations. Catch-at-age and size data indicate that most adult suckers presently in Upper Klamath Lake spawning populations were hatched around 1991. While, a lack of egg production and emigration of young fish (especially larvae) may contribute, catch-at-length and age data indicate high mortality during the first summer or winter of life may be the primary limitation to the recruitment of young adults. The causes of juvenile sucker mortality are unknown.

We compiled and analyzed catch, length, age, and species data on juvenile suckers from Upper Klamath Lake from eight prior studies conducted from 2001 to 2015 to examine annual variation in apparent production, survival, and growth of young suckers. We used a combination of qualitative assessments, general linear models, and linear regression to make inferences about annual differences in juvenile sucker dynamics. The intent of this exercise is to provide information that can be compared to annual variability in environmental conditions with the hopes of understanding what drives juvenile sucker population dynamics.

Age-0 Lost River suckers generally grew faster than age-0 shortnose suckers, but the difference in growth rates between the two species varied among years. This unsynchronized annual variation in daily growth may be an indication that environmental conditions are affecting growth rates of these species in different ways.

The combined evidence outlined in this report and in Simon and others (2012) indicates that years of relatively high age-0 sucker production occurred in the late 1990s through at least 2000, in 2006, and in 2011. Our analysis of annual age-0 sucker catch per unit effort (CPUE), which accounted for zero inflated data and annual variation in sampling gears and locations, indicated that 2006 had the greatest apparent relative production of age-0 suckers ≥ 45 mm standard length (SL) during the time

period examined. Midsummer trap net effort by the U.S. Geological Survey (USGS) was too sparse to examine age-0 sucker CPUE from 2011 to 2013. Relatively frequent catches of age-1 suckers in 2001, 2007, and 2012 corroborated relatively high CPUE for age-0 suckers during 1999–2000, 2006, and 2011, as reported by USGS or Simon and others (2012).

There were several indications in the data that juvenile sucker survival is low from at least midsummer of the first year of life through mid-September of the second year of life. Our estimated index of relative apparent age-0 sucker late-summer survival, which accounted for zero inflated data and variations in sampling gears and locations, was higher in 2009 than in 2004. Our index of apparent age-0 sucker mortality for all other years from 2001 to 2015 was similar among years. Seventy-five percent of age-1 suckers were captured prior to July 17 each year. In 2007, the one year with substantial age-1 sucker summertime catches, the proportion of nets to capture age-1 suckers decreased from July to mid-September. Maximum annual age-2+ sucker CPUE was 0.02 fish per net, 10,000 times less than the maximum annual age-0 sucker CPUE.

Analysis of species data indicated that juvenile Lost River suckers may have greater apparent mortality than shortnose suckers. Lost River suckers made up a smaller proportion of age-0 suckers captured in July each year than would be expected, based on the abundance of adult Lost River suckers relative to shortnose suckers, and higher Lost River than shortnose sucker fecundity. The proportion of age-0 suckers captured that were Lost River suckers decreased from July to September in several years. Only 14 percent of age-1 or older juvenile suckers identified to species over the 15-year time period were Lost River suckers.

Background

Historically, Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) suckers were abundant in Upper Klamath Lake, providing a major subsistence fishery for the indigenous peoples (National Research Council, 2004). Decreasing sucker population sizes were noted in the first quarter of the 20th century (National Research Council, 2004), but it was not until 1985 that the severity of the situation was realized (U.S. Fish and Wildlife Service, 1993). By 1974, both species were listed as endangered in California (Moyle, 2002), and in 1988, they were listed as federally endangered (U.S. Fish and Wildlife Service, 1988). Only after the Federal listing were the two sucker species proposed as endangered in Oregon (Oregon Natural Heritage Data Base, 1989). Decreases in sucker populations were attributed to damming of rivers; dredging and draining lake-fringe wetlands; water diversions; hybridization; competition with and predation by exotic species; insularization of habitat; and suboptimal water quality associated with timber harvest, removal of riparian vegetation, livestock grazing, and agricultural practices (U.S. Fish and Wildlife Service, 1988). Lost River and shortnose suckers historically were found in most lakes throughout the Upper Klamath Basin, but presently are primarily found in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California, with smaller populations of one or both species found in Keno Reservoir (also known as Lake Ewauna), Gerber Reservoir, Tule Lake, and the Lost River (National Research Council, 2004).

Several endangered sucker species, including Lost River and shortnose suckers, in the Western United States are limited by recruitment into the adult spawning aggregations. The primary, short-term threat to the persistence of Lost River and shortnose suckers in Upper Klamath Lake is a prolonged lack of substantial and sustained recruitment of new individuals into spawning populations (Hewitt and others, 2015). Age structure and catch size composition indicate that the cohorts originating in the early 1990s presently compose most adult suckers in Upper Klamath Lake populations of both species (Hewitt and others, 2015). Low survival during early life stages, limited egg production, and emigration of young fish, may all contribute to the lack of young mature suckers in Upper Klamath Lake populations. Hypothesized causes of low survival include competition with non-native fishes, predation by birds, factors related to poor water quality, cyanotoxins, parasites, dietary deficiencies, and overwinter starvation (Martin and Saiki, 1999; Foott and Stone, 2005; Markle and Dunsmoor, 2007; Burdick, 2013; Kent and others, 2014; Burdick and others, 2015; Evans and others, 2016). Lack of recruitment to the adult Cui-ui (*Chasmistes cujus*) populations endemic to Pyramid Lake, Nevada, was a result of a lack of connectivity between rearing and spawning habitats that lead to a failure to reproduce (Scoppettone and Rissler, 2012). Low survival of early life stages due to predation has been hypothesized as the cause of limited adult recruitment for Razorback suckers (*Xyauchen texanus*) native to the Colorado River and June suckers (*Chasmistes liorus)* native to Utah Lake, Utah (Andersen and others, 2006; Marsh and others, 2015).

Sampling of suckers throughout Upper Klamath Lake, in the lake's tributaries, and near the lake outlet indicate that emigration and reduced susceptibility to gear alone cannot explain the near absence of older juvenile suckers (Hendrixson and others, 2007a, 2007b; Bottcher and Burdick, 2010). Summertime movement of juvenile suckers along the eastern shore and toward the lake outlet was not detected from July to September during 2002–06 (Hendrixson and others, 2007a), nor was there a shift in abundance of age-0 juvenile suckers from northern and eastern parts of the lake near spawning areas to areas near lake outlets in lakewide sampling from June to September during 2007–09 (Bottcher and Burdick, 2010). Instead, juvenile suckers captured in Upper Klamath Lake were progressively larger from June to September throughout Upper Klamath Lake and CPUEs decreased in all parts of the lake simultaneously (Hendrixson and others, 2007a, 2007b; Bottcher and Burdick, 2010). Extensive studies of juvenile sucker distribution indicated that age-0 suckers are habitat generalists in Upper Klamath Lake once they reach about 45 mm SL and, therefore, indicated that mid- to late-summer decreases in CPUEs were not due to fish changing habitats (VanderKooi and others, 2004; Hendrixson and others, 2007a, 2007b; Bottcher and Burdick, 2010; Burdick and Hewitt, 2012). Furthermore, age-0 to age-6 Lost River and shortnose suckers have been captured in Clear Lake Reservoir with the same gear as used in Upper Klamath Lake, indicating that gear avoidance cannot completely explain the near-complete annual disappearance of juvenile suckers from Upper Klamath Lake (Burdick and others, 2015). Therefore, low survival within the first year of life likely is a major factor contributing to the lack of older and larger juvenile suckers captured in Upper Klamath Lake.

Annual variability in juvenile sucker production, growth, and survival are unknown. Understanding the variability in juvenile sucker dynamics may lead to new hypotheses about environmental factors controlling juvenile sucker dynamics. Catch per unit effort, length, age, and species identification data for juvenile suckers were collected as part of habitat use and sucker health research by the U.S. Geological Survey (USGS) from 2001 to 2015 in Upper Klamath Lake. These data previously were analyzed to understand habitat use, sucker distribution, and migration patterns (VanderKooi and Buelow, 2001; VanderKooi and others, 2004; Burdick and others, 2007; Hendrixson and others, 2007a, 2007b; Burdick and others, 2009a, 2009b; Bottcher and Burdick, 2010; Burdick and Brown, 2010; Burdick and VanderKooi, 2010; Burdick, 2012a, 2012b; Burdick and Hewitt, 2012; Burdick, 2013; Burdick and others 2015). We examined trends in these data to describe annual variability in sucker dynamics that in future research may be correlated with environmental conditions to better assess the reasons for the failure of suckers to thrive in Upper Klamath Lake.

Study Area

The study area is located in the U.S. Fish and Wildlife Service Upper Klamath Lake recovery unit for Lost River and shortnose suckers, including Upper Klamath Lake and its tributaries (U.S. Fish and Wildlife Service, 2012; fig. 1). Upper Klamath Lake has a large surface area (36,260 ha), yet has a shallow depth of about 2 m throughout most of the lake and, therefore, is a discontinuous polymictic lake (National Research Council, 2004). Consequently, the water column is intermittently stratified during summer whenever winds are calm for several days, leading to lower dissolved-oxygen concentrations near the benthos than at the surface. Furthermore, dissolved-oxygen concentrations can decrease to as low as 0.2 mg/L throughout the water column in response to a combination of high water temperature, algal senescence, and limited vertical mixing of the water column.

Upper Klamath Lake is hypereutrophic and the phytoplankton community is dominated by the cyanobacteria species *Aphanizomenon flos-aquae* (National Research Council, 2004). Historically, lake phytoplankton was not dominated by a single species. In 1913, diatoms comprised most of the summertime phytoplankton in Upper Klamath Lake (Kemmerer and others, 1923), *Aphanizomenon flos-aquae* was first reported in 1939 (Bonnell and Mote, 1942), and by the 1960s, there was a virtual monoculture of *Aphanizomenon flos-aquae* (Miller and Tash, 1967). Furthermore, *Microcystis aeruginosa*, which can produce a toxin, proliferates following the rapid and widespread death of *Aphanizomenon flos-aquae* cells and subsequent release of nutrients into the water column (Eldridge and others, 2012).

Several large wetlands remain hydrologically connected to Upper Klamath Lake during periods of high water (fig. 1). Historically, there were far more wetlands associated with the lake margin (National Research Council, 2004). Between 1915 and 1995, an estimated 66 percent of wetlands adjacent to Upper Klamath Lake were eliminated through diking and draining (Larson and Brush, 2010). In 1999, The Nature Conservancy began restoring the Williamson River Delta, and in 2007 connectivity to about 1,000 ha was achieved northwest of the Williamson River (Tulana). In October 2008, connectivity of another 1,000 ha was achieved southeast of the river (Goose Bay) (Erdman and Hendrixson, 2011).

The non-native fathead minnow (*Pimephales promelas*) is the most abundant species in Upper Klamath Lake and can be several orders of magnitude more numerous than other species during the summer (Bottcher and Burdick, 2010). The native blue chub (*Gila coerula*) and the Klamath tui chub (*Siphateles bicolor bicolor*) also are abundant in the Lake and often will dominate the catch in the spring (Bottcher and Burdick, 2010). Other species often captured in lower numbers include yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), Upper Klamath marbled sculpin (*Cottus klamathensis klamathensis*), slender sculpin (*Cottus tenuis*), Klamath Lake sculpin (*Cottus princeps*), pumpkinseed (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), Klamath speckled dace *(Rhinichthys osculus klamathensis*), Klamath redband trout (*Oncorhynchus mykiss newberri*), and lamprey (*Lampetra spp.)*. The endangered suckers generally made up less than 10 percent of catches for any given net from 2001 to 2015 (VanderKooi and Buelow, 2001; VanderKooi and others, 2004; Burdick and others, 2007; Hendrixson and others, 2007a, 2007b; Anderson and others, 2009; Burdick and others, 2009a, 2009b; Bottcher and Burdick, 2010; Burdick and Brown, 2010; Burdick and VanderKooi, 2010; Burdick, 2012a, 2012b; Burdick and Hewitt, 2012; Burdick, 2013; Burdick and others, 2015).

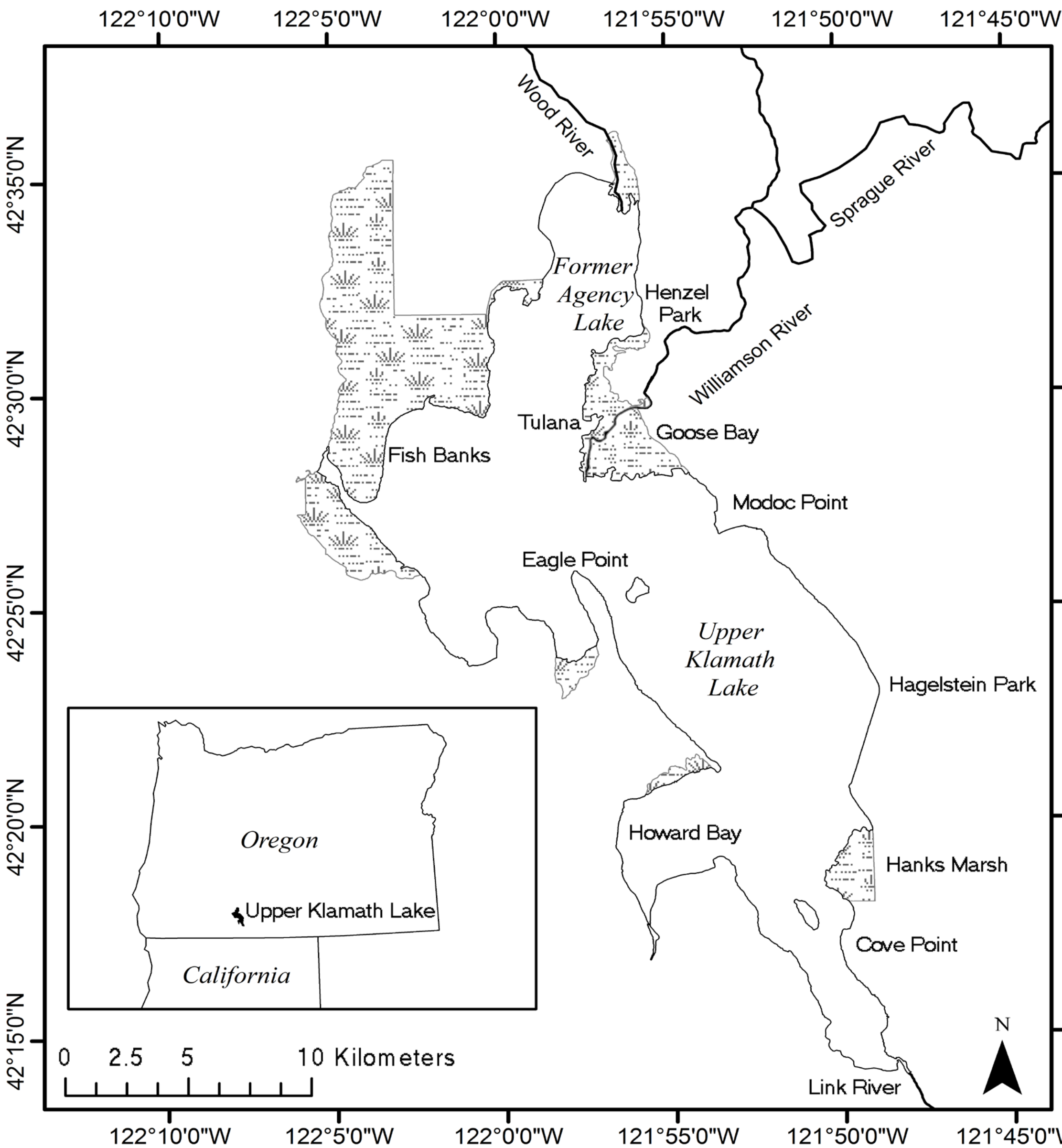

Figure 1. Map showing Upper Klamath Lake, Oregon. Horizontal datum is North American Datum of 1983 (NAD 83).

Methods

We compiled catch, length, age, and species data for juvenile suckers from eight separate USGS studies conducted in Upper Klamath Lake, Oregon, from 2001 to 2015. Specifically, we examined length at age and by day of the year to estimate apparent summertime growth rates. We examined annual variability in CPUEs of age-0 suckers as an index of relative (among years) apparent production. We examined the rate of summertime decrease in CPUEs to understand relative (among years) apparent survival. We examined annual and seasonal variability in species composition to better understand the potential for differential mortality between species. Finally, we compared CPUEs of age-0 suckers with proportion of nets to catch age-1 suckers the following year to better understand apparent overwinter survival. While, growth, production, and survival are the most probable and influential factors affecting the trends we observed, other factors may affect trends and cannot be discounted as insignificant. Therefore, we qualify our measures as apparent and (or) relative rates or values and explain alternative explanations for observed patterns.

Summary of Available Data

Eight different studies with various goals were conducted on juvenile suckers in Upper Klamath Lake from 2001 to 2015 (table 1; Burdick and others, 2017). Study 1 investigated juvenile sucker use of vegetated and unvegetated shoreline habitats. Study 2 examined use of nearshore and offshore habitat and examined summertime age-0 sucker migration patterns along the eastern shore of Upper Klamath Lake. Study 3 was a quantitative estimation of age-0 and age-1 sucker habitat use in the Upper Klamath Lake system including Agency Lake and the restoration sites in the Williamson River Delta. Study 4 examined summertime juvenile sucker use of Hanks Marsh. Study 5 compared health and condition of suckers in Upper Klamath Lake with those in Clear Lake Reservoir, California. In 2015, a juvenile sucker monitoring project was implemented to track cohorts through time (study 6). Two studies focused on springtime distributions of suckers—study 7, a study on the spring-time distribution of age-1 suckers in 2007, and study 8, an effort to capture and tag age-1 suckers. The duration of time that nets were set was similar among years (mean ± standard deviation [SD], 22.1 ± 2.5 hours), but the locations sampled during each study, the numbers of nets set, and the within-year timing of sampling differed (table 2).

Sampling gear differed among years, studies, and sometimes within a study (table 1). Round trap nets were exclusively used in nearshore habitats in both vegetated and unvegetated habitats. Both large and small rectangular trap nets were used in various habitats that included nearshore, offshore, vegetated, and unvegetated habitats, and over various substrates. Large rectangular trap nets were set in water as deep as 7.7 m, and small rectangular trap nets were set in water as deep as 15 m. The Williamson River Delta and Agency Lake were exclusively sampled with small rectangular trap nets.

Table 1. List and description of samples that were used in analyses summarized by study.

[Studies, in which gear or location varied among years, were noted with letters A–D, which correspond with map panels in figures 2 and 3. Types of passive gear used and listed in the table are as follows: (1) 0.61-meter (m) round trap nets, which had a 0.61-m diameter round opening, five wire hoops for structural support, two internal round traps nets, a 9.1-m lead and two 4.6-m wing nets; (2) 0.91-m round traps, which were the same as the 0.61-m trap net, except with a 0.91-m diameter opening; (3) small rectangular trap nets, which had mouth dimensions of 0.61 × 0.91 m, a 10-m lead, and three internal fykes; and (4) large rectangular trap nets, consisting of a 1.2 × 16-m lead, a 1.2 × 1.8 × 1-m rectangular frame, and four 1-m diameter circular hoops (1 m apart). The 0.61-m round trap nets had either green or black nylon netting, whereas all other nets only had green nylon netting. All gears had 6.4-millimeter bar mesh. Sample locations for each study are shown in figures 2 and 3]

Study No.	Gear type	Years	Months	Citations
1A	0.61- and 0.91-m round trap nets	2001–02	July–Sept.	VanderKooi and Buelow, 2001; VanderKooi and others, 2004; Hendrixson and others, 2007a, 2007b Burdick and others, 2007
1B	0.61- and 0.91-m round trap nets	2004–06	July–Sept.	
2	Large rectangular trap nets	2001–06	July–Sept.	VanderKooi and Buelow, 2001; VanderKooi and others, 2004; Hendrixson and others, 2007a, 2007b Burdick and others, 2007
3A	Small rectangular trap nets	2007	June–Sept.	Burdick and others, 2009a, 2009b; Burdick and Brown, 2010;
3B, C, and D	Small rectangular trap nets	2008–10	April–Sept.	Burdick and VanderKooi, 2010; Bottcher and Burdick, 2010; Burdick, 2012a; Burdick and Hewitt, 2012
4	0.91-m round trap nets	2007	July–Aug.	Anderson and others, 2009
5	Small rectangular trap nets	2013–15	July–Sept.	Burdick and others, 2015a
6	Small rectangular trap nets	2015	March and May–Sept.	Burdick and others, 2016
7	Large rectangular trap net	2007	April–May	Burdick and others, 2009b
8	Small rectangular trap nets	2011–12	May–June	Burdick, 2012b, 2013

Table 2. Number of nets fished per month by year for purpose of sampling for juvenile Lost River and shortnose suckers, Upper Klamath Lake, Oregon, 2001–15.

[Detailed description of studies contributing to this table, including a description of nets, is provided in table 1]

Years	March	April	May	June	July	August	September	Annual total
2001	0	0	0	0	147	346	24	517
2002	0	0	0	19	238	274	113	644
2003	0	0	0	0	0	110	107	217
2004	0	0	0	0	241	443	208	892
2005	0	0	0	0	176	338	169	683
2006	0	0	0	0	75	152	64	291
2007	0	23	28	279	382	365	98	1,175
2008	0	0	108	376	1,288	395	195	2,362
2009	0	12	653	756	809	762	473	3,465
2010	0	50	468	652	591	668	386	2,815
2011	0	0	184	277	0	0	0	461
2012	0	0	242	104	0	85	0	431
2013	0	0	0	0	12	59	36	107
2014	0	0	0	0	90	103	52	245
2015	20	0	34	62	75	207	154	552
Total	20	85	1,717	2,525	4,124	4,307	2,079	14,857

The locations where nets were set varied among studies and years as well (figs. 2 and 3). In studies 1, 5, and 7, all nets were set next to shore. In study 2, nets were set in a line perpendicular to shore starting next to shore and extending 600 m from shore. Study 1 sites were located in two areas in 2001—(1) south of the mouth of the Williamson River, and (2) at Modoc Point. Whereas, study 1 sites extended south to Cove Point from 2002 to 2006 (fig. 2, panels 1A and 1B). All sites in study 4 were set along the periphery of Hanks Marsh. Studies 3, 6, and 8 included both nearshore (<100 m from shore) and offshore (≥100 m from shore) sites. The area sampled in study 3 changed each year from 2007 to 2010 to include the Williamson River Delta as it was restored (figs. 2 and 3; panels 3A–3D).

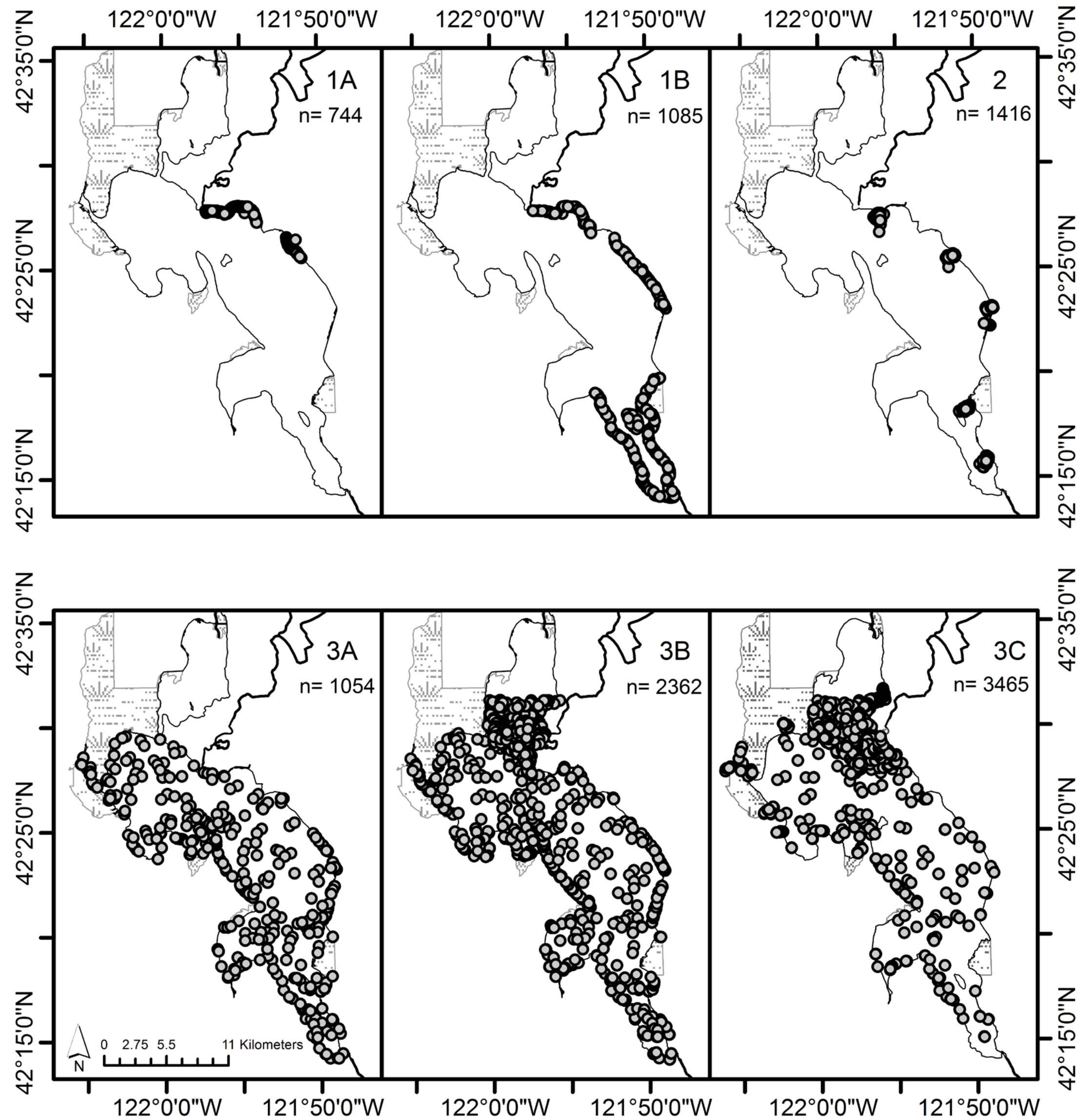

Figure 2. Maps showing locations sampled for juvenile suckers (circles) during studies 1–3, Upper Klamath Lake, Oregon. Numbers in the upper left corner of each panel indicate the study number as described in table 1. Numbers of nets set in each study are given in each panel (n). Gear types used and months sampled are given in table 1. Place names are given in figure 1. The Williamson River Delta is not shown for studies 1A–3A and is only partially shown for study 3B, because these studies occurred prior to the re-inundation of this wetland. Years associated with each panel are 1A, 2001–02; 1B, 2004–06; 2, 2001–06; 3A, 2007; 3B, 2008; and 3C, 2009.

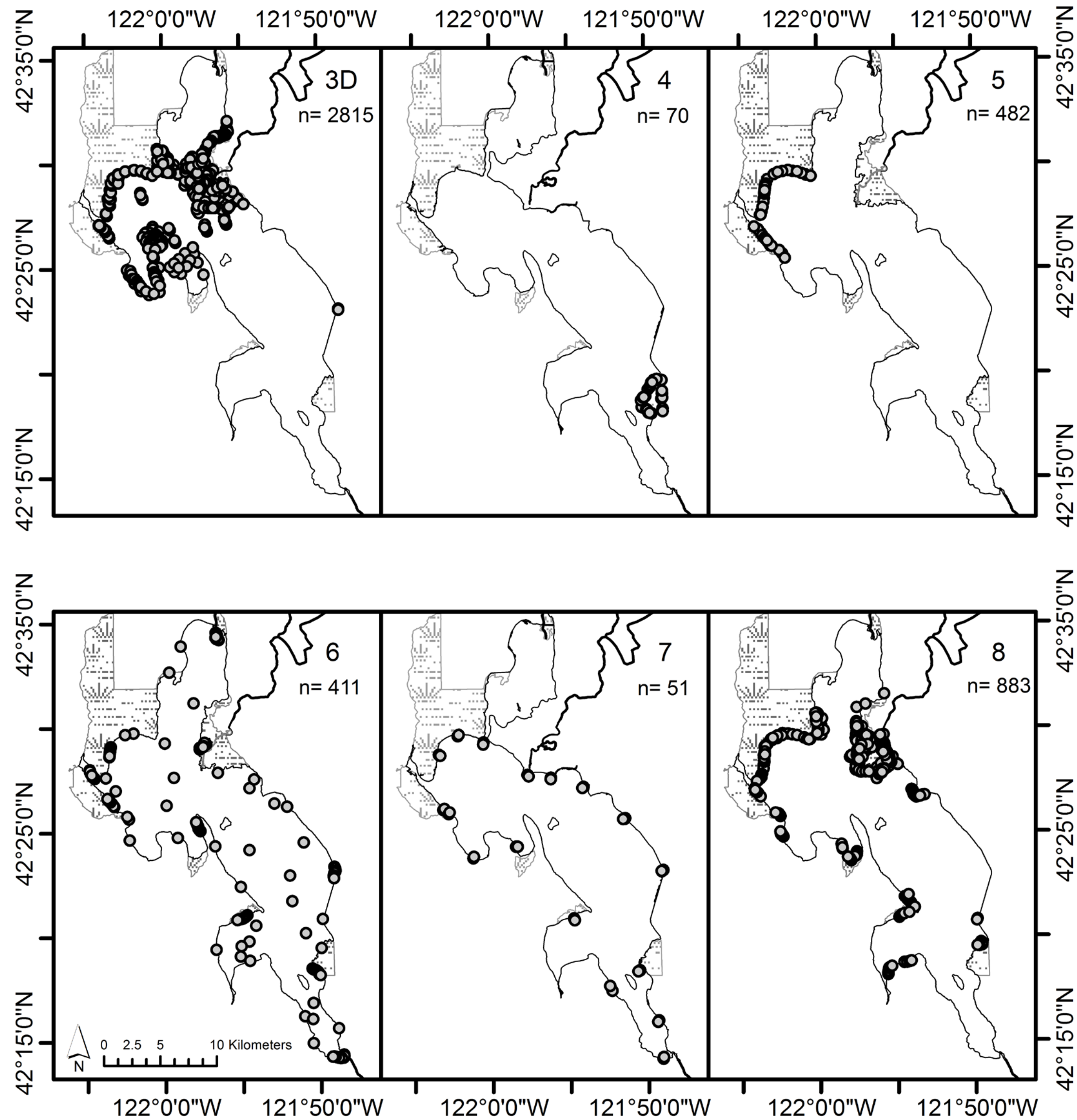

Figure 3. Maps showing locations sampled for juvenile suckers (circles) during studies 3–8, Upper Klamath Lake, Oregon. Numbers in the upper left corner of each panel indicate the study number as described in table 1. Numbers of nets set in each study are given in each panel (n). Gear types used and months sampled are given in table 1. Place names are given in figure 1. The Williamson River Delta is not shown for studies 4, and 7 because these studies occurred prior to the re-inundation of this wetland. Years associated with each panel are 3D, 2010; 4, 2007; 5, 2013–15, 6, 2015; 7, 2007; and 8, 2011–12.

Due to different goals among the studies, the primary habitats sampled varied among years, but various habitats were sampled in all years. Most nets were set in 0.5–1.9 m of water in all years except during 2007–2009, and 2007–2010 were the only years when nets were set in water 3.5 m deep and deeper (fig. 4). Most nets were fished within 100 m of shore in all years except 2003, when 53 percent were fished offshore (≥100 m from shore, fig. 5). From 2002 to 2005, and from 2007 to 2009, at least 25 percent of nets were fished offshore. In contrast, from 2011 to 2015, only 9 percent or fewer nets were fished offshore. Nets fished nearshore were not always fished near the edge of wetlands, as there is more wetland-like habitat in the northern end of Upper Klamath Lake than the southern end. The number of nets fished near a wetland edge increased from 2009 to 2011, when the evaluation of the Williamson River Delta was a focus of USGS research (fig. 6).

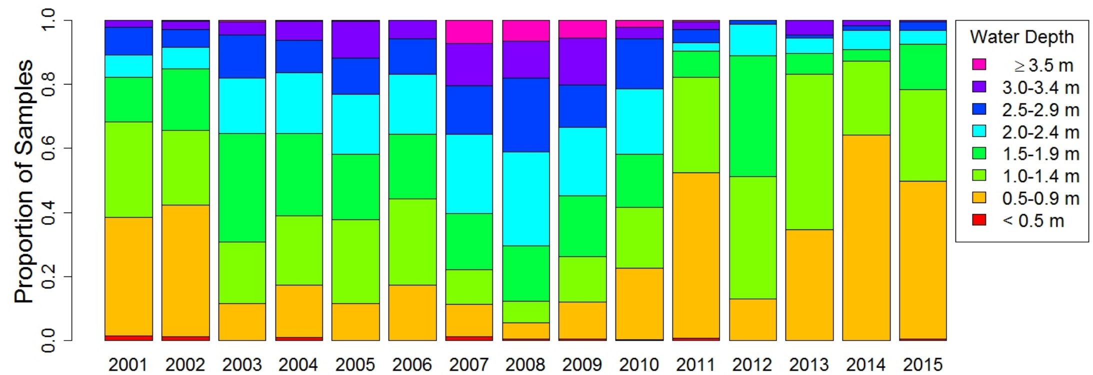

Figure 4. Proportion of nets fished for suckers by water depth (in meters [m]) and year, Upper Klamath Lake, Oregon, 2001–15.

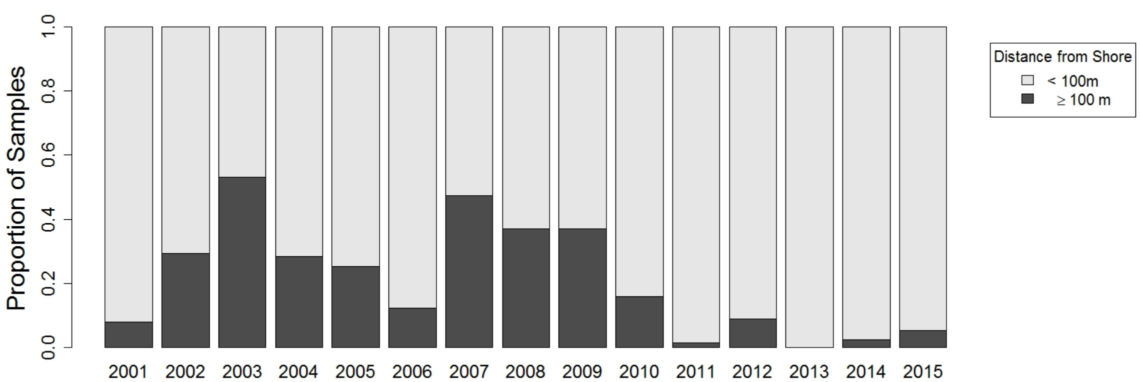

Figure 5. Proportion of nets fished for suckers that were nearshore (< 100 meters [m] from shore) or offshore (100 or more meters from shore), Upper Klamath Lake, Oregon, 2001–15.

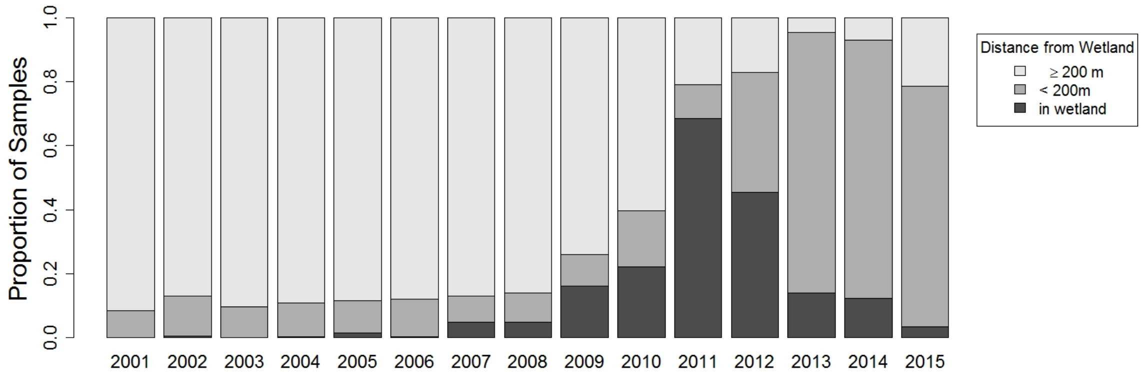

Figure 6. Proportion of nets fished for suckers that were in a wetland, near a wetland (< 200 meters [m] from) or distant from a wetland edge (200 m or more from) each year, Upper Klamath Lake, Oregon, 2001–15.

Net sets within Upper Klamath Lake were replicated in various ways in different studies and among years, and are not all truly independent samples. In study 1, nets were set in pairs, with one net set facing away from shore and one set facing toward shore. In 2001 and 2002 in study 1, net pairs were located along vegetation. In 2004 and 2005 in study 1, one-half of net pairs were set along vegetation and one-half were set along unvegetated shoreline. In study 2, transects started nearshore (1 and 50 m from shore) and ended offshore (100, 200, 400, and 600 m from shore). In 2007, 2008, and 2009, trap net samples were spatially replicated by fishing three nets simultaneously with openings facing different directions (studies 3A–3C). In 2010, trap net samples were replicated by fishing the same site with a single net set 3 days in a row (study 3D). There were no differences in sucker CPUEs between or among replicates of any kind (that is, nearshore compared to offshore, vegetation compared to unvegetated, direction of net set relative to shore; VanderKooi and Buelow, 2001; VanderKooi and others, 2004; Burdick and others, 2007; Hendrixson and others, 2007a, 2007b; Burdick and others, 2009a, 2009b; Bottcher and Burdick, 2010; Burdick and Brown, 2010; Burdick and VanderKooi, 2010; Burdick, 2012a; Burdick and Hewitt, 2012).

The numbers of suckers captured per net were recorded on most sampling occasions. The exceptions occurred in 2006 when two nets had 28 and 11 kg of suckers. In these nets, the numbers of suckers were enumerated in a subsample of about 30 percent by weight. Total catches were estimated from subsamples by extrapolating using the ratios of subsample to total sample weights.

Species Identification

Juvenile suckers from Upper Klamath Lake cannot be identified to species using external characteristics alone (Markle and others, 2005). Therefore, two methods were used to identify sucker taxa. From 2001 to 2013, a subset of up to 33 percent of captured juvenile suckers < 70 mm SL were sacrificed and preserved in 95-percent denatured ethanol or frozen. Sacrificed suckers were identified to species using a method based on vertebral and gill raker counts and lip morphology (Markle and others, 2005). Images of calcified structures were created using either high or low dose x-ray techniques and vertebrae were enumerated. Suckers with 45 or more post-Webarian vertebrae were identified as Lost

River suckers, whereas those with 43 or fewer post-Webarian vertebrae were considered a mix of shortnose and Klamath largescale suckers. Suckers with 44 post-Webarian vertebrae could be any of the three species. In order to better clarify the taxa of fish with 44 post-Webarian vertebrae or fewer, the numbers of gill rakers (compared with the length of the fish) were examined. This was done in all years for fish with 44 post-Webarian vertebrae. From 2001 to 2007, gill rakers of age-0 suckers with 43 post-Webarian vertebrae or fewer vertebrae were not examined and the separation of shortnose and Klamath largescale suckers was based on lip morphology. Starting in 2008, gill rakers were counted on all fish with 43 post-Webarian vertebrae or fewer, and fish were identified as shortnose and Klamath largescale suckers based on gill raker counts.

In 2014 we began using non-lethal genetic techniques to identify all captured suckers to the lowest taxonomic level possible with this technique. The method described by Hoy and Ostberg (2015) generates a probability that a sucker was a Lost River sucker (prob[LRS]). Presently, genetic methods can distinguish Lost River suckers from shortnose or Klamath largescale suckers but cannot distinguish the latter two from each other. Our growth and species composition analyses required that we categorically assign species. Therefore, following the example given by Burdick and others (2015), we called suckers having a Prob [LRS] ≥ 0.95 Lost River suckers and those with a Prob[LRS] ≤ 0.05 shortnose suckers. To facilitate comparisons between 2014 and 2015 and other years, we grouped suckers identified as shortnose and Klamath largescale suckers into a single category. Given that less than 1 percent of meristic-identified species were Klamath largescale suckers, we decided for the sake of simplicity to call all Klamath largescale/shortnose suckers shortnose suckers throughout this report. Because we only had species identification data on a small proportion of suckers, we grouped all suckers into a single category for all CPUE-based analyses.

Determination of Length and Estimation of Age

To determine the length at which young-of-year suckers became fully vulnerable to our gear, we plotted length frequencies for both sucker taxa combined. The most common length (45 mm SL) was considered the size at which juvenile suckers were fully vulnerable to our gear. Smaller suckers were assumed to have a lower probability of capture and were excluded from analyses.

Sixty-eight percent of suckers were measured to SL, fork length (FL), or both. Due to large catches, an estimated 4,664 suckers were not measured. A total of 90 percent of these were captured in 2006, 9 percent in 2002, and less than 1 percent in any other year. Another 6,838 suckers were estimated to have been captured in 2006 and not counted based on subsample extrapolation. Of the suckers with length measurements, 280 suckers collected in 2004 only had FL data. These fish ranged from 40 to 68 mm FL. To convert FL to SL, we fit a linear model to data on 822 suckers collected from Upper Klamath Lake in 2014 and 2015, for which both FL and SL data were available. In this regression, the dependent variable was SL and the independent variable was FL. For this analysis we assumed the following; 1) each fish was an independent sample, 2) the relationship between FL and SL over the size range of the suckers in our data was linear, 3) SL and FL were normally distributed, and 4) measurement errors were random and normally distributed about the mean. Univariate normality of SL and FL data were graphically assessed. The assumption of random and normally distributed measurement errors was graphically assessed by plotting residuals. We then used the regression parameters from this model to estimate the SL of the 280 suckers for which only FL data were available. All calculations were conducted in Program R (R Core Team, 2013).

Ages of suckers were estimated based on length at date from 2001 to 2015, and also were estimated based on the number of annuli on fin ray sections in 2014 and 2015. Separate age classes were qualitatively determined for suckers based on the separation of data point clusters within year-specific SL compared to time plots (appendix A). We did not attempt to separate species in this analysis because species was only determined for a small portion of suckers collected. Using this approach, we were able to develop a standard set of rules (table 3) for assigning ages as age-0, age-1, and age-2+ that could be used to identify these clusters within all years of our study for Upper Klamath Lake suckers. Suckers > 350 mm SL were considered to be adults and removed from this analysis because that is the smallest size of suckers captured at spawning sites (Hewitt and others, 2015). The USGS began collecting fin rays from juvenile suckers in Upper Klamath Lake in 2014. Fin rays were sectioned and annuli were counted using transmitted light microscopy to estimate age. Fin-ray aging methods and among-reader precision for juvenile Lost River and shortnose suckers are described by Burdick and others (2015). Length-based age assignment was compared to fin-ray-based age assignment to determine if the two methods agreed. The suckers from Upper Klamath Lake that were neither measured nor had a fin ray removed were assumed to be age-0 based on the length-based age estimates of measured suckers in subsamples.

Table 3. Age assignment (years) for Upper Klamath Lake juvenile suckers based on standard length and day of the year, Upper Klamath Lake, Oregon.

[Age assignment was qualitatively determined based on standard length at date frequency in each year (appendix A). A common set of rules was then developed that correctly identified clusters in all years]

Standard length (millimeters)	Day of year												
	<5-30	5-31–6-24	6-25–6-28	6-29–7-23	7-24–7-26	7-27–7-29	7-30–8-6	8-7	8-8–8-12	8-13–8-24	8-25–9-6	9-7–9-15	>9-15
< 41	0	0	0	0	0	0	0	0	0	0	0	0	0
41–54	1	1	0	0	0	0	0	0	0	0	0	0	0
55–66	1	1	1	0	0	0	0	0	0	0	0	0	0
67–69	1	1	1	1	1	0	0	0	0	0	0	0	0
70–79	1	1	1	1	1	1	0	0	0	0	0	0	0
80–83	1	1	1	1	1	1	1	0	0	0	0	0	0
84–93	1	1	1	1	1	1	1	1	1	0	0	0	0
94–96	1	1	1	1	1	1	1	1	1	1	0	0	0
97–99	1	1	1	1	1	1	1	1	1	1	1	0	0
100–119	1	1	1	1	1	1	1	1	1	1	1	1	0
120–124	1	1	1	1	1	1	1	1	1	1	1	1	1
125–144	2+	1	1	1	1	1	1	1	1	1	1	1	1
145–159	2+	2+	2+	2+	1	1	1	1	1	1	1	1	1
160–189	2+	2+	2+	2+	2+	2+	2+	2+	1	1	1	1	1
> 189	2+	2+	2+	2+	2+	2+	2+	2+	2+	2+	2+	2+	2+

Apparent Summertime Growth Rates

We fit general linear models to estimate the effects of year and sucker taxa on summertime apparent growth rates of age-0 suckers. We define apparent growth as the mean change in length of suckers captured over time. Our growth estimates are of apparent growth rather than actual growth because we measured different fish at each time step rather than making multiple measurements of the same fish over time. For these models, we only used data for fish that we had either morphometric or genetic species identification information. We used power analysis to examine our ability to detect strong growth rates from 0.1 to 0.7 mm per day with sample sizes across our range of data (1–757). Based on the power analysis, we excluded data from 2011 to 2013 due to small sample sizes (table 4). In the simplest model fit to the data, SL was modeled as a linear function of the number of days since January 1 (day of the year). More complex models included (1) year and species effects, (2) year effect only, (3) species effect only, and (4) a completely interactive year and species model. Year was included in models as a categorical variable, rather than a random effect, because it was the main variable of interest. We assumed the following; (1) each fish was an independent sample, (2) the relationship between SL and day of the year over the size range and time period of our sampling was linear, and (3) measurement errors were random and normally distributed about the mean. The assumption of random and normally distributed measurement errors was graphically assessed by plotting residuals. Goodness of fit was assessed using chi-squared goodness of fit test on the interactive year and species model. We compared models using Akaike's information criterion adjusted for sample size (AICc), which ranks models based on parsimony and accounts for sample size (Burnham and Anderson, 2002). We report the daily apparent growth rate based on the most parsimonious model. All analyses were conducted in Program R (R Core Team, 2013).

Table 4. Numbers of age-0 suckers captured for which length and species identification data were both available, Upper Klamath Lake, Oregon, 2001–15.

[Data on these fish were used in an apparent growth analysis, except for data from 2011 to 2013 when sample sizes were small]

Year	Lost River suckers	Shortnose suckers
2001	384	179
2002	624	256
2003	82	169
2004	431	143
2005	299	68
2006	477	449
2007	176	139
2008	65	100
2009	78	172
2010	153	267
2011	0	0
2012	2	1
2013	4	8
2014	95	64
2015	144	134

To determine if there were annual differences in age-1 sucker apparent growth rates, we fit and compared three general linear models. Because there were very few age-1 suckers sacrificed for species identification, our analysis of age-1 sucker apparent growth is not species-specific. Power analysis indicated that sample sizes were only sufficient to detect strong growth rates effect sizes with a probability of ≥ 0.5 in 2001 and during 2006–2012 (table 5). Therefore, all other years in our dataset were excluded from this analysis. We also excluded 2001, 2006, and 2011 from this analysis because almost all age-1 suckers were collected within a single month in these years, making growth trends difficult to detect. In our simplest model, SL was a linear function of day of the year. We included a model where the initial standard length (intercept) was allowed to vary among years but the growth rate was the same among years (Day of Year + Year). Finally, we included a model where both the initial standard length and growth rate were allowed to vary among years (Day of Year *Year). As with the age-0 apparent growth analysis, year was a categorical variable rather than a random effect because it was a key parameter of interest. We ranked models based on parsimony using AICc. Assumptions for this analysis were the same as for the age-0 sucker apparent growth analysis and were verified using the same techniques.

Table 5. Numbers of age-1 suckers captured each month in Upper Klamath Lake, Oregon, 2001–15.

[Numbers of nets fished are given in table 2. These numbers are for all age-1 sucker species combined]

Years	March	April	May	June	July	August	September	Annual total
2001	0	0	0	0	16	39	3	58
2002	0	0	0	3	13	3	2	21
2003	0	0	0	0	0	0	1	1
2004	0	0	0	0	4	12	0	16
2005	0	0	0	0	14	8	2	24
2006	0	0	0	0	15	22	1	38
2007	0	8	43	93	111	34	5	294
2008	0	0	8	35	62	8	3	116
2009	0	29	245	187	98	10	9	578
2010	0	7	74	19	18	6	3	127
2011	0	0	15	195	0	0	0	210
2012	0	0	148	70	0	9	0	227
2013	0	0	0	0	0	0	0	0
2014	0	0	0	0	3	1	0	4
2015	2	0	0	10	1	4	1	18
Total	2	44	533	612	355	156	30	1,732

Assessment of Annual Variation in Apparent Age-0 Sucker Production

To estimate a relative annual index of age-0 sucker production based on age-0 suckers fully susceptible to our gear (≥ 45 mm SL), we fit general linear models to age-0 CPUE data. We removed uninformative zeros from all years by truncating catch data before the earliest day in any year in which an age-0 sucker was captured (June 26). In the remaining data, we accounted for a large number of zeros by assuming a negative binomial distribution. We analyzed CPUE during 2001–06 and 2007–15 separately to account for a complete change in gear type in 2007. We qualified indices discussed in this section of the report as “apparent” because this value is a product of larval production and survival to the size that is fully recruited to our gear. We also qualified the estimates as “relative” among years because we were unable to account for capture probability. Because we were unable to identify suckers to species in the field, there was no way to calculate species-specific CPUEs.

We accounted for variation due to sample locations and gear types by including explanatory variables. In these models, the response variable was age-0 sucker CPUE. Explanatory variables included categorical variables for year, gear type, distance to shore (Shore), and distance to nearest wetland (Wetland) (table 6), and continuous variables for numbers of hours that nets were set (Hours), and water depth (Depth). We chose to include both habitat (Wetlands, Shore, Depth) and sampling variables (Gear and Hours) in our analysis to account for variation in the age-0 sucker CPUEs that may have been due to capture probability, abundance, or both (table 6). Habitat use was not the focus of this analysis but is reported on in Burdick and Hewitt (2012). A categorical parameter for gear type (Gear; table 6) was included in the analysis of 2001–06 data when three gear types were used. We restricted our analysis of the 2007–15 data to that collected by small trap nets, and thus avoided the need for inclusion of a gear-type covariate. Number of hours that nets were fished (Hours) were included to account for potential variation in sampling efficiency. Previous research indicates that the presence and absence of age-0 suckers varies by water depth but not by distance to wetland or nearness to shore (Burdick and Hewitt, 2012). However, it is unknown if capture probability or abundance (number of) of age-0 suckers also vary by distance to wetland or nearness factors. Therefore, Wetland, Shore and Depth were all included to account for potential variation in CPUEs due to a combination of abundance and capture probability, which we do not attempt to disentangle in this analysis. Continuous covariates were standardized by dividing the mean by the standard deviation to improve the optimization efficiency (McCune and Grace, 2002).

Models were compared using AICc and estimates for the effect of year on CPUEs based on the most parsimonious model are reported (Burnham and Anderson, 2002). We took a progressive approach to model set development. We started by fitting the intercept only model, and then fit single parameter models. Variables that reduced AICc by more than two times the number of added parameters were considered informative and were included in an additional three and four parameter models. Our final model set included 26 models. We assumed that each net set was an independent sample, that the ages of fish in each sample were correctly identified, and that the number of age-0 fish were correctly counted or estimated (Cameron and Trivedi, 2013). We assessed goodness of fit of the most parameterized model by examining the distribution of the log of the deviance residuals. Normally distributed log deviance residuals indicate an unbiased model specification (Cameron and Trivedi, 2013). Models were fit with program R using package pslc and the glm.nb function (R Core Team, 2013; Jackman, 2015).

We estimated the year effect on CPUEs from the most parsimonious models that carried nearly all the model weights. To describe how the positively skewed data varied among years, we reported the portion of nets to catch age-0 suckers, the mean CPUE in nets that captured age-0 suckers, and the median CPUE in nets that captured age-0 suckers.

Table 6. Descriptions of categorical variables used in catch per unit effort analyses.

Variable	Description	Categories
Year	Year	2001–15
Gear	Type of net	0.61-meter (m) round trap net, 0.91-m round trap net, 0.91-m rectangular trap net, or 1.8-m rectangular trap net
Wetland	Distance to the edge of a mapped wetland	In wetland, ≤ 200 m from wetland edge, or > 200 m from wetland edge
Shore	Distance to the nearest mapped shoreline	≤100 m from mapped shoreline, or > 100 m from mapped shoreline

Annual Variation in Apparent Age-0 Sucker Survival

To estimate an index of relative apparent summertime age-0 sucker survival, we truncated data and made several key assumptions. Data for this analysis include only nets set on or after the date in each year with the greatest daily mean CPUE to exclude the period each year when suckers were still growing to the size of susceptibility to our nets. The years 2011–13 were not included in this analysis because most or all sampling occurred prior to what we consider the peak of age-0 sucker catches. We assumed that recruitment of new suckers to the sampled population was constant among years within this truncated dataset. We assumed that rates of emigration and declining gear susceptibility due to growth, age, or some other factor were constant among years. We qualified our index as "apparent" survival because we were unable to separate emigration from survival. We did not separate data into before and after the 2007 gear change because we assumed that, although the type of gear may affect the magnitude of catches, the rate of within-year decrease in catches would not be gear-specific. This assumption was based on a lack of evidence in the literature for fish size selectivity due to any of the differences among gears used in this study. We assumed that each net set was an independent sample, that the ages of fish in each sample were correctly identified, and that the number of age-0 fish was correctly counted or estimated. We also presumed that our catch data had a negative binomial distribution and confirmed that covariates were uncorrelated by examining scatter plots.

We fit three general linear models to our truncated dataset to determine if there was annual variation in apparent relative age-0 sucker survival. The response variable in all models was age-0 sucker CPUE. Our most basic model included a year effect and an interaction between gear and depth (Year+Gear*Depth). We choose this model structure because the previous analysis indicated that these parameters were the most important for explaining variation in CPUE. With this basic model, we examined the hypothesis that mean annual CPUEs were sufficient to describe variation in data. We added a parameter for the number of days since the peak catch rate to a second model (Year+Day+Gear*Depth) to examine the hypothesis that CPUE decreased at the same rate each year. Finally, we fit a model with a Year by Day effect (Year*Day+Gear*Depth) to examine the hypothesis that CPUE decreased at different rates among years.

All three models were compared with AICc and model weights were calculated to show the probability of each model being the most parsimonious within the model set. The distribution of the log of the residuals was examined for normality as an assessment of goodness of fit for the Year*Day+Gear*Depth model (Cameron and Trivedi, 2013). The most parsimonious model was considered to be the one most supported by the data. Models were fit with program R using package pslc and the glm.nb function (R Core Team, 2013, Jackman, 2015).

Assessment of Annual Variation in Apparent First-Year Survival

To determine if there were large variations in first winter apparent mortality, we compared quantitatively derived indices of age-1 abundance to the apparent relative age-0 sucker production in the prior year. We presumed that if indices of age-1 sucker abundance tracked with the apparent relative production in the prior year, production was a large factor in the probability of catching age-1 suckers. In contrast, if the indices of age-1 sucker abundance were the same among years or were relatively high following years of relatively low apparent age-0 sucker production, then annual variation in over-winter mortality may have been a relatively large contributing factor compared to age-0 production. We assumed that changes in gear selectivity and (or) emigration from Upper Klamath Lake were constant among years.

Our quantitative index of age-1 sucker abundance was the odds of catching one or more age-1 sucker per net within a given year. The relative odds of capturing one or more age-1 sucker per net in each year were estimated using logistic regression applied to a subset of data. Because catches of age-1 suckers were infrequent, we selected subsets of data for this analysis in which catch frequencies were greater than typical frequencies. Because we derived our odds estimates from a subset of data, the estimates can be considered relative (among years) odds but do not represent lakewide annual odds of capturing age-1 suckers. To be included in our analysis, subsets of data were required to include at least 3 years. Each subset of data included net of the same type, fished in a single month, within the same distance from wetland category, and within the same distance from shore category. All nets within a subset of data had water depths within 1 m. We identified 14 subsets of data that met our requirements for inclusion in our analysis (table 7). One of the data subsets was unique in that all samples were collected in August prior to 2007 using 0.91-m round trap nets, and was analyzed separately and qualitatively. In the other 13 data subsets, 0.91-m trap nets were set nearshore (table 7). Each of the subsets of data included 121–723 net sets that captured 8–110 age-1 suckers. We combined these 13 subsets of data to create a dataset for analysis (table 8).

Table 7. Subsets of data used to calculate the odds of capturing one or more age-1 suckers per net within given years.

[All selected subsets of data except 14 used the 91-centimeter (cm) rectangular trap nets in nearshore habitats. Data subset 14 used 91-cm round nets and—because it was unique in gear type, month, and years—it was analyzed separately. Subsets of data in this list, with the exception of subset 14, were combined into a single dataset that was analyzed to estimated odds of capturing one or more age-1 suckers per year.]

Subset	Number of nets	Proportion non-zeros	Month	Wetland	Depth (meters)	Years
1	203	0.36	5	In wetland	<1	2008–12, 2015
2	262	0.41	5	In wetland	1–2	2008–12, 2015
3	208	0.25	5	Near wetland	1–2	2008–12, 2015
4	372	0.54	6	In wetland	<1	2008–12
5	263	0.29	6	In wetland	1–2	2008–12
6	177	0.15	6	Near wetland	1–2	2007–12, 2015
7	137	0.24	6	No wetland	1–2	2007–12, 2015
8	438	0.14	6	No wetland	2–3	2007–11, 2015
9	171	0.24	6	No wetland	3–4	2007–11
10	243	0.11	7	No wetland	1–2	2007–10
11	723	0.13	7	No wetland	2–3	2007–10
12	128	0.24	7	No wetland	3–4	2007–10
13	121	0.11	7	No wetland	5+	2007–09
14	227	0.14	8	No wetland	1–2	2001–02, 2004–06

We fit a logistic regression model to the combined subsets in order to determine if the probability of capturing an age-1 sucker varied among years and data subsets. The response in our logistic regressions was a binary variable for the presence (1) or absence (0) of age-1 suckers in nets. We did not fit models with any separate explanatory variables listed in table 7 because Wetland, Month, and Depth were all at least somewhat correlated. Instead, we included a random effect for data subset. We also included a categorical parameter for year. Year was not included as a random effect because it was our main variable of interest. We calculated relative odds of catching age-1 suckers per year.

Table 8. Data used in logistic regression analysis to estimate odds of catching one or more age-1 sucker per net within a year.

[Number of age-1 suckers captured (numerator) and number of nets set (denominator) are given by data subset and year. Each subset of data had similar wetland designation, month, and water depth (table 7). All subsets of data include only nearshore net sets. NA means data were not collected.]

Subset	2007	2008	2009	2010	2011	2012	2015
1	NA	0/7	18/35	14/92	6/44	10/20	0/5
2	NA	0/3	16/58	5/48	6/58	36/93	0/2
3	NA	0/1	3/27	2/48	0/27	28/84	0/21
4	NA	2/25	11/57	2/75	81/176	14/30	NA
5	NA	3/11	9/68	1/99	12/38	17/36	NA
6	2/8	3/11	6/34	1/60	0/4	6/20	3/28
7	5/13	1/21	6/27	1/31	5/19	3/5	3/15
8	11/39	4/58	20/89	2/199	0/14	NA	2/7
9	11/21	1/45	13/90	0/7	0/8	NA	NA
10	5/46	1/83	1/36	1/84	NA	NA	NA
11	10/46	17/302	16/155	0/249	NA	NA	NA
12	5/19	5/55	2/47	0/5	NA	NA	NA
13	5/25	3/78	1/18	NA	NA	NA	NA
Totals	54/192	40/615	122/688	29/905	110/344	114/268	8/73

Differential Mortality Between Taxa

To examine potential differential mortality between sucker taxa, we examined variation in species composition of age-0 suckers among weeks and of age-1 suckers among years. We calculated the proportion of the catch that could be identified to species as Lost River suckers within each age class. For age-0 suckers, we calculated the proportion of Lost River suckers by week in weeks that we had both age and species data for at least 10 suckers. For age-1 suckers, we calculated the annual proportion of Lost River suckers captured in years in which we had both age and species data for at least 10 suckers. Proportions greater than 0.5 indicated that there were more Lost River suckers relative to shortnose suckers, and proportions less than 0.5 indicated the opposite.

Assessment of Apparent Survival of Age-1 Suckers in Summer 2007

To assess the rate of decrease in the proportion of nets successfully capturing age-1 suckers, we examined 2007 catch data. The 2007 catch data were unique in that a single gear type was used, nearly all of Upper Klamath Lake was randomly sampled, and sampling and capture of age-1 suckers occurred over a protracted time period. Captures of age-1 suckers were relatively high in 2007 when compared to other years. Because numbers of suckers captured per net were substantially skewed toward zero, we examined the proportion of nets catching one or more sucker, rather than the number of suckers per net. We calculated proportions and their 95 percent confidence intervals of nets catching one or more sucker per week during the core sampling period; June 4th to September 10th.

Results

Length and Age

Standard length data were available for 24,694 juvenile suckers and was estimated from FL of another 46 juvenile suckers. There was a strong correlation between FL and SL ($p<0.0002$, coefficient of determination [R^2]=0.99, degrees of freedom [df]=820). The relation between the SL and FL was SL = -1.02 + 0.92 FL. Juvenile suckers captured in trap nets in Upper Klamath Lake ranged from 17 to 205 mm SL, but 95 percent were 38–83 mm SL. Length frequency peaked at 45 mm SL (fig. 7).

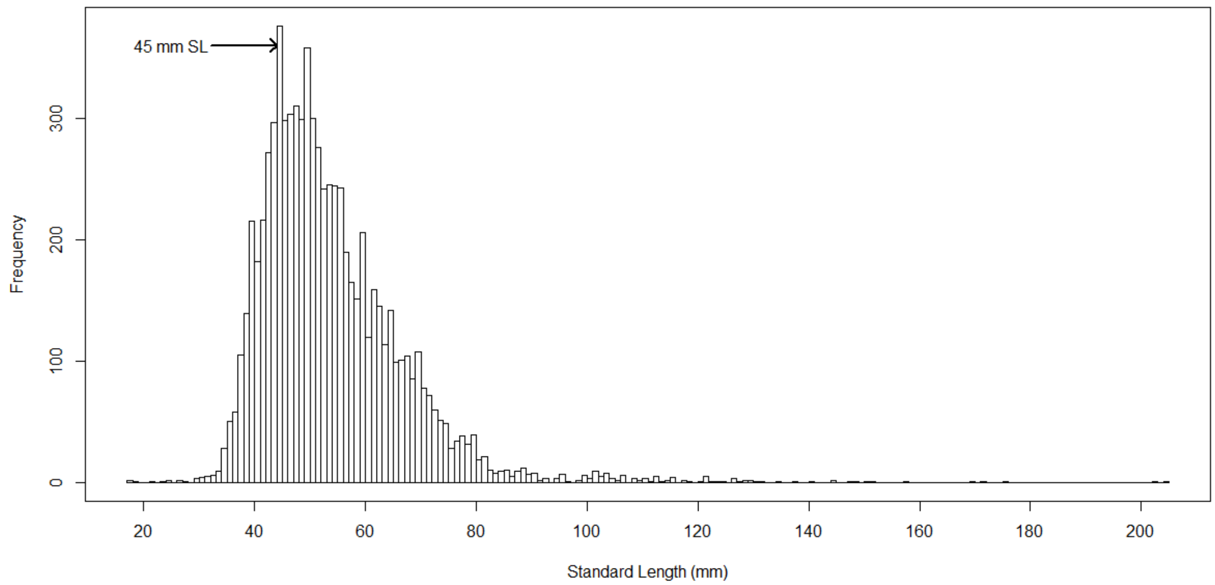

Figure 7. Length frequency (number of suckers) for suckers captured in trap nets set in Upper Klamath Lake, Oregon, 2001–15. Data are grouped into 1-millimeter (mm) length bins. The size class at which frequency was maximized (45 mm standard length [SL]) is considered the size at which suckers are most susceptible to trap nets.

Length-based age assignment and fin-ray-based age assignment were the same in most (97.2 percent) cases for Upper Klamath Lake suckers (table 9). There were clear distinctions between presumed age clusters in length by day of the year plots for Upper Klamath Lake suckers, when considered on an annual basis (appendix A). Estimated ages based on fin rays were dissimilar from those based on length for only 2.8 percent of the 822 suckers collected in Upper Klamath Lake for which both types of data were available (table 9). Discrepancies occurred when the fish length and day of year were near the threshold for age assignment and never differed by more than one age category. Ninety-nine percent of suckers estimated to be age-0 based on either method also were estimated as age-0 based on the other method (table 9), whereas 65 and 62 percent of suckers estimated to be age-1 or older, respectively, based on at least one method were estimated as the same age based on both methods.

Table 9. Numbers of suckers assigned ages based on length and day of year and numbers of annuli identified in fin rays, Upper Klamath Lake, Oregon.

[Numbers are only for fish for which both types of data were collected]

Number of annuli	Length-based age estimate		
	0	1	≥ 2
0	762	6	0
1	8	45	6
≥ 2	0	4	17

We estimated there were 164 age-2+ juvenile suckers, 1,732 age-1 suckers, and 34,560 age-0 suckers captured between 2001 and 2015 in Upper Klamath Lake. A total of 3,251 of the age-0 suckers were < 45 mm SL. One or more age-2+ juvenile suckers were captured annually in all years except during 2004–06 and 2013. There was never more than one age-2+ sucker captured in a net. Total annual age-2+ sucker CPUE exceeded 0.01 during 2001, 2007–10, and 2015 (table 10). A total of 26 (72 percent) age-2+ suckers captured in 2010 were ≥ 250 mm SL.

Table 10. Catch per unit effort (CPUE) and number of age-2+ suckers captured, Upper Klamath Lake, 2001–15.

[Annual number of age-2+ suckers and number of suckers per trap net set (CPUE) in Upper Klamath Lake, Oregon]

Year	Suckers	CPUE
2001	9	0.017
2002	5	0.008
2003	2	0.009
2004	0	0.000
2005	0	0.000
2006	0	0.000
2007	13	0.011
2008	47	0.020
2009	39	0.011
2010	36	0.013
2011	2	0.004
2012	3	0.007
2013	0	0.000
2014	1	0.004
2015	7	0.013

Apparent Growth of Suckers

Model selection indicated that the apparent growth rate of age-0 suckers ≥ 45 mm SL in Upper Klamath Lake varied by sucker species independently within years (table 11). The most parameterized model (Day of Year + Species*Year) also was the most parsimonious and fit the data well ($p<0.00002$; df=5123). All apparent growth models fit to length by day of year data converged and residuals were normally distributed around zero.

Table 11. Akaike's information criterion statistics for age-0 sucker growth models.

[For each model, the following are shown: Number of model parameters (n), Akaike's information criterion adjusted for sample size (AICc), difference in AICc between a given model and the best model (ΔAICc), and probability that the model is the most parsimonious of the models in the set (w)]

Model name	n	AICc	ΔAICc	w
Day of Year+Species*Year	26	34,873.02	0	1
Day of Year+Species+Year	15	35,085.57	212.56	0
Day of Year+Year	14	35,459.23	586.21	0
Day of Year+Species	4	36,070.60	1,197.58	0
Day of Year	3	36,525.83	1,652.81	0

Within sucker species, apparent daily growth rates of age-0 fish varied somewhat among years (fig. 8; appendix B). Lost River suckers appeared to grow faster than shortnose suckers in most years, although the difference was only significant in 5 of the 12 years examined. Years in which age-0 Lost River suckers appeared to grow slower were not the same as years in which age-0 shortnose suckers appeared to grow slower.

The rate of apparent growth varied among years for age-1 suckers (table 12). The most complex model also was the most parsimonious model in our set and fit the data well (chi squared $p<0.0002$; df=1705). This model indicated that apparent summertime growth was slower in 2012 than in 2007 or 2009 (fig. 9; appendix C). Confidence intervals overlapped among other years examined, indicating no significant difference in growth rates among other years.

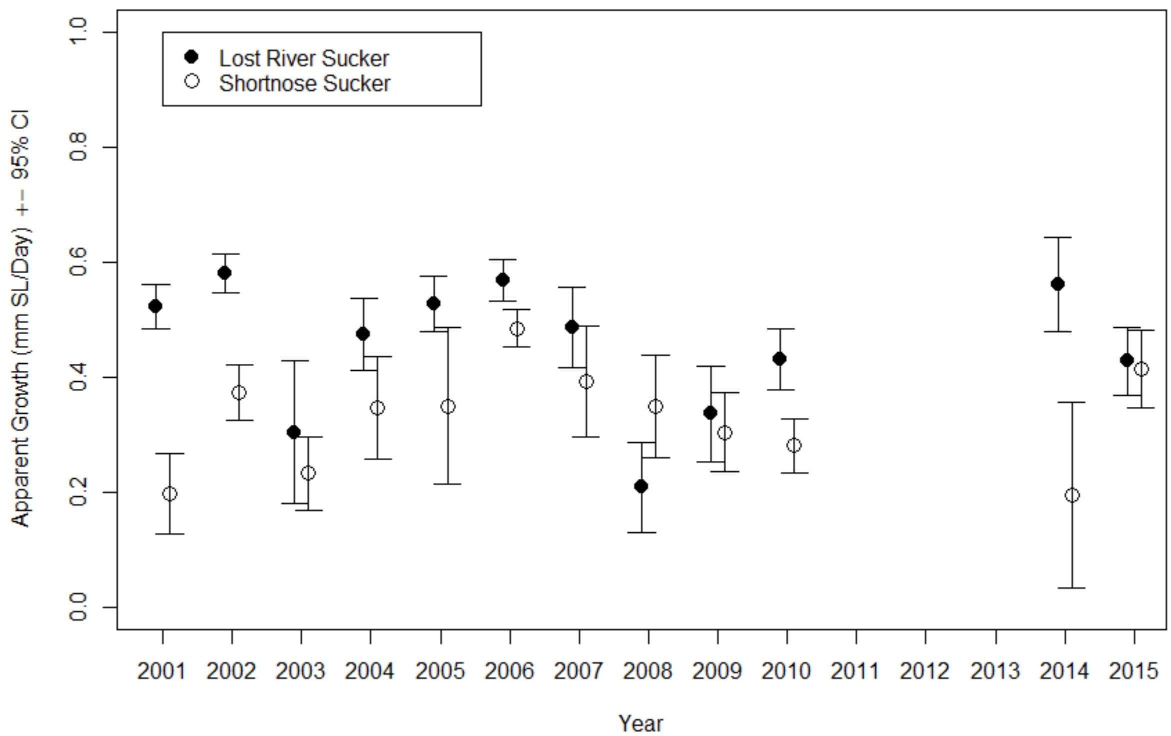

Figure 8. Mean estimated apparent growth rates of age-0 Lost River and shortnose suckers collected from Upper Klamath Lake, Oregon, 2001–15. The 95-percent confidence intervals (CI) are indicated by whiskers. Data were insufficient ($n \leq 8$) to estimate daily change in length from 2011 to 2013. Sample sizes used to estimate each point are given in table 4.

Table 12. Akaike's information criterion statistics for age-1 sucker growth models.

[For each model, the following are shown: Number of model parameters (n) Akaike's information criterion adjusted for sample size (AICc), difference in AICc between a given model and the best model (ΔAICc), and probability that the model is the most parsimonious of the models in the set (w)]

Model name	n	AICc	ΔAICc	w
Day of Year*Year	14	11,773.39	0.00	1
Day of Year+Year	8	11,784.31	10.92	0
Day of Year	2	11,926.05	152.67	0

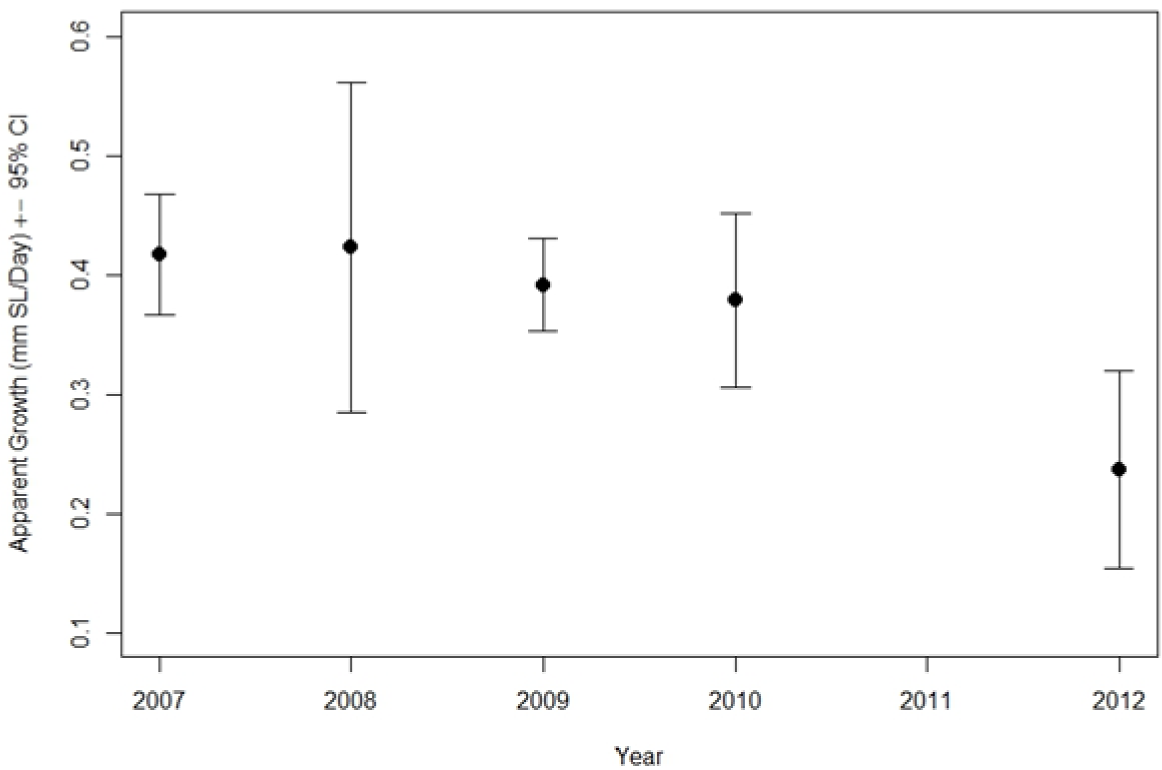

Figure 9. Apparent July–September growth rates of age-1 suckers collected from Upper Klamath Lake, Oregon by year. The 95-percent confidence intervals (CI) are indicated by whiskers. Power analysis indicated that July–September sample sizes were only sufficient to estimate daily change in length from 2007 to 2010 and in 2012. Sample sizes and regression lines are shown in appendix C.

Annual Variation in Apparent Age-0 Sucker Production

Model ranks for the 2001–06 dataset indicated that age-0 sucker CPUE could be best explained by year, distance from wetland edges, and a gear by depth interaction (table 13). The log of residuals from the best fit model (Year+Wetland+Gear*Depth) were roughly normally distributed, indicating good model fit. Year was the parameter most correlated with variation in age-0 sucker CPUE. Water depth alone was uninformative for describing variation in age-0 sucker CPUE, and gear type alone was somewhat less informative than a gear by depth interaction. The number of hours and the distance from shore that nets were fished also were essentially uninformative parameters. Despite the Wetland parameter improving parsimony of the model over models without this parameter, the effect size of Wetland in the most parsimonious model (Year+Wetland+Gear*Depth) was insignificant ($p \geq 0.14$) and biologically trivial. Indices of relative abundance based on the Year+Wetland+ Gear*Depth model were 0.77 ± SE 0.54 greater at sites located >200 m from a mapped wetland edge than at sites located in a wetland, and 0.74 ± 0.53 greater than sites located within 200 m of a mapped wetland. Most of the explanatory power of the most parsimonious model was in the year effect and the gear-by-depth interaction. Indices of relative abundance were greater when large rectangular trap nets (180 cm) were used than when either of the two smaller hoops nets were used at water depths of ≤ 1.8 m, and when 61 cm hoop nets were used at water depths up to 3.9 m.

Table 13. Akaike's information criterion statistics for models fit to catch data collected, 2001–06.

[For each model, the following are shown: Number of model parameters (n), Akaike's information criterion adjusted for sample size (AICc), difference in AICc between a given model and the best model (ΔAICc), and the relative model weight (w). Model weight can be interpreted as the probability that a model is the most parsimonious in this model set given the data]

Model name	n	AICc	Δ AICc	w
Year+Wetland+Gear*Depth	14	13,957.65	0.00	0.97
Year+Wetland+Gear	11	13,964.44	6.79	0.03
Year+Gear*Depth	12	13,985.97	28.32	0.00
Year+Gear	9	13,988.97	31.32	0.00
Year+Wetland	9	14,048.37	90.72	0.00
Year+Shore+Wetland	10	14,050.11	92.46	0.00
Year	7	14,069.87	112.23	0.00
Year+Hours	8	14,070.32	112.67	0.00
Year+Depth	8	14,071.67	114.02	0.00
Year+Shore	8	14,071.83	114.18	0.00
Year+Gear*Depth	8	14,720.45	762.80	0.00
Hours+Gear*Depth	8	14,743.98	786.33	0.00
Shore+Wetland+Gear	7	14,756.53	798.88	0.00
Gear*Depth	7	14,759.25	801.60	0.00
Shore+Gear	5	14,768.67	811.02	0.00
Hours+Gear	5	14,806.13	848.48	0.00
Wetland+Gear	6	14,832.92	875.27	0.00
Gear	4	14,844.86	887.21	0.00
Hours+Shore	4	14,931.02	973.37	0.00
Hours+Wetland	5	14,944.76	987.11	0.00
Hours	3	14,958.88	1,001.23	0.00
Shore+Wetland	5	14,993.77	1,036.12	0.00
Shore	3	15,009.04	1,051.39	0.00
Wetland	4	15,027.15	1,069.51	0.00
Depth	3	15,043.53	1,085.88	0.00
Intercept Only	2	15,044.88	1,087.24	0.00

Model ranks for the 2007–15 dataset indicated that all parameters except Hours explained some variation in age-0 sucker CPUE (table 14). The log residuals for the most parameterized model, which also was the most parsimonious model, were roughly normally distributed indicating good model fit. All models that included a year parameter substantially outranked similar models that omitted year, indicating year was an important explanatory variable. Catch per unit effort (CPUE) decreased with water depth at a rate of 0.69 ± standard error [SE] 0.05 ($p < 0.002$) per meter. While Wetland and Shore improved the parsimony of the model fit, they had insignificant effects within the Year+Wetland+Shore+Depth model ($p \geq 0.09$), and the effect sizes associated with Wetland and Shore parameters had wide confidence intervals that overlapped zero.

Table 14. Akaike's information criterion statistics for models fit to catch data collected, 2007–10 and 2012–15.

[For each model, the following are shown: Number of parameters (Pars), Akaike's information criterion adjusted for sample size (AICc), difference in AICc between a given model and the best model (ΔAICc), and the relative model weight (w). Model weight can be interpreted as the probability that a model is the most parsimonious in this model set given the data]

Model name	Pars	AICc	ΔAICc	w
Year+Wetland+Shore+Depth	12	13,571.67	0.00	0.99
Year+Shore+Depth	10	13,582.09	10.42	0.01
Year+Wetland+Depth	11	13,595.43	23.76	0.00
Year+Depth	9	13,604.08	32.40	0.00
Year+Shore	9	13,766.19	194.52	0.00
Year+Wetland+Shore	11	13,766.24	194.57	0.00
Year+Wetland	10	13,810.65	238.98	0.00
Year	8	13,819.32	247.65	0.00
Depth+Wetland+Hours	6	13,891.35	319.67	0.00
Depth+Hours	4	13,900.71	329.04	0.00
Depth+Wetland+Shore	6	13,924.13	352.46	0.00
Depth+Shore	4	13,932.13	360.46	0.00
Depth+Wetland	5	13,936.55	364.87	0.00
Depth	3	13,941.14	369.47	0.00
Wetland+Hours+Shore	6	14,085.4	513.73	0.00
Hours+Shore	4	14,086.57	514.89	0.00
Hours+Year	4	14,086.57	514.89	0.00
Wetland+Hours	5	14,109.31	537.63	0.00
Hours	3	14,120.9	549.22	0.00
Wetland+Shore	5	14,139.05	567.37	0.00
Shore	3	14,144.48	572.80	0.00
Wetland	4	14,172.08	600.41	0.00
Intercept	2	14,194.02	622.34	0.00

Indices of relative abundance for age-0 suckers were greatest in 2006, and smaller intra-annual differences in indices also were detected within the two time periods examined. All summary statistics indicated that CPUE was greater in 2006 compared to other years in the study. Of all age-0 suckers captured in the 15 years examined in this study, 57 percent were captured in 2006. The estimated effect size also indicated that CPUEs were greater in 2006 than from 2001 to 2005.Within the 2001–06 dataset age-0 sucker CPUEs were greatest in 2006, moderate in 2002, and lowest during 2003–05 (table 15). The index of relative apparent abundance (± SE) of 2006 was greater ($p<0.0002$) than in any other year (table 15). The index of relative abundance for 2002 was greater ($p<0.0002$) than for the years 2003–05. Within the 2007–10 and 2012–15 dataset, CPUEs of age-0 suckers were the lowest in 2012 and slightly greater in 2007, 2010, 2014, and 2015 than in 2008 or 2009 (table 16). The standard error of the index of relative abundance for 2013 was large and this year could only be distinguished as having higher index than 2012.

Table 15. Catch and model fit statistics for age-0 suckers ≥ 45 millimeters standard length captured during 2001–06.

[Uninformative nets (considered to be those that were fished before June 26, which is the earliest day in any year in which an age-0 suckers was captured) were removed from the dataset used to generate this table. For each year, the following are shown: Number of nets in the dataset (n); proportion of nets to catch one or more suckers (Proportion non-zero); median (Median of non-zero), mean, and standard deviation (Mean [±SD] of non-zero) of catches in nets that captured at least one sucker; maximum numbers of suckers captured in one net (Max); and an index of relative abundance plus or minus standard error (Index of relative apparent abundance [±SE]). This combination of statistics is presented to describe the distribution in the highly skewed and zero-heavy data. The maximum number of suckers captured in one net was estimated in 2006 based on an extrapolation from a sub-sample. The relative estimated effect of year, given a negative binomial distribution, is shown. Annual effect size is given relative to the year with the lowest effect size (2003) so that all relative values are positive]

Year	n	Proportion non-zero	Median of non-zero	Mean (±SD) of non-zero	Max	Index of relative apparent abundance (±SE)
2001	517	0.50	3	7.65 ± 12.09	94	0.87 ± 0.54
2002	638	0.61	4	9.32 ± 15.42	131	1.11 ± 0.12
2003	217	0.55	2	5.59 ± 8.16	48	0.00 ± 0.18
2004	892	0.44	2	4.99 ± 6.83	54	0.05 ± 0.12
2005	683	0.40	2	5.68 ± 13.00	178	0.14 ± 0.12
2006	291	0.79	17	84.66 ± 270.37	3304	3.44 ± 0.15

Table 16. Catch and model fit statistics for age-0 suckers ≥ 45 millimeters standard length captured during 2007–10 and 2012–15.

[Uninformative nets (considered to be those that were fished before June 26, which is the earliest day in any year in which at least one age-0 sucker was captured) were removed from the dataset used to generate this table. Data are not shown for 2011 because no nets were fished after June 26. For each year, the following are shown: Numbers of nets in the dataset (n), proportion of nets to catch one or more sucker (Proportion non-zero), median (Median of non-zero), mean and standard deviation (Mean [±SD] of non-zero) of catches in nets that captured at least one sucker, maximum numbers of suckers captured (Max), and an index of relative abundance plus or minus standard error (Index of relative apparent abundance [±SE]). This combination of statistics is presented to describe the distribution in the highly skewed and zero-heavy data. The relative estimated effect of year, given a negative binomial distribution, is shown (Index of relative apparent abundance [± SE]). Annual effect size is given relative to the year with the lowest effect size (2012) so that all relative values are positive]

Year	n	Proportion non-zero	Median of non-zero	Mean (±SD) of non-zero	Max	Index of relative apparent abundance (± SE)
2007	875	0.37	2.0	3.27 ± 3.88	34	2.72 ± 0.37
2008	2,091	0.12	1.0	2.11 ± 2.04	16	1.09 ± 0.37
2009	2,135	0.17	1.0	2.09 ± 2.07	17	1.29 ± 0. 37
2010	1,725	0.29	2.0	3.39 ± 3.99	36	2.02 ± 0. 33
2012	280	0.02	1.0	1..2 ± 0.41	2	0.00 ± 0.00
2013	107	0.19	1.0	1.95 ± 1.47	6	0.96 ± 0.42
2014	245	0.34	2.0	3.00 ± 3.40	24	2.02 ± 0. 37
2015	436	0.40	1.5	2.29 ± 2.16	18	1.82 ± 0. 34

Annual Variation in Apparent Age-0 Sucker Survival

Daily mean CPUEs for age-0 suckers ≥ 45 mm SL peaked in August in all years except 2009 when they peaked on July 28 (table 17). In 2001, 2002, 2004, 2005, 2006, and 2010 there appeared to be a clear increase followed by a clear decrease in mean non-zero catches (appendix D). However, in 2001 and 2006 the proportion of nets to catch one or more sucker did not decrease substantially after it peaked in August. In 2003, we did not sample until mid-August and there was a strong decrease in mean non-zero catches and proportion of nets to catch at least one sucker. In 2008 and 2009, CPUEs did not decrease after an August peak in catches, and these years were removed from our survival analysis. In 2014 and 2015, CPUEs were consistently low throughout the sampling seasons.

The Day*Year + Gear*Depth model fit to daily catch data carried 100 percent of the model weight, indicating that age-0 sucker CPUE decreased at different rates among years (table 18). The index of relative apparent sucker survival was lowest in 2004 (fig. 10). Differences in the indices of apparent relative age-0 sucker survival were not detected among any other years. There appeared to be an apparent decrease in summertime survival from 2001 to 2004 and an increase in survival from 2004 to 2007, but there was a lack of statistical support for this pattern.

Table 17. Greatest mean daily catch for age-0 suckers each year and day of the year on which it occurred.

[Number of nets fished (n) was used to calculate the daily mean (Mean) and standard deviation (SD) for age-0 suckers captured on each day. Suckers < 45 millimeters standard length were removed from these calculations because they were considered too small to be fully vulnerable to our nets.]

Year	Date	Mean	SD	n
2001	August 2	15.92	25.2	12
2002	August 2	19.9	30.6	18
2003	August 5	20.4	11.6	5
2004	August 26	10.1	13.5	18
2005	August 6	47.0	73.9	5
2006	August 11	618.4	1,099.9	8
2007	August 22	6.8	8.8	8
2008	August 29	3.7	4.6	16
2009	July 28	1.5	3.3	46
2010	August 25	3.2	5.8	46
2012	August 8	0.2	0.4	32
2013	August 15	1.2	2.1	12
2014	August 14	3.9	8.5	8
2015	August 11	2.5	4.5	17

Table 18. Model selection statistics for three models fit to data truncated at the day in each year when the mean catches per unit effort peaked.

[Dates used to truncate data are given in table17. Day is a parameter for the number of days since the peak catch of age-0 suckers in each year. All other parameters are described in table 6. For each model, the following are shown: Number of parameters (Pars), Akaike's information criterion adjusted for sample size (AICc), difference in AICc between a given model and the best model (ΔAICc), and the relative model weight]

Model name	Pars	AICc	ΔAICc	w
Day*Year + Gear*Depth	31	15,461.14	0.00	1.0
Day + Year + Gear*Depth	19	15,717.39	256.26	0.0
Year + Gear*Depth	18	16,023.69	562.55	0.0

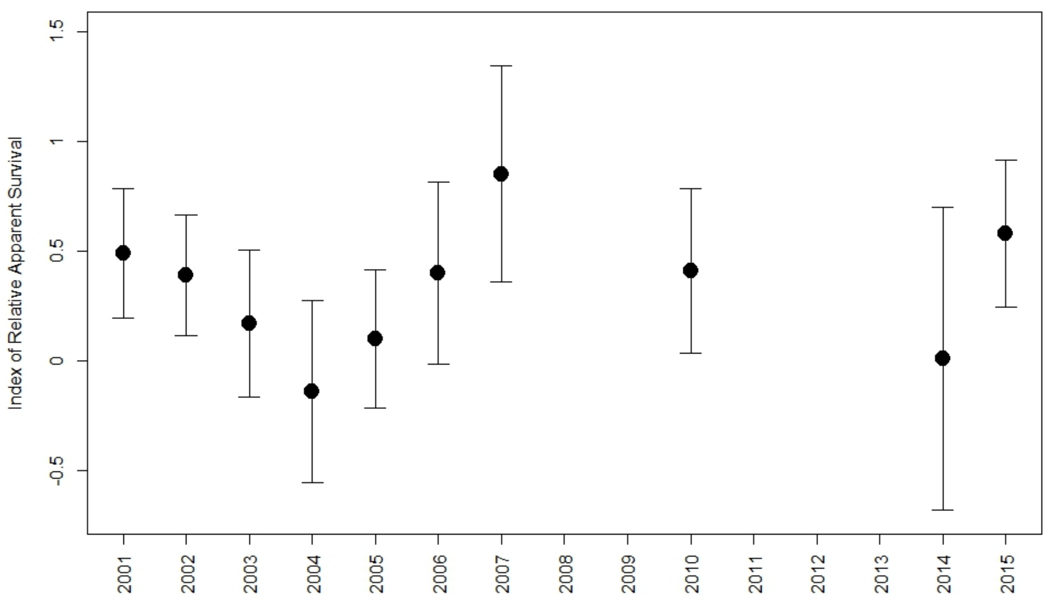

Figure 10. Annual index of relative apparent survival of age-0 suckers, Upper Klamath Lake, Oregon, mid-August to mid-September, 2001–15. Whiskers indicate 95-percent confidence intervals.

Annual Variation in Apparent First-Year Survival

Age-1 suckers were rare in our catches and varied somewhat among years. A total of 1,732 age-1 suckers were captured over the 15 years (table 19). Age-1 suckers were captured in only 11 percent of all nets fished. However, the proportion of nets within a year to capture one or more age-1 suckers ranged from 0.00 to 0.33. Seventy-five percent of age-1 suckers were captured prior to July 17 each year. Of the nets that captured age-1 suckers, 72 percent captured only one and 95 percent captured four or fewer. The maximum number of age-1 suckers captured in a single net was 32, which occurred on May 7, 2009, in the Tulana restoration area of the Williamson River Delta. When we focused our qualitative examination of age-1 sucker catch data on dataset number 14 (table 7), we found higher median and mean CPUEs in 2001 and 2006 than in 2002, 2004 and 2005 (table 20).

Table 19. Catch statistics for age-1 suckers in Upper Klamath Lake, Oregon, 2001–15.

[For each year, the following are shown: Total number of nets fished in each year (n), proportion of nets that captured one or more age-1 suckers (Proportion non-zero), median catch in nets that captured at least one age-1 sucker (Median of non-zero), mean (± standard deviation [SD]) catch per unit effort in nets that captured one or more age-1 sucker (Mean [±SD] non-zero), maximum catch of age-1 suckers in one net (Max), and total number of age-1 suckers captured (Total). This combination of statistics is reported to describe the distribution of skewed and very zero-heavy data. Not all age-1 suckers were identified to species; therefore, this table is for all sucker taxa combined. Ages were presumed based on length at date and rules described in table 3. NA means that data were not available]

Year	n	Proportion non-zero	Median of non-zero	Mean (± SD) non-zero	Max	Total
2001	517	0.08	1	1.38 ± 0.76	4	58
2002	645	0.03	1	1.24 ± 0.56	3	21
2003	217	<0.01	1	1.00 ± 0.00	1	1
2004	892	0.01	1	1.23 ± 0.44	2	16
2005	683	0.03	1	1.33 ± 0.97	5	24
2006	291	0.09	1	1.41± 1.05	7	38
2007	1,175	0.13	1	1.86 ± 1.87	15	294
2008	2,362	0.03	1	1.41 ± 0.97	7	116
2009	3,465	0.10	1	1.66 ± 2.35	32	578
2010	2,815	0.04	1	1.25 ± 0.47	3	127
2011	461	0.25	1	1.84 ± 1.53	9	210
2012	422	0.33	1	1.61 ± 1.44	13	227
2013	107	0.00	NA	NA	0	0
2014	242	0.02	1	1.00 ± 0.00	1	4
2015	544	0.03	1	1.13 ± 0.34	2	18

Table 20. Catch statistics for age-1 suckers in data subset 14, in which a single gear type was used and habitat parameters are similar, 2001–02 and 2004–06.

[Data subset 14 (table 7) includes 91-centimeter round nets that were set in August nearshore in 1–2 meters (m) of water, more than 200 m from a wetland edge. These data were chosen because there were a large number of similar samples that could be compared across years; therefore, the need to account for habitat and sampling differences was eliminated. For each year, the following are shown: Total number of nets fished in each year (n), proportion of nets that captured one or more age-1 suckers (Proportion non-zero), median catch in nets that captured at least one age-1 sucker (Median of non-zero), mean (±standard deviation [SD]) catch per unit effort in nets that captured one or more age-1 sucker (Mean [±SD] non-zero),maximum catch of age-1 suckers in one net (Max), and total number of age-1 suckers. This combination of statistics is reported to describe the distribution of skewed and very zero-heavy data. Not all age-1 suckers were identified to species; therefore, this table is for all sucker taxa combined. Ages were presumed based on length at date and rules described in table 3. NA means data were not available.]

Year	n	Proportion non-zero	Median of non-zero	Mean (±SD) non-zero	Max	Total
2001	58	0.12	2	1.7 ± 0.76	3	12
2002	13	0.00	NA	NA	0	0
2004	68	0.01	1	1.0 ± 0.0	1	1
2005	45	0.02	1	1.0 ± 0.0	1	1
2006	43	0.19	1.5	2.3 ± 2.1	7	18

The estimated relative odds (± SE) of capturing one or more age-1 sucker per net were greatest in 2007 (0.93 ± 0.25) and 2012 (0.84 ± 0.25). However, non-overlapping confidence intervals indicated that odds in 2007 were only greater than in 2008 and 2010 and the odds in 2012 were only greater than in 2010 (fig. 11). The odds of success were 18.5 times greater in the best year (2007) than in the worst year (2010) for catching age-1 suckers within the subset of data analyzed.

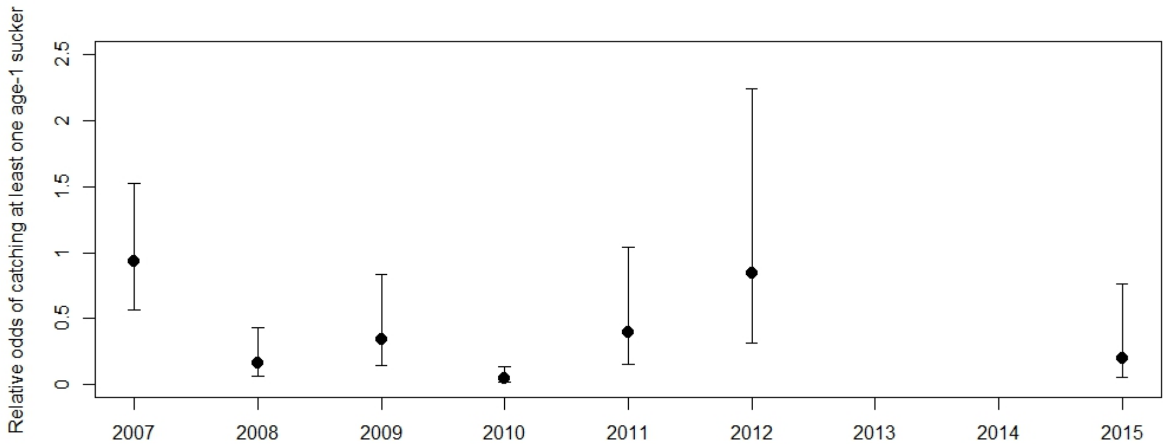

Figure 11. Relative odds of catching one or more age-1 sucker per net by year, based on selected data collected in Upper Klamath Lake, Oregon, 2007–15. Estimates are qualified here as relative odds because they were based on a subset of comparable data and do not represent the true lakewide odds. Data used in analysis associated with this figure are summarized in tables 7 and 8. The 95-percent confidence intervals are shown. Significant differences among years are indicated by non-overlapping confidence intervals. Odds greater than one indicate success is more likely than failure, odds less than one indicate failure is more likely than success, and odds of one indicate equal probability of success and failure.

Differential Mortality Between Taxa

Weekly patterns in species composition of age-0 suckers varied among years (fig. 12). Lost River suckers were the more common sucker species in all weeks of 2004 and 2005. Shortnose suckers were the more common species in all weeks in 2003 and 2010. There was a strong downward trend in the proportion of Lost River suckers captured over the sampling seasons of 2003, 2007, 2009, and 2015. There was never an increasing trend in the proportion of Lost River suckers throughout a sampling season.

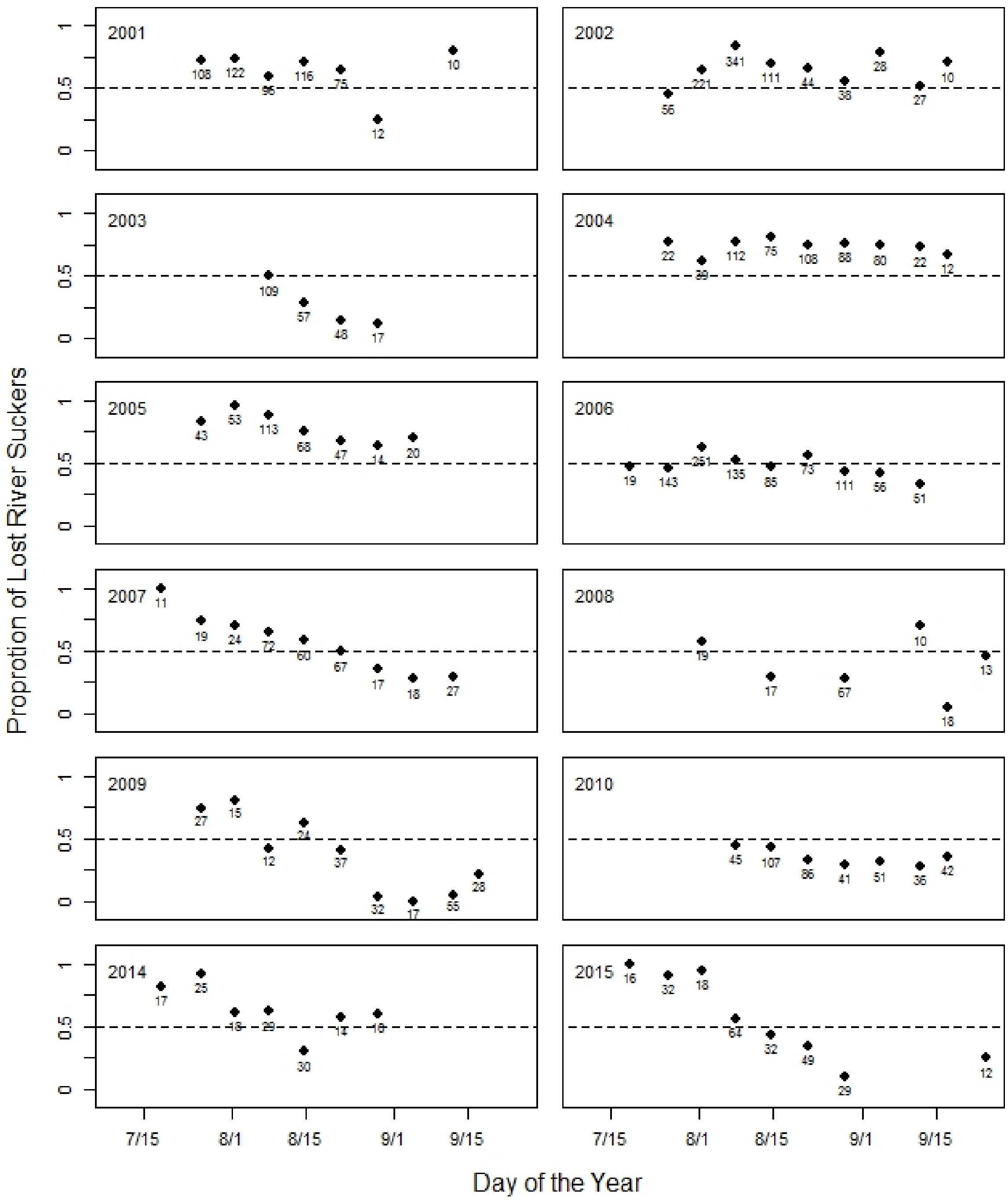

Figure 12. Proportions of weekly catches of age-0 suckers ≥ 45 millimeters standard length identified to species that were Lost River suckers in Upper Klamath Lake, Oregon, 2001–10 and 2014–15. Values greater than 0.5 indicate more Lost River suckers; whereas, values less than 0.5 indicate more shortnose suckers. Total number of fish used to calculate proportions are shown under each data point (diamond).

Lost River suckers comprised only 14 percent of 159 total age-1 suckers identified to species during 2001–15. Shortnose suckers were the most common taxa in the 5 years in which 10 or more age-1 suckers were identified to species (table 21). Lost River suckers comprised between 4 and 30 percent of age-1 suckers identified to species in each of these 5 years (table 21). Somewhat smaller proportions of the identified age-1 suckers were Lost River suckers in 2001, 2009 and 2010 than in 2006 and 2007.

Table 21. Numbers of age-1 suckers with sample sizes of at least 10 suckers identified to species in 5 years, Upper Klamath Lake, Oregon, 2001, 2006–07, and 2009–10.

[Proportions of the suckers sampled that were Lost River Sucker also are given. Data are only shown for years in which at least 10 age-1 suckers were identified to species]

Year	Lost River sucker	Shortnose sucker	Klamath largescale sucker	Proportion Lost River sucker
2001	2	21	0	0.09
2006	3	5	2	0.30
2007	4	16	2	0.18
2009	2	50	1	0.04
2010	1	10	1	0.08

Decrease in Proportion of Nets to Capture Age-1 Suckers During Summer 2007

CPUE of non-zero catches for age-1 suckers did not decrease noticeably during summer 2007 (fig. 13). However, the proportion of nets catching at least one age-1 sucker generally decreased between the weeks of June 4 and September 10, 2007 (fig. 14). The proportion (± SE) of nets catching one or more age-1 suckers was greatest the week of June 25, (0.31 ± 0.004) and least during the week of August 13 (0.01 ± 0.00).

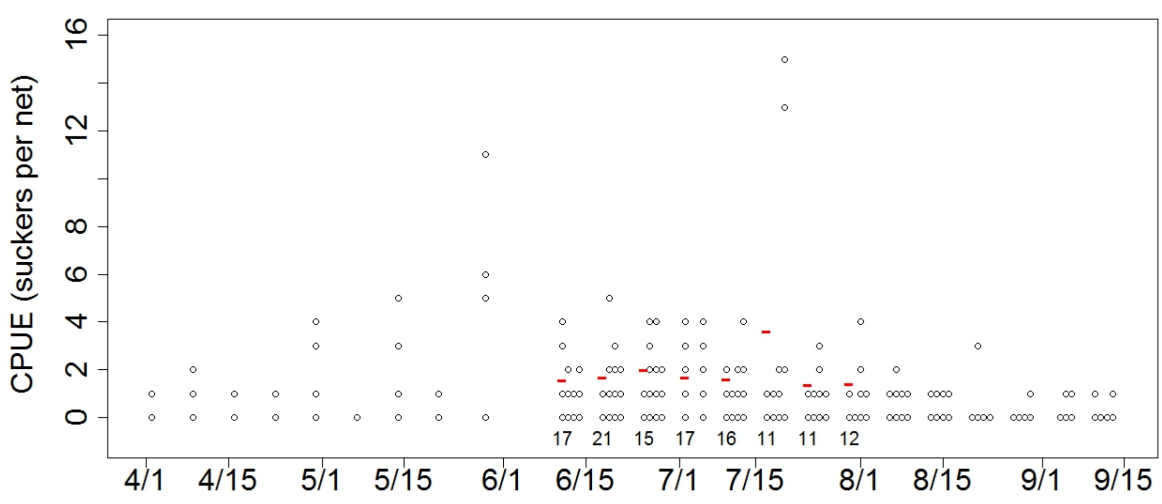

Figure 13. Catch per unit effort (CPUE; suckers per net) for age-1 suckers by day of the year, Upper Klamath Lake, Oregon, 2007. Circles indicate CPUE and bars indicate mean weekly non-zero catches where at least 10 nets within a week captured age-1 suckers. Numbers of nets used to calculate means and proportions are given in the figure near the x axis.

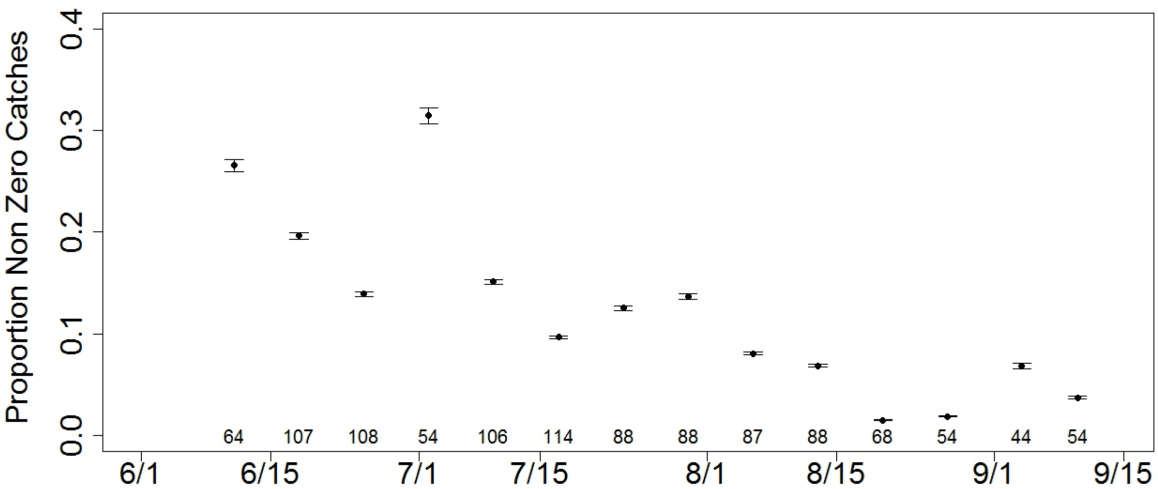

Figure 14. Weekly proportions of nets catching one or more suckers for weeks in which at least 10 nets were fished, Upper Klamath Lake, Oregon, 2007. Numbers of nets used to calculate means and proportions are given in the figure near the x axis. Dots and whiskers on graph show means and 95-percent confidence intervals.

Discussion

Apparent Growth

There was more variation in apparent summertime growth rates of age-0 (≥ 45 mm SL) Lost River suckers than for age-0 shortnose suckers. We identified 2001, 2002, 2005, 2006, 2014 as years when Lost River suckers appeared to grow relatively fast. Simon and others (2012) noted that mean SLs of Lost River suckers captured in cast nests in late August were relatively high in all these years except 2014, when they did not sample. They also reported relatively long Lost River suckers in late August 2004, a year that we were unable to identify as having relatively fast growth due to large confidence intervals. For shortnose suckers, we identified 2001 and 2006 as years with relatively slower and faster growth rates than other years, respectively (fig. 8). Simon and others (2013) reported relatively long age-0 shortnose suckers captured in late August cast nets in 2006, adding support to the claim that 2006 was a year in which shortnose suckers grew relatively fast. They also reported relatively long but variable SLs of late-August shortnose suckers captured in 2001 and 2002, highly variable lengths in 2003, and short but variable lengths in 2010. Apparent inconsistencies between our relative growth estimates and the relative late-August SLs of shortnose suckers reported in Simon and others (2013) likely are due to a combination of slightly different distributions in sample locations, different methods, variable growth rates, or some combination of these factors. Relatively early hatching in 2002 (Simon and others, 2009) meant that age-0 suckers had more time to grow and might help to explain why Simon and others (2013) found relatively large shortnose suckers in August, when we did not detect relatively fast growth.

Simon and others (2009) estimated daily growth rates by dividing fish length by the number of lapillus-otolith increments for suckers captured from the second week of August to the first week of September each year from 1994 to 2008. Their estimates of daily growth rates are faster than ours, and they did not detect the differences among years that we detected in our analysis of apparent daily growth. The differences between the two sets of growth estimates can be explained by the methods. The method used by Simon and others (2009) averaged growth rates over juvenile and larval life stages, which may have resulted in faster estimated growth rates because larval fish typically grow faster than juvenile fish (Butler, 1989; Wieser and Medgyesy, 1990). Our method was specific to the summertime apparent growth of age-0 suckers.

Sampling locations and gear could cause negative bias in estimated growth rates if suckers leave the sampled areas and (or) outgrow size selectivity of specific gears. This would be of particular concern if the slowest growth years also were years with restricted areas of sampling. Differences in growth rates among areas of the lake also could create artificial differences in growth rates among years. However, we did not find correlations between annual apparent growth rates that can be explained by different sampling areas. For example, there were differences in apparent growth rates among years during 2001–06, when all samples were collected on the east shore. Most sample sites were located in the Williamson River Delta and the north end of the lake during 2008–10 and 2014–15, but there was variation in growth rates among those years.

Factors affecting juvenile sucker growth may be age- and species-specific. The unsynchronized variation in annual growth rates between age-0 suckers of the two species indicates that environmental conditions may be affecting the species differently. Although apparent age-0 sucker growth rates varied among years, we did not detect annual variation in age-1 sucker growth rates. The lack of variation in age-1 sucker growth rates may be partially due to the averaging effect of combining species, although only 14 percent of age-1 suckers identified to species were Lost River suckers.

Annual Variation in Age-0 Apparent Production

Relative to other years during 2002–10 or 2014–15, 2006 was a year of relatively high apparent juvenile sucker production. A gear change in 2007 makes it inappropriate to discuss minor differences in CPUEs during 2001–06 and 2007–15. A joint analysis may be done in the future if data are collected using all gear types in a single year, so that a gear effect can be evaluated. Mean and median of non-zero catches in 2006 were an order of magnitude greater than in any other year in our analysis, and the relative estimated index of relative apparent abundance was at least three times greater than in any other year during 2001–05 (table 15). Our results were corroborated by Simon and others (2013), who identified 2006 as a year with relatively high midsummer CPUEs when compared to other years during 2002–10.

The time period considered in this report may have encompassed relatively low production years, particularly when viewed relative to the longer 1991–2011 record examined by Markle and Cooperman (2002) and Simon and others (2013). These studies identified years with relatively high apparent juvenile sucker production in which USGS did not sample or target age-0 suckers. Their mean mid-July beach seine CPUEs in 1996, 1997, 1999, and 2000 were at least twice as great as in 2001, 5.6 times greater than in 2006, and 8.1 times greater than in any other year in which both USGS and Simon and others (2013) sampled. They also reported relatively high frequencies of cast net and otter trawl samples that captured 10 or more juvenile suckers in August of 2011, a year in which USGS only targeted age-1 suckers in spring sampling. Relatively high catches of age-1 suckers in USGS trap nets in 2012 corroborate relatively high 2011 age-0 sucker apparent abundance.

Relative (among years) summertime age-0 sucker CPUEs are the result of relative (among years) spawning success, survival from egg fertilization to larval egress, in-lake larval survival, and juvenile survival to the size of gear recruitment (45 mm SL). We presume that fecundity varied minimally or decreased slightly among years and, therefore, cannot explain relatively high apparent age-0 sucker production years. The number of adult suckers returning to spawn decreases slightly each year because of a lack of recruitment to spawning aggregations and low annual adult sucker mortality (Hewitt and others, 2015); these factors are not likely to be a major contributor to the annual variation in age-0 sucker CPUEs. Investigation of factors that could affect spawning success or early life stage survival in spawning and rearing habitats may lead to a better understanding of the causes of annual variation in the abundance of juvenile suckers in midsummer.

Annual Variation in Apparent Age-0 Sucker Survival

A combination of recruitment to our gear, survival, and emigration can explain the variation in within-season catches of age-0 suckers. The seasonal increase in age-0 CPUEs and the proportion of nets catching one or more suckers can be explained by suckers continuing to recruit to our gear as they grew to a fully vulnerable size around 45 mm SL. Dates on which age-0 sucker catch rates peaked each year do not necessarily indicate the start of annual mortality; rather, they indicate the point in time when most suckers were of a size vulnerable to capture in our nets. Annual decreases in CPUE are a result of emigration from sampled areas, survival, and potential reductions in sampling efficiency for larger suckers (appendix D). Sampling in various habitats in each year of our study reduced the risk of emigration as a major contributor to declining CPUEs. Directed movement of age-0 suckers ≥ 45 mm SL along the eastern shore of Upper Klamath Lake from north to south and nearshore to offshore areas was examined from 2001 to 2006. No nearshore to offshore movement was detected, and apparent summertime age-0 sucker north to south movement was only detected in 2004 (Hendrixson and others, 2007b). Finally, our analysis is based on declining CPUEs after annual peaks in mean CPUEs, and is only relevant to trends that occurred from mid-August to mid-September each year. The lack of decrease in CPUEs in 2007 to 2009 (appendix D) likely is due to a combination of shortnose suckers continuing to recruit to gear as late as September in these years (appendix B) and very low CPUEs overall.

Our index of apparent relative age-0 sucker survival was similar among all years except 2004 and 2007 (fig. 10). Our inability to detect annual differences among years was partly due to a high proportion of zero catches and variability in catch rates within weeks. Slightly higher apparent mortality occurred in 2004, a year when there was some indication of midsummer southward movement patterns of age-0 suckers (Hendrixson and others, 2007b). The combination of these two findings is consistent with emigration from the study area in 2004.

A seasonal decrease in the proportion of nets catching one or more age-1 suckers in 2007 may have been caused by decreasing susceptibility to our gear, mortality, or both. Age-1 to age-6 juvenile suckers as large as 300 mm SL make up most of the suckers captured in similar trap nets fished in Clear Lake Reservoir, California (Burdick and others, 2015), indicating that reduced selectivity alone is unlikely to be the cause of the steep decrease in the proportion of nets catching age-1 suckers in Upper Klamath Lake. Despite the relatively high apparent production in 2006, by mid-September of 2007 the probability of capturing one of these suckers was not significantly different than zero (fig. 11). That is, the largest year class produced (2006) in the years examined in this report was nearly undetectable by the second September of life.

Annual Variation in Apparent First-Year Survival

Although the juvenile sucker catch data were not sufficient to estimate overwinter survival, survival likely is to be very low. The negative correlation between CPUE and age class is due to a combination of emigration from the lake, reduced susceptibility to the gear with age, mortality, or some combination of these factors. Evidence from other studies suggests that emigration from the lake and reduced susceptibility to gear cannot completely explain decreases in catch rates. Hendrixson and others (2007b) only found evidence of age-0 July and August emigration from the lake along the eastern shore in 1 of 5 years examined. Similarly, Burdick and Brown (2010) did not observe mass age-0 sucker emigration in lakewide July and August sampling in 2007 to 2009. However, catches of age-0 suckers vary among years in 8 weeks of annual sampling at the A-canal bypass system at the lake outlet, indicating that at least thousands of suckers emigrate from the lake in some years (J. Bottcher, Bureau of Reclamation, oral commun.). September–June emigration has yet to be ruled out and may play a role in the low catch rates of age-1 suckers. Catches of age-1 and older suckers in Clear Lake Reservoir, California, using 0.91-m trap nets during 2007–15 indicate that age-1 and older suckers should have been at least somewhat susceptible to capture (Burdick and others, 2015), but does not rule out reduced susceptibility of suckers with age.

Age-1 catches from data subset 14 indicated relatively greater abundance of age-1 suckers in 2001 and 2006 (table 20). Relative age-0 sucker abundance is unknown for 2000 and was not remarkably great in 2005. The lack of a relational pattern between relative age-0 sucker abundance indices and age-1 sucker catch statistics may indicate that overwinter survival varies among years. However, too few positive age-1 sucker catches in this data subset made it difficult to detect among-year patterns.

The odds of catching age-1 suckers, based on our restricted dataset analysis for 2007–12 and 2015, roughly tracked with age-0 sucker apparent relative production the prior year. Following a somewhat high apparent relative age-0 production year of 2006, the odds of catching an age-1 sucker in 2007 were greater than during 2008–10. The odds of catching an age-1 sucker also were slightly but insignificantly elevated in 2012 relative to 2008–10. The higher odds detected in 2012 followed 2011, a year in which Simon and others (2012) reported higher than typical age-0 CPUE in cast nets.

Captures of age-2+ suckers in Upper Klamath Lake were rare, and years in which catches of this age class were slightly elevated generally followed 2 or more years after years of relatively high age-0 CPUEs. Simon and others (2009) reported relatively high CPUE of age-0 suckers during 1998–2000. Following the 1998 and (or) 1999 cohorts, our age-2+ CPUE was relatively high in 2001. Following an apparently abundant 2000 year class, we captured relatively more age-1 suckers in 2001 and a total of five age-2+ suckers in 2002. Following a relatively abundant age-0 sucker year class of 2006, we captured age-2+ suckers during 2008–10. The larger size of a large portion of age-2+ suckers captured in 2010 indicates that these fish likely were older and perhaps members of the 2006 cohort. Simon and others (2013) also reported relatively high CPUE of age-0 suckers in 2011. We did not capture any age-2+ suckers in 2013, likely because of a small sample size (n=107) in 2013 and low capture rates for this age class. Age-2+ sucker CPUE also was relatively high in 2015, which did not follow 2 years after a year of relatively high age-0 sucker abundance.

Differential Mortality Between Taxa

Age-0 Lost River suckers made up a smaller proportion of summertime sucker catches than is expected based on the prevalence of Lost River sucker adult spawners. Approximately 10 times as many adult Lost River suckers as shortnose suckers make spawning migrations up the Williamson and Sprague Rivers every year (Hewitt and others, 2015). A second spawning population of Lost River Suckers occurs on the eastern shoreline of Upper Klamath Lake (Hewitt and others, 2015). Lost River suckers also are about three times more fecund than shortnose suckers (Scoppettone and Vinyard, 1991). Therefore, most (>97 percent) juvenile suckers captured in mid-July should be Lost River suckers, if spawning success, egg survival, larval survival, early (≤ 45 mm SL) juvenile survival, and gear susceptibility were similar between the two species. The percentage of juvenile suckers identified as Lost River suckers exceeded 95 percent during 1 week in July in 2007 and 2015. In all other years, the percentage of juvenile suckers identified as Lost River suckers ranged from 40 to 85 percent in mid-July. Lost River suckers also were seemingly underrepresented in catches of out-migrating larvae from the Williamson River, indicating that species-specific differences in some combination of spawning success, egg survival, and hatch rates may be the cause. Larval suckers sampled from the lower Williamson River during the spring outmigration seasons of 2004–10 were between 42 percent (2008) and 76 (2009) percent Lost River suckers (Ellsworth and others, 2008, 2009, 2011; Ellsworth and Martin, 2012).

The decrease in the proportion of Lost River suckers captured over the sampling seasons of 2003, 2007, 2009, and 2015 could be explained by several factors or a combination of factors. A protracted or delayed recruitment to the gear for shortnose suckers could have caused this decrease. Shortnose suckers within 5 mm of the size of full recruitment (45–50 mm SL) continued to be captured 1–4 weeks after Lost River suckers of the same size were last captured each year, except in 2006 and 2008 (appendix B). This dynamic could explain seasonal decrease in the proportion of age-0 Lost River suckers in our catches in 2003, 2007, 2009, and 2015. Lost River sucker specific emigration from the study area is another potential cause of this pattern in 2003 and 2015, when the spatial extent of sampling was limited; however, similar emigration from sampled areas was unlikely in 2007 and 2009, when nearly all known summertime habitats for juvenile suckers were sampled. Steep decreases in the proportion of Lost River suckers may have been facilitated in some years by higher or earlier mortality of Lost River suckers. This explanation corroborated the finding that most age-1 suckers that were identified to species were shortnose, not Lost River suckers (table 21).

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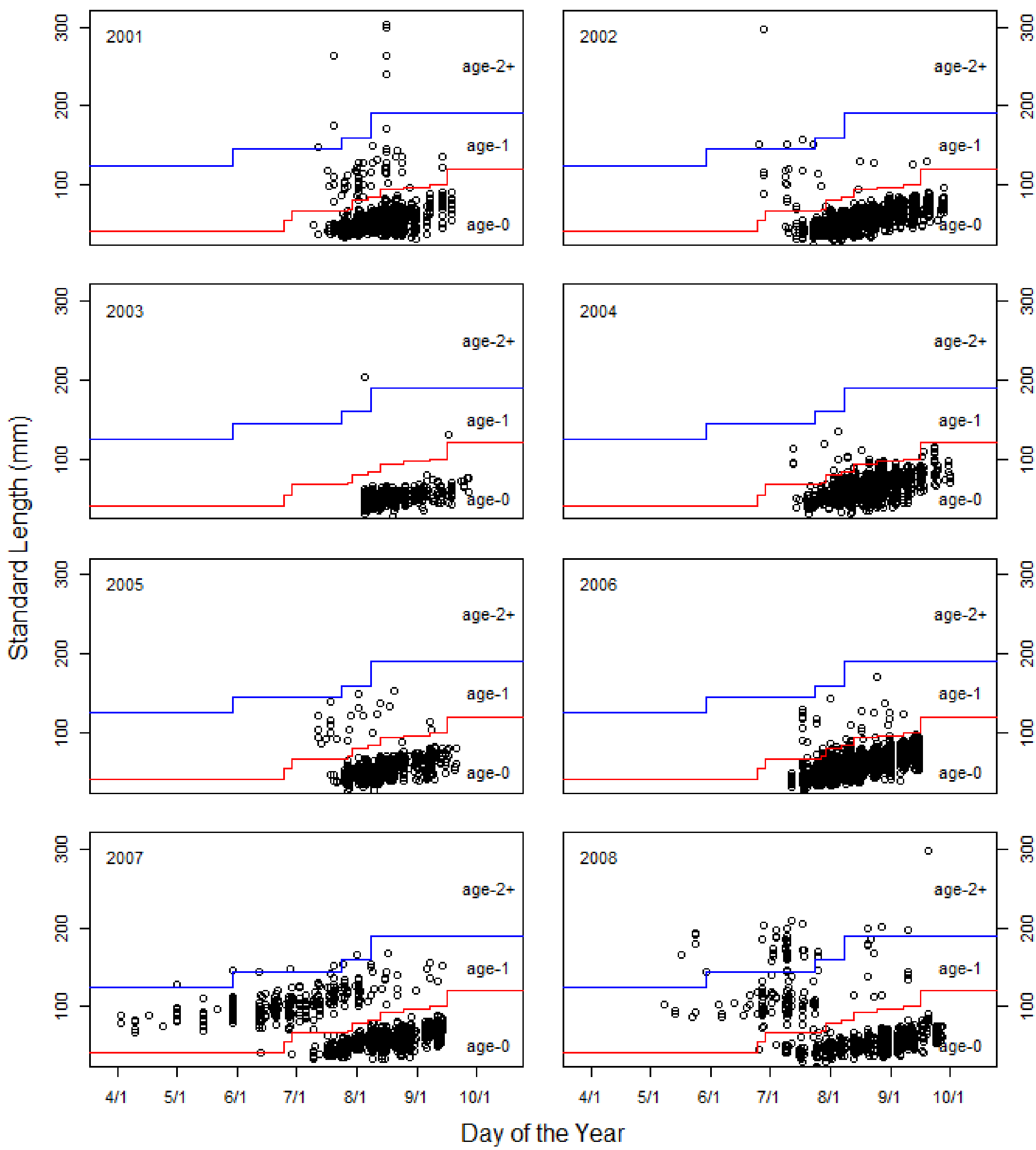
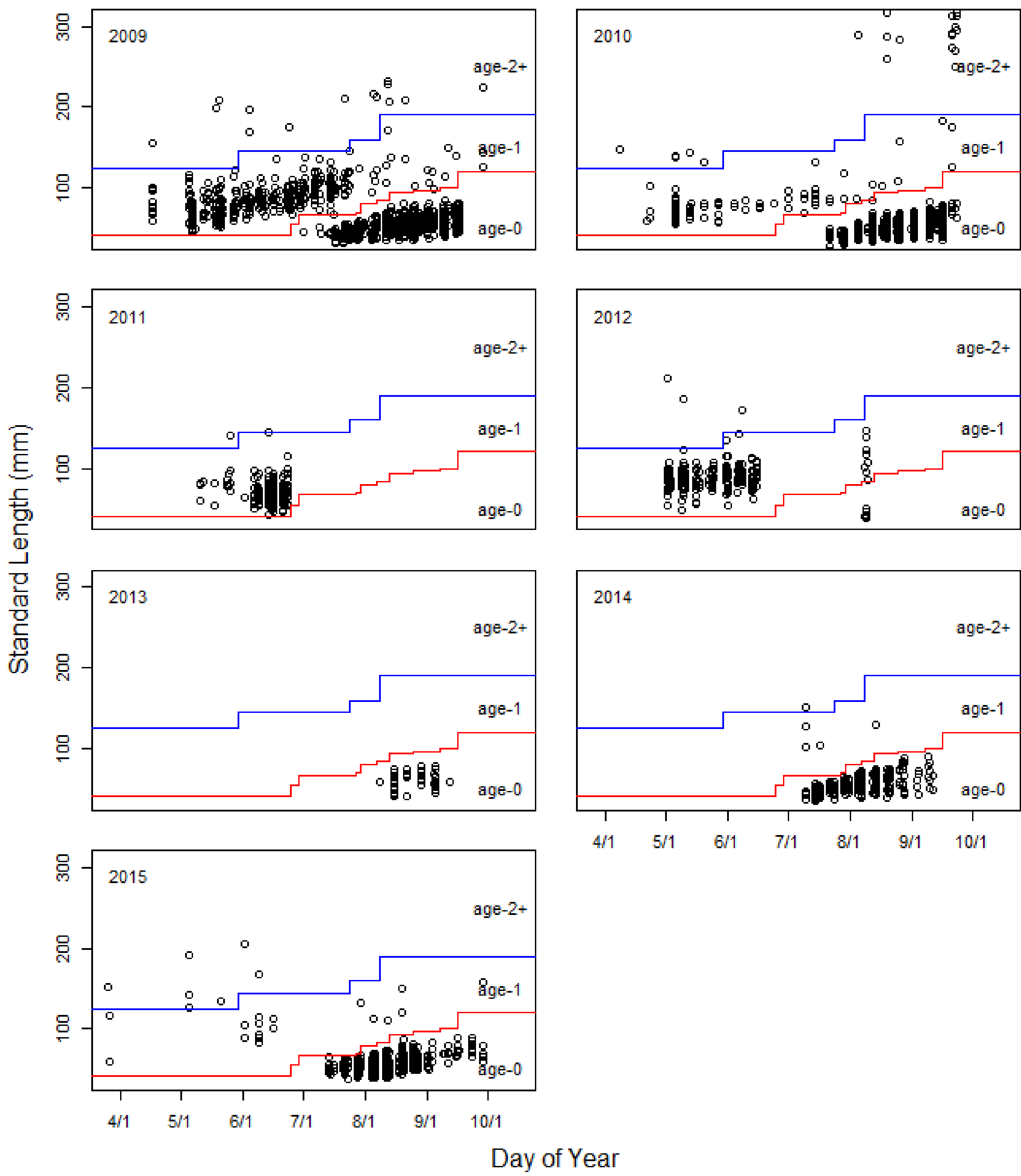
Appendix A. Age Assignment of Juvenile Suckers Based on Day of Year and Standard Length of Suckers Captured in Upper Klamath Lake, Oregon, 2001–15

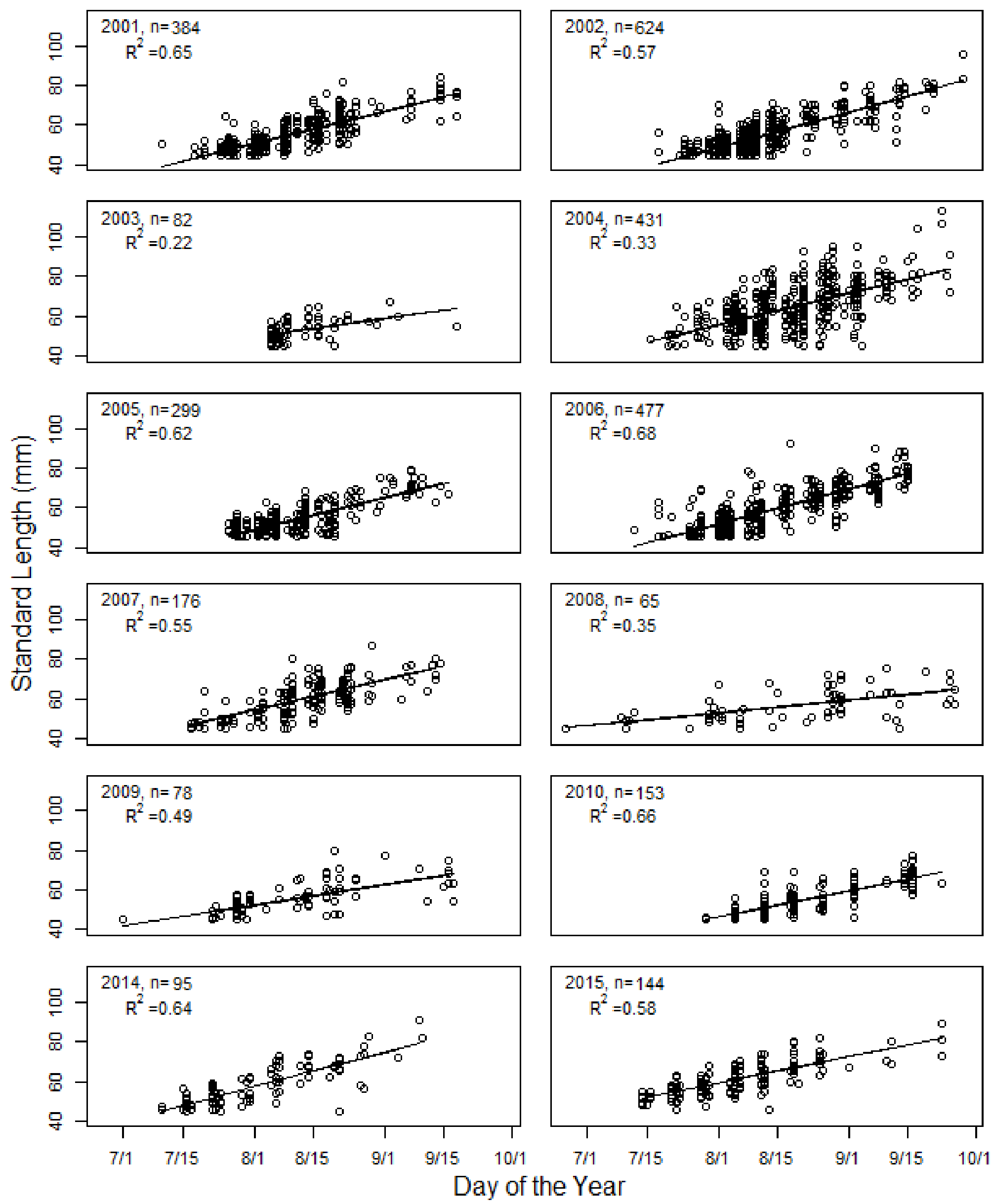
The following graphs show length (in millimeters [mm]) frequency graphs of juvenile suckers captured in Upper Klamath Lake, Oregon, 2001–15. Day of year on the x-axis is chronological day (days since January 1 in each year). Graphical assessment of data point (circle) clusters were used to develop a set of rules for age assignment. Lines indicate separation into different age groups based on this rule set.



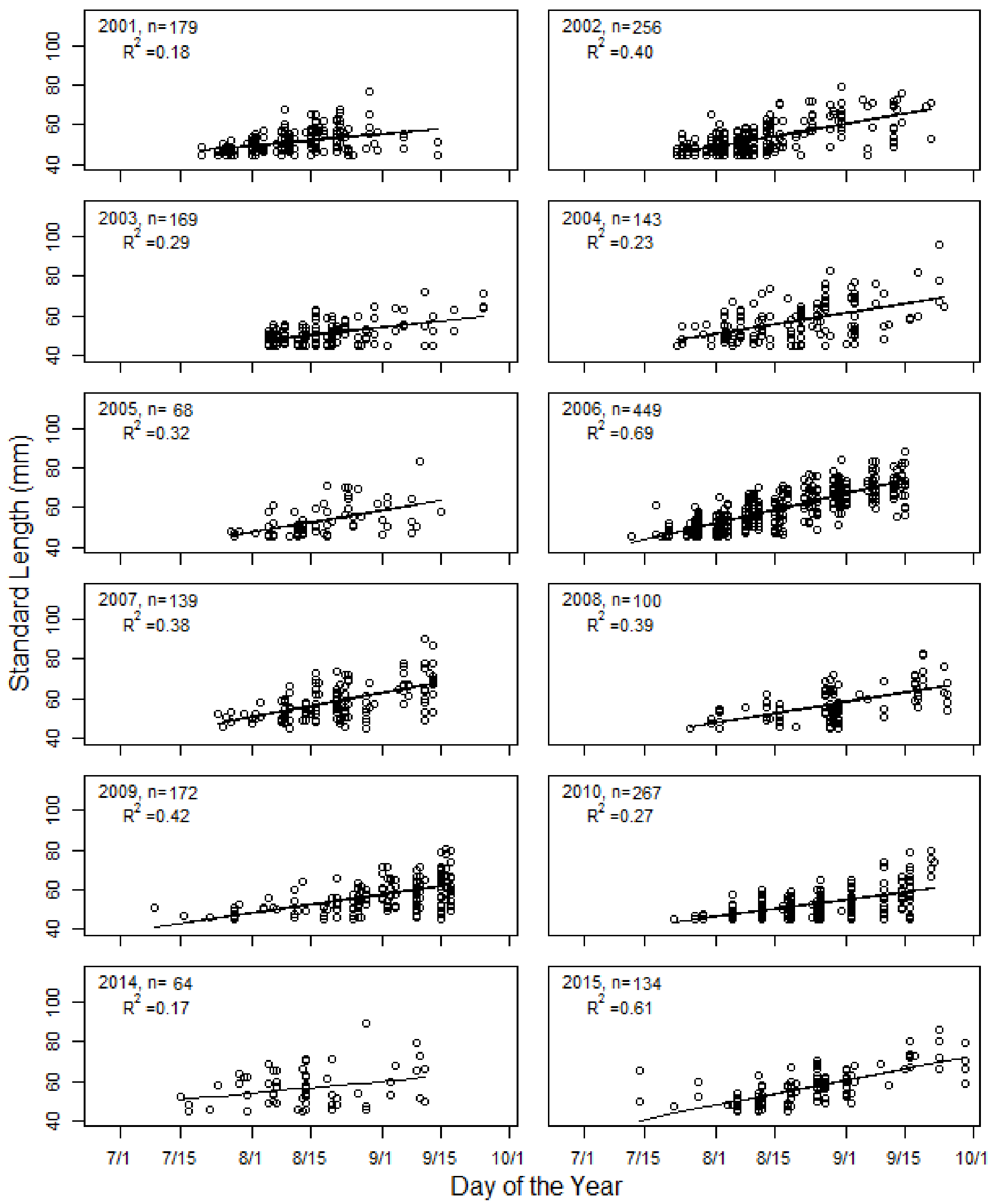

2009
2010
2011
2012
2013
2014
2015
age-2+
age-1
age-0
Standard Length (mm)
Day of Year
100
200
300
4/1
5/1
6/1
7/1
8/1
9/1
10/1

Appendix B. Age-0 Sucker Standard Length by Chronological Day and Year and Apparent Growth Regression Lines

The following graphs show standard length by day of the year for presumed age-0, 45-mm or greater SL shortnose suckers collected from Upper Klamath Lake, Oregon, 2001–15. Sample size (n), coefficient of determination (R^2) fit statistic, and regression line are shown for each year. Data points are shown as circles. Because of small samples sizes, 2011–13 were omitted from this analysis (table 4). Age was presumed based on length frequency and rules defined in table 3.

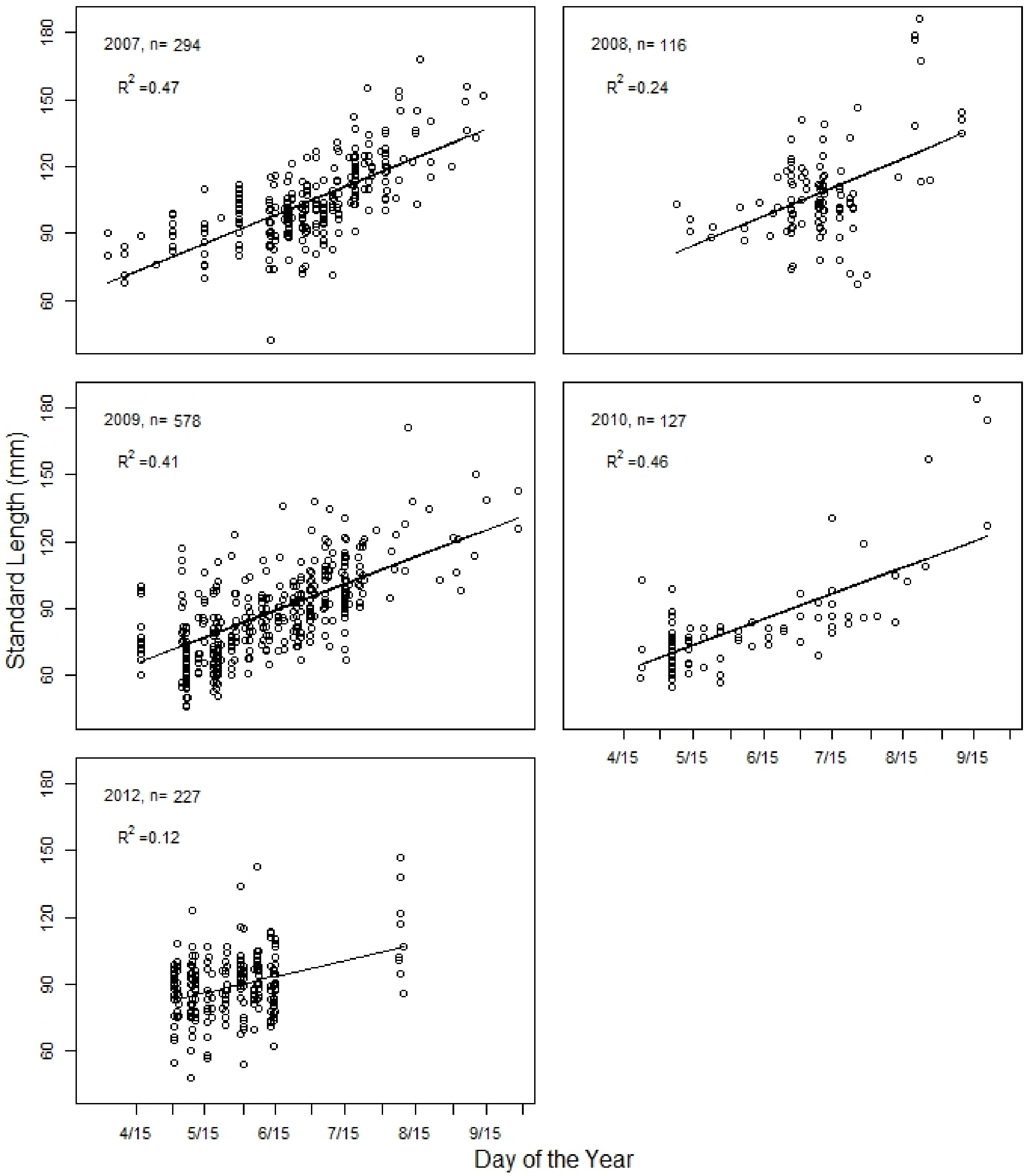


The following graphs show standard length by day of the year for presumed age-0, 45 mm or greater SL Lost River suckers collected from Upper Klamath Lake, Oregon, 2001–15. Sample size, (n) coefficients of determination (R^2), and regression line are shown for each year. Data points are shown as circles. Because of small samples sizes, 2011–13 were omitted from this analysis (table 4). Age was presumed based on length frequency and rules defined in table 3.



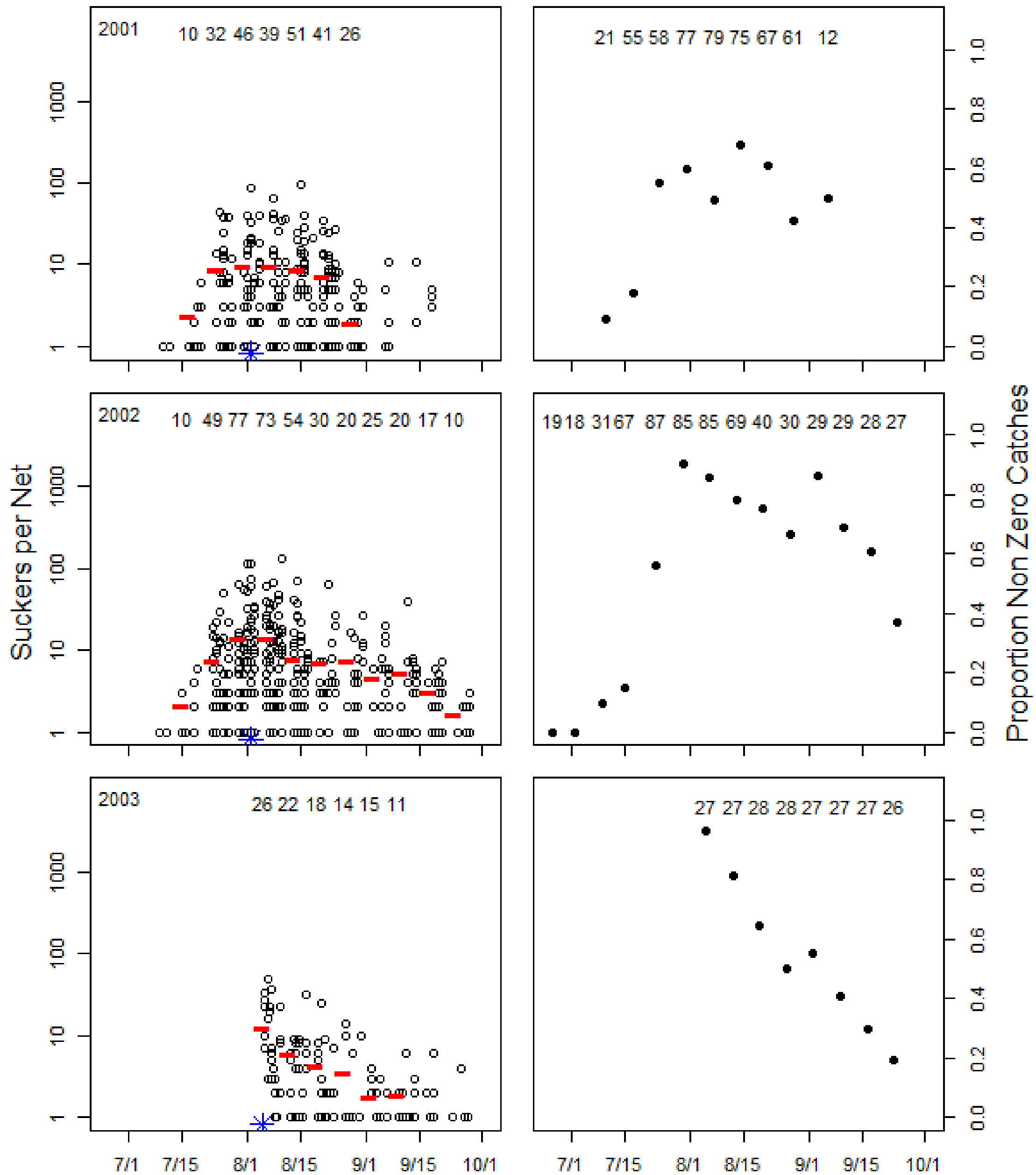
Appendix C. Age-1 Sucker Standard Length by Day of the Year Plots with Apparent Growth Rate Regressions

The following graphs show standard length (in millimeters [mm]) by day of the year for age-1 suckers captured during 5 years when the power to detect growth over 2 or more months exceeded 0.5 (table 5), in Upper Klamath Lake, Oregon, 2007–12. Sample size (n), coefficient of determination (R^2) fit statistic, and regression line are shown for each year. Data points are shown as circles.

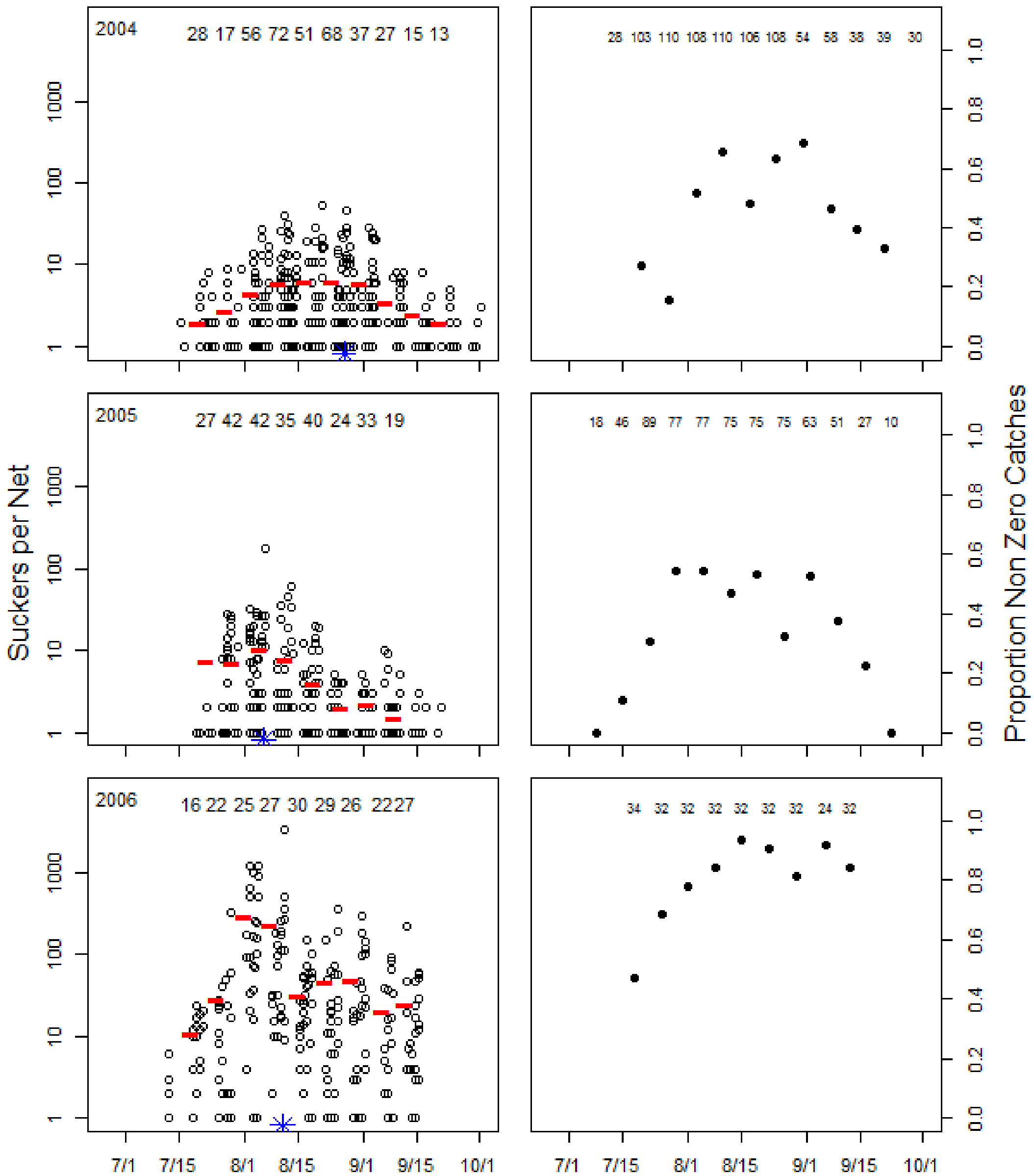


Appendix D. Age-0 Sucker Catch Per Unit Effort per Day and Proportion of Weekly Non-Zero Catches Shown by Year

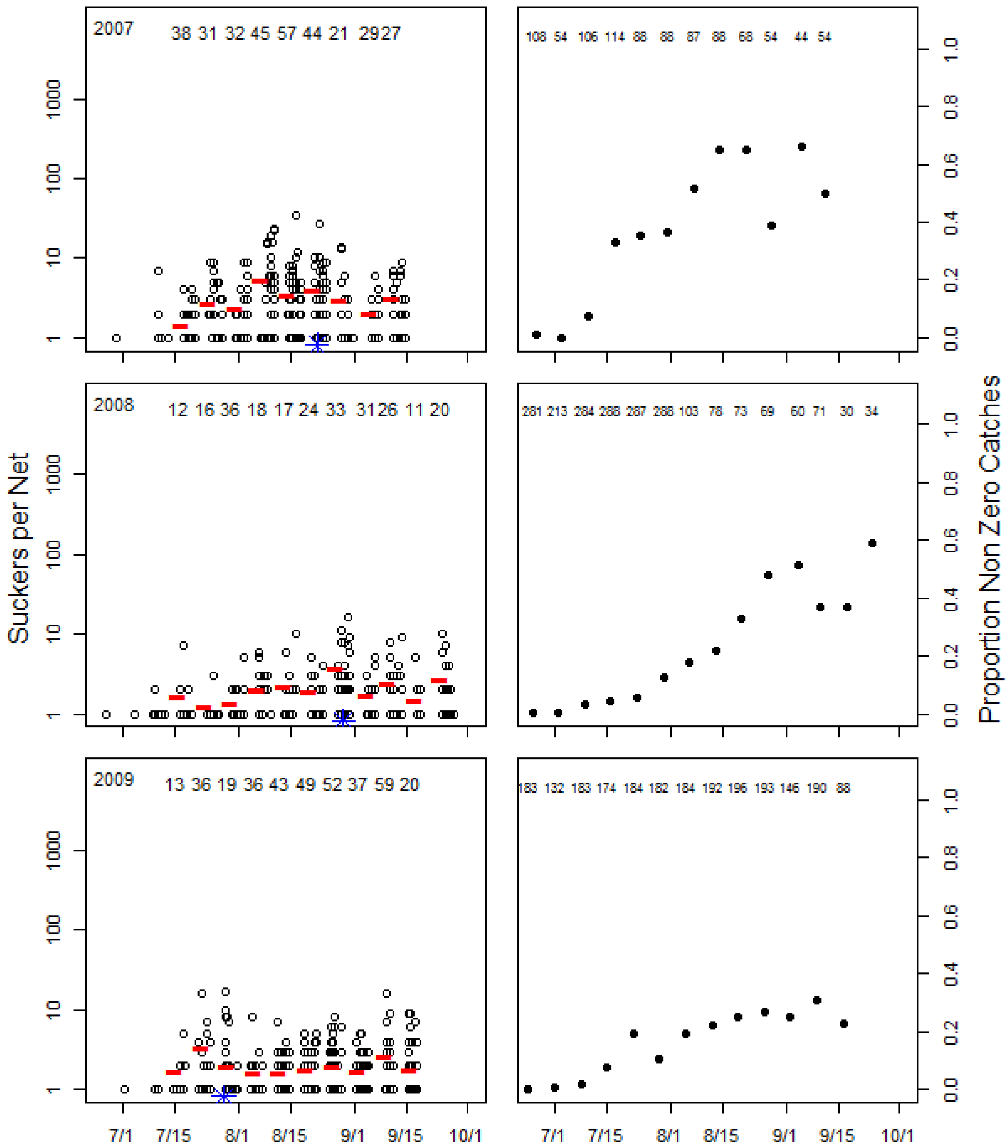
The following graphs show catches of age-0 suckers ≥ 45 millimeters standard length per net by day of the year, Upper Klamath Lake, Oregon, 2001–10 and 2014–15. Graphs in left columns show catches per net (circles) and mean daily non-zero catches (bars) where at least 10 nets captured suckers. Weekly proportions of nets catching one or more sucker are presented in graphs in right columns for weeks in which at least 10 nets were fished. Number of nets used to calculate means and proportions are given in the figures near the top of each graph. Stars on the x-axis indicate the day on which the greatest mean daily catch occurred in each year. Catch data that occurred on or after the stars were used in analysis of the rate of decrease in catches.

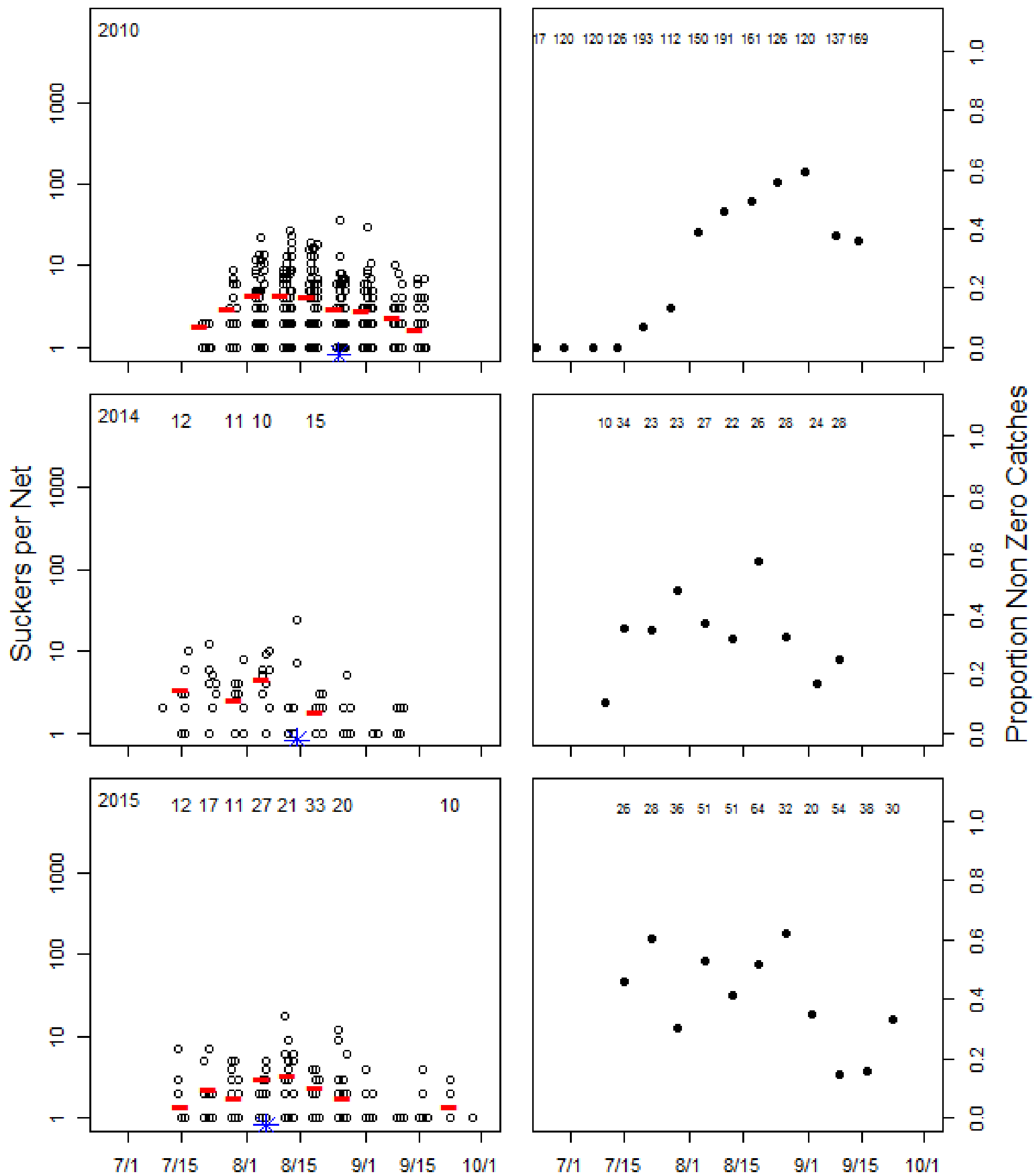


2001
10 32 46 39 51 41 26
21 55 58 77 79 75 67 61 12
2002
10 49 77 73 54 30 20 25 20 17 10
1918 3167 87 85 85 69 40 30 29 29 28 27
2003
26 22 18 14 15 11
27 27 28 28 27 27 27 26
Suckers per Net
Proportion Non Zero Catches
7/1 7/15 8/1 8/15 9/1 9/15 10/1



2004
28 17 56 72 51 68 37 27 15 13
28 103 110 108 110 106 108 54 58 38 39 30
2005
27 42 42 35 40 24 33 19
18 46 89 77 77 75 75 75 63 51 27 10
2006
16 22 25 27 30 29 26 2227
34 32 32 32 32 32 32 24 32
Suckers per Net
Proportion Non Zero Catches
7/1 7/15 8/1 8/15 9/1 9/15 10/1


2007
38 31 32 45 57 44 21 29 27
108 54 106 114 88 88 87 88 68 54 44 54
2008
12 16 36 18 17 24 33 31 26 11 20
281 213 284 288 287 288 103 78 73 69 60 71 30 34
2009
13 36 19 36 43 49 52 37 59 20
183 132 183 174 184 182 184 192 196 193 146 190 88
Suckers per Net
Proportion Non Zero Catches
7/1 7/15 8/1 8/15 9/1 9/15 10/1


2010
2014
12 11 10 15
2015
12 17 11 27 21 33 20 10
17 120 120 126 193 112 150 191 161 126 120 137 169
10 34 23 23 27 22 26 28 24 28
26 28 36 51 51 64 32 20 54 38 30
Suckers per Net
Proportion Non Zero Catches
7/1 7/15 8/1 8/15 9/1 9/15 10/1

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