

LARVAL SUCKER DISTRIBUTION AND CONDITION BEFORE AND AFTER LARGE-SCALE RESTORATION AT THE WILLIAMSON RIVER DELTA, UPPER KLAMATH LAKE, OREGON

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ABSTRACT.—We monitored the response of endangered Lost River sucker (*Deltistes luxatus*) larvae and shortnose sucker (*Chasmistes brevirostris*) larvae prior to, and during the first 2 seasons after, restoration of historic wetlands at the mouth of the Williamson River, Upper Klamath Lake, Oregon. In 2006 and 2007 (prerestoration) and in 2009 and 2010 (postrestoration), we used pop nets set in shallow-water (<1-m-deep) wetland habitats to document the distribution and condition of larval fish throughout the Williamson River Delta Preserve, as well as at a reference site along the Goose Bay shoreline in Upper Klamath Lake. From prerestoration to postrestoration, we witnessed significant declines in abundance of larval suckers at the reference site along the Goose Bay shoreline but no similarly significant declines in the 2 pilot restoration projects ($t = 9.92$, $df = 400$, $P < 0.0001$; $t = 0.8$, $df = 400$, $P = 0.3438$). In 2009 and 2010, larvae were documented using the newly restored portions of the delta. Larval suckers captured during pre- and postrestoration in the pilot areas and during postrestoration in the restored areas of the preserve were more likely to have fuller guts than larvae captured at the reference site along the Goose Bay shoreline. Throughout the study, length trends were more variable than gut fullness trends: larvae captured in pilot areas prior to restoration were larger than those captured after restoration, and larvae captured at the reference site postrestoration were on average larger than postrestoration sucker larvae from the restored and pilot areas.

RESUMEN.—Observamos la respuesta de las larvas de las especies de peces en peligro de extinción *Deltistes luxatus* y *Chasmistes brevirostris* antes de y durante las 2 primeras temporadas después de la restauración de los humedales históricos en la desembocadura del Río Williamson, Lago Upper Klamath, Oregón. En 2006 y 2007 (antes de la restauración) y 2009 y 2010 (después de la restauración), colocamos redes en hábitats de aguas poco profundas (<1 m de profundidad) en los humedales para documentar la distribución y condición de las larvas de peces a lo largo de la Reserva del Delta del Río Williamson; también, colocamos otras en un sitio de referencia sobre la costa de la Bahía Goose en el Lago Upper Klamath. En el sitio de referencia sobre la costa de la Bahía Goose, se observó un descenso significativo en la abundancia de las larvas de estos peces del tiempo previo a la restauración al tiempo posterior a la misma; sin embargo, no se observaron descensos significativos similares en 2 proyectos piloto de restauración ($t = 9.92$, $gl = 400$, $P < 0.0001$; $t = 0.8$, $gl = 400$, $P = 0.3438$). En los años 2009 y 2010, se documentaron larvas usando las zonas recientemente restauradas del Delta. Además, las larvas de estos peces que se capturaron tanto antes como después de la restauración en las áreas piloto y después de la restauración en las áreas restauradas de la reserva tendían a tener los estómagos más llenos, en comparación con las larvas capturadas en el sitio de referencia a lo largo de la costa de la Bahía Goose. Las tendencias en la longitud variaron más durante el estudio, ya que se capturaron larvas más grandes en las áreas piloto antes de la restauración, mientras que las larvas que se capturaron en los sitios de referencia después de la restauración eran en promedio más grandes que las larvas de las áreas restauradas y piloto.

Restoring hydrologic function to wetland ecosystems previously drained and filled for agriculture or development has become an important strategy in reducing nutrient loading in rivers and lakes, increasing ecosystem function, mitigating unavoidable damages to protected habitats, and maintaining or increasing native biodiversity (Falk 1990, Gearhart et al. 1995, Zedler 1996, Kaushal et al. 2008). Examining the impacts of wetland restoration projects on the natural fauna, especially on endangered species, is an important step in informing future restoration and management efforts and

creating an improved framework for understanding whether a project is ecologically beneficial (Mitsch and Wilson 1996, Palmer et al. 2005). In Upper Klamath Lake, Oregon, reduction of wetland habitat by roughly 65% during the last century (National Research Council 2004) through dredging and draining for agriculture was one factor that contributed to the decline and subsequent listing of 2 endangered suckers, the Lost River sucker (*Deltistes luxatus*) and the shortnose sucker (*Chasmistes brevirostris*; U.S. Fish and Wildlife Service 1993).

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Lost River sucker and shortnose sucker are both lake-dwelling catostomids that spawn in early spring, from about the middle of March through May. In Upper Klamath Lake, suckers spawn in the Williamson River and its largest tributary, the Sprague River, and at springs on the eastern shore (Buettner and Scopettone 1990, Janey et al. 2008). The 2 species, along with a third nonlisted catostomid, Klamath large-scale sucker (*Catostomus snyderi*), are endemic to the Upper Klamath Basin, but current population strongholds remain in Upper Klamath Lake and Clear Lake only (U.S. Fish and Wildlife Service 1993, Barry et al. 2009). These fish are highly fecund, iteroparous, and long-lived (up to 57 years; Scopettone and Vinyard 1991, Terwilliger et al. 2010). Larval suckers hatched in the Williamson and Sprague rivers emerge from gravels and immediately begin a downstream, nocturnal out-migration toward the lake that can take as little as one day (Cooperman and Markle 2004). Historically, wetlands surrounding Upper Klamath Lake were probably used by suckers for rearing (National Research Council 2004). Wetlands in Upper Klamath Lake, and the associated macrophytic vegetation, are important for protecting sucker larvae from non-native fathead minnow (*Pimephales promelas*) by providing vegetative cover and refuge (Markle and Duns Moor 2007); supporting ample growing opportunities resulting from warmer water temperatures during the out-migration period than occur in Upper Klamath Lake (Crandall et al. 2008, Wong et al. 2010); and retaining larvae, especially shortnose sucker, from the clockwise gyre that dominates surface currents in Upper Klamath Lake (Cheng et al. 2005) and thus delaying the emigration of larvae out of Upper Klamath Lake to downstream areas of low survivability (Lake Ewauna–Keno Impoundment; Markle et al. 2009).

The conversion of a vast expanse of wetland habitat at the mouth of the Williamson River to agriculture land in the 1940s with the resultant loss of larval- and juvenile-rearing habitat was cited as a major contributing factor in the listing of both sucker species in 1988 (U.S. Fish and Wildlife Service 1993). Restoring former wetlands at the Williamson River Delta (the delta) was a recovery strategy aimed at increasing nursery habitat for larval and juvenile suckers by hydrologically reconnecting approximately 2200 ha to Upper Klamath and Agency lakes and the Williamson River. Expanding the availability

of suitable rearing habitat in Upper Klamath Lake may equate to substantial advantages for larval suckers in growth and juvenile overwinter survival and eventually to better recruitment into adult stages, as small changes in early-life mortality can have a large impact on later-life history stages of highly fecund fish (Ricker 1981, Houde 2002, Harvey et al. 2006).

In 2000 and 2003, The Nature Conservancy and partners completed 2 small-scale (<75 ha), pilot wetland restoration projects (areas 1 and 5, Fig. 1) at the delta—Riverbend and South Marsh. Subsequent monitoring at these pilot restoration areas documented use by sucker larvae and validated the hypothesis that restoring habitat at the delta would benefit larval suckers by providing better growth and feeding conditions (Crandall et al. 2008). Hydrologic reconnection of the 2200-ha delta was completed by 2008 through the breaching of levees and the flooding of old agricultural fields at 2 larger areas (>1000 ha each) of the delta—Tulana and Goose Bay (areas 2 and 3, Fig. 1). The objective of this study was to gauge larval sucker response to large-scale wetland restoration at the delta by assessing habitat use (distribution and abundance) and condition (length and gut fullness) of larval suckers before and after restoration of Tulana and Goose Bay in pilot, restored, and reference wetlands.

Study Area

The study area consisted of 2 pilot restoration sites (Riverbend and South Marsh), 1 reference site (Goose Bay shoreline), and 2 restored sites (Tulana and Goose Bay)—all areas located in or adjacent to the delta. At Riverbend, roughly 11 ha of former deltaic wetlands approximately 5 km from the mouth of the Williamson River (area 1, Fig. 1) were flooded in 2000 by lowering approximately 1300 m of levee. The South Marsh pilot site is located at the southernmost boundary of the delta, adjacent to Upper Klamath Lake (area 5, Fig. 1). Restoration here was completed in 2003 when levees were breached in 3 locations and roughly 70 ha of deltaic wetlands were created. Vegetation composition at both sites is dominated by patches of hardstem bulrush (*Schoenoplectus acutus*) and creeping spikerush (*Eleocharis palustris*) interspersed among areas of open water. In Riverbend, willows (*Salix* spp.) provide cover during high river flows and high lake elevations.

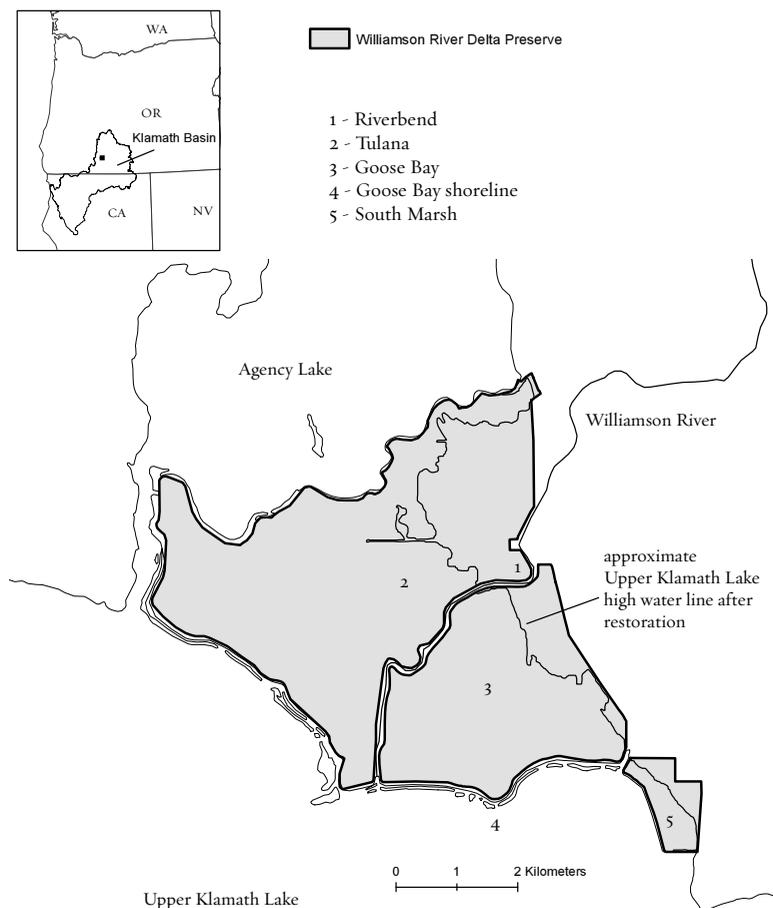


Fig. 1. Map of The Nature Conservancy's Williamson River Delta Preserve, showing 5 sampled locations (Riverbend, Tulana, Goose Bay, Goose Bay shoreline, and South Marsh), Upper Klamath Lake, Oregon. Areas 1 and 5 were pilot restoration projects where levees were breached; hydrology was restored in 2000 and 2003, respectively. Area 2 was restored in late 2007 and area 3 in late 2008. The reference site, area 4, is along Upper Klamath Lake's shoreline and contains some remnant wetland habitat.

The reference site was located along the Goose Bay shoreline, extending from the mouth of the Williamson River to the northwest corner of the South Marsh pilot site (area 4, Fig. 1). This reference site was chosen because previous research on larval sucker habitat use had focused on this area (Cooperman and Markle 2003, Crandall et al. 2008). This area is characterized by patchy bands of hardstem bulrush extending a maximum of 5 m from the shoreline and a thin margin of overhanging willow branches. Curly pondweed (*Potamogeton crispus*), an exotic, is also present in substantial patches, usually on the lakeside of the hardstem bulrush. Prior to restoration, this area was the first substantial habitat larvae encountered

upon entering Upper Klamath Lake after exiting the Williamson River.

Roughly 1200 ha of former deltaic habitat was hydrologically reconnected in Tulana through the explosive and mechanical removal of over 3 km of levees in the fall of 2007. Prior to flooding, Tulana had been managed as a wetland, which allowed for the establishment of some wetland vegetation, most notably large patches of hardstem bulrush (Elseroad et al. 2006). However, due to substantial subsidence, the western portion of Tulana is inundated year-round, resembling more lake-like conditions. The eastern half of Tulana is considerably shallower and therefore functions as a seasonally flooded emergent wetland. In the fall of 2008, 1000 ha in

Goose Bay was flooded after the mechanical removal of approximately 2 km of levee. Because this area was not managed as a wetland prior to restoration, there is much less perennial wetland-vegetation growth compared to Tulana, and currently much of the area is open water. However, Elseroad et al. (2010) reported that roughly 35% of the 1-m² plots sampled in 2009 in Goose Bay contained perennial emergent vegetation.

METHODS

Prerestoration sampling occurred during 2006 and 2007 at 3 different locations within the study area: 2 pilot restoration projects and 1 reference wetland site along the Goose Bay shoreline. Postrestoration sampling, occurring during 2009 and 2010, was conducted in both pilot and reference sites, as well as in the 2 restored wetland sites, Tulana and Goose Bay.

Larval sampling was conducted from mid-May until mid-July every other week in 2006 and 2007 and weekly in 2009 and 2010. Sampling points in the reference, pilot, and restored sites were randomly generated using Hawth's Tools version 3.2X in ArcMap. Additionally, in 2009 and 2010, we incorporated data from 4 fixed sites in the restored wetlands that were visited weekly and were sampled in conjunction with the development of a larval sucker transport model for the delta (Wood et al. in review). All points were located in water <1 m deep, because daytime larval nursery habitat is generally shallow and vegetated or in close proximity to aquatic vegetation (Buettnner and Scopettone 1990, Cooperman and Markle 2003).

Pop nets were set during daylight hours, replicated at both vegetated (>25% emergent or submerged aquatic vegetation) and open water sites (<25% macrophyte cover; Hendrixson 2008, Anderson et al. 2009). Two to 4 pop nets were set in close proximity to each other at each sampling point. These nets consisted of 2 PVC frames (1-inch-diameter pipe, 1.6 m × 1.6 m, area = 2.56 m²), one weighed down with rebar to serve as the lead line and the other wrapped in foam core to act as a float, with fine-mesh mosquito netting connecting the 2 frames. Nets lacked a top and bottom, enabling them to be set in vegetation. Each net was allowed to soak for a minimum of 30 minutes to ensure that the site recovered from disturbances associated with setting the net. After the net was remotely "popped" we measured water depth at the center

of the net, wind speed, UTM coordinates, and water temperature, dissolved oxygen, pH, and conductivity (Hydrolab Quanta[®]). Small aquarium dip nets were then used to collect the fish enclosed in the net, and each net was swept at least 5 times after the last fish was caught to ensure that no larvae were missed. Stalks of vegetation were occasionally removed from the net in order to facilitate fish capture. Samples were immediately stored in 95% ethanol.

A variable power (7X–30X) dissecting microscope was used to identify and measure dorsal and lateral melanophore patterns and morphological characteristics (D. Simon, Oregon State University, personal communication, 2004) of preserved larval fish. All suckers were grouped together for analysis because shortnose sucker and Klamath largescale sucker are indistinguishable at the larval stage (Markle et al. 2005). However, we assume that most of the larvae captured are either shortnose sucker or Lost River sucker due to the close proximity of the study site to Upper Klamath Lake, the most important habitat for these 2 species (Buettnner and Scopettone 1990), and to the rare presence of juvenile Klamath largescale sucker in proximity to the lake (Cooperman and Markle 2004, Markle et al. 2009). Based on visual estimation, larval suckers were qualitatively assigned to 1 of 5 gut-fullness levels as described by Cooperman and Markle (2004): 0% full, 25% full, 50% full, 75% full, and 100% full.

Statistical Methods

We examined variation in catch per unit effort (CPUE) and gut fullness from pre- (2006–2007) to postbreach (2009–2010) and among reference, pilot, and restored habitat types by fitting generalized linear mixed models (GLMM) with PROC GLIMMIX in SAS 9.2. The LaPlace method was used for obtaining maximum likelihood estimates of model parameters (Bolker et al. 2009). Month and site nested within habitat were included, as were habitat and year effects in the initial models and 2- and 3-way interactions. The simplest, best-fit model was selected by omitting nonsignificant effects and choosing the model with the lowest AIC_c value (Anderson 2008). Replicates (random sample points at each year) and subsamples nested within replicates were included as random effects.

CPUE data were analyzed with Poisson regression using a logarithmic link. The final model included year and the habitat × year,

TABLE 1. Number of pop nets set (P) and larval suckers captured (*n*) during pre- and postrestoration sampling along the Goose Bay shoreline (reference site), Riverbend and South Marsh (pilot sites), and Tulana and Goose Bay (restored sites) at the Williamson River Delta Preserve, Upper Klamath Lake, Oregon.

Site	Prerestoration				Postrestoration			
	2006		2007		2009		2010	
	P	<i>n</i>	P	<i>n</i>	P	<i>n</i>	P	<i>n</i>
Reference	66	1667	82	1093	64	59	80	74
Pilot	72	385	96	502	70	226	80	1053
Restored	—	—	—	—	142	688	160	409

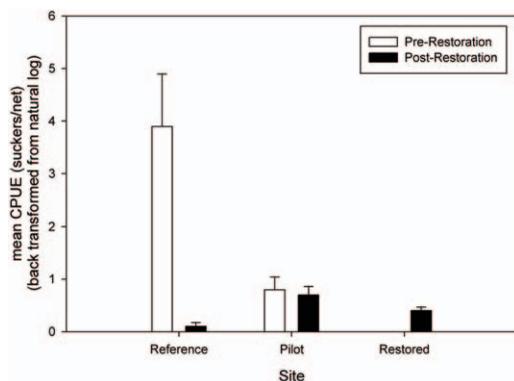


Fig. 2. Pre- and postrestoration mean larval sucker catch per unit effort (CPUE) and standard error bars in the 3 sampling areas at the Williamson River Delta Preserve, Upper Klamath Lake, Oregon. Goose Bay shoreline is the reference site; Riverbend and South Marsh are the pilot sites; and Tulana and Goose Bay are the restored sites. Geometric means were back-transformed from the natural log. Prerestoration sampling occurred in 2006 and 2007, and postrestoration sampling occurred in 2009 and 2010.

year \times month, and year \times site (habitat) interactions. Because the habitat \times year effect was highly significant, we used contrasts to compare CPUE (1) between pre- and postbreaching for pilot and reference habitats separately and (2) among habitats before and after breaching. We present back-transformed results for these contrasts, along with 95% confidence intervals.

In order to analyze pre- and postrestoration variation in standard length data across sites, oneway ANOVAs were used in JMP[®] version 8.0.1. The distribution of residuals did not show large departures from normality. Mean standard lengths along with standard errors are presented for comparisons of pre- and postrestoration size differences in pilot and reference habitats and postrestoration differences in restored and reference sites.

Gut fullness data were analyzed with logistic regression, assuming a binomial distribution

with a logit link. We collapsed gut fullness scores into 2 categories, high (≥ 75) and low (< 75), to obtain adequate counts per cell and avoid the assumption of proportional odds (i.e., parameter estimates are equal for all component binary models, such as 0 vs. 50, 50 vs. 75, etc.). The final model included habitat, year, and month. We used contrasts to compare the odds of having high versus low gut fullness at pre- versus postbreach averaged over habitat, and similarly to compare the odds of fuller guts among habitats averaged over time. For these comparisons, we report odds ratios along with 95% confidence intervals.

RESULTS

Annual trends in larval sucker catch varied substantially among habitats ($F_{6,400} = 8.44$, $P < 0.0001$; Table 1). Pre- to postrestoration changes were evident only in reference sites, where catch rate was 26.4 times greater (95% CI 13.85–50.74) prior to levee breaching ($t = 9.92$, $df = 400$, $P < 0.0001$; Fig. 2). Catch rate remained relatively constant from pre- to postbreach in pilot sites (mean ratio = 1.3, 95% CI 0.70–2.34; $t = 0.8$, $df = 400$, $P = 0.3438$). Over all available habitats, prerestoration CPUE was 1.8 suckers per net (95% CI 1.34–2.46), but postrestoration CPUE was only 0.3 suckers per net (95% CI 0.25–0.45). CPUE also varied significantly among habitats both before and after levee breaching. Before restoration, the CPUE was 4.7 times higher in reference sites (95% CI 2.73–8.24) than in pilot sites ($t = 5.54$, $df = 400$, $P < 0.0001$). Data collected in 2006 and 2007 indicated that large numbers of larvae occupied the reference site along the Goose Bay shoreline (area 4, Fig. 1). Conversely, during postrestoration sampling, pilot sites had 4.4 times more larvae (95% CI 2.28–8.33) per unit effort than the reference site ($t = 4.47$, $df = 400$, $P < 0.0001$; Fig. 2). Pilot sites also had 1.7 more

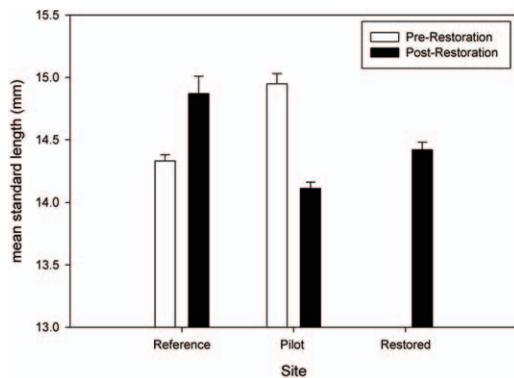


Fig. 3. Pre- and postrestoration larval sucker mean standard length (mm) and standard error bars in the 3 sampling areas at the Williamson River Delta Preserve, Upper Klamath Lake, Oregon. Goose Bay shoreline is the reference site; Riverbend and South Marsh are the pilot sites; and Tulana and Goose Bay are the restored sites. Prerestoration sampling occurred in 2006 and 2007, and postrestoration sampling occurred in 2009 and 2010.

fish (95% CI 1.01–2.83) than restored sites at Tulana and Goose Bay ($t = 2.02$, $df = 400$, $P < 0.0442$), while restored sites had 2.6 times more sucker larvae (95% CI 1.42–4.55) than reference sites ($t = 3.18$, $df = 400$, $P = 0.0016$).

Larval suckers in the pilot prerestoration areas (areas 1 and 5) were on average larger than fish captured prerestoration in the reference site along the Goose Bay shoreline; however, this trend did not exist postrestoration, when larvae captured in the reference site were larger than those captured in the 2 restored areas. Mean standard length of sucker larvae captured in 2006 and 2007 in pilot restoration areas (areas 1 and 5) was 14.95 mm (SE = 0.08) and only 14.33 mm (SE = 0.05) in the reference areas along the Goose Bay shoreline ($F = 43.0157$, $df = 2700$, $P < 0.0001$; Fig. 3). Conversely, in 2009 and 2010, mean standard length of suckers captured in the pilot areas was 14.11 mm (SE = 0.05) and 14.87 mm (SE = 0.14) in the reference wetlands along the Goose Bay shoreline ($F = 27.5077$, $df = 1410$, $P < 0.0001$). Mean standard length of larvae in the restored areas in 2009 and 2010 was 14.42 mm (SE = 0.06), significantly smaller than fish captured at the reference site during the same years ($F = 5.999$, $df = 1228$, $P = 0.0145$; Fig. 3).

Despite the size differences among habitats across years, variation in gut fullness among habitats was more consistent throughout the study. Location was a robust predictor of gut fullness

in larvae captured pre- and postrestoration, as larvae from pilot areas were more likely to have high gut fullness ($\geq 75\%$ full) than those in the reference or restored sites. The odds of high gut fullness in pilot sites were 3.3 times greater (95% CI 2.09–5.18) than those in reference sites ($t = 3.18$, $df = 162$, $P < 0.0001$) and 2.0 times greater (95% CI 1.12–3.38) than those in restored sites ($t = 2.40$, $df = 162$, $P = 0.0176$). The odds of fuller guts were not significantly different between restored and reference areas ($t = 2.40$, $df = 162$, $P = 0.1021$; mean difference = 1.7, 95% CI 0.90–3.16). In the pilot and restored areas, the probability of high gut fullness was 75% (95% CI 69%–81%) and 61% (95% CI 49%–73%), respectively, compared to only 48% (95% CI 39%–58%) at the reference site along Goose Bay.

DISCUSSION

Postrestoration catch per unit effort in the reference wetland along the Goose Bay shoreline was significantly reduced compared to catches at this site prior to restoration of the Tulana and Goose Bay portions of the delta ($P < 0.0001$). Reduced catches in 2009 and 2010 could be caused by numerous factors: (1) lower larval production in 2009 and 2010 than in 2006 and 2007 due to interannual variation in spawning, fertilization success, or egg and larval mortality through swim-up and drift down the Williamson River (Janey et al. 2008, Ellsworth et al. 2009, Cooperman et al. 2010); (2) increased larval dispersion at the delta leading to reduced capture probability; (3) interannual differences in the species composition of larvae migrating down the Williamson River or variability in potential larval habitat preferences which could lead to our sampling methods being biased toward either shortnose sucker or Lost River sucker; or (4) restoration of the 2 larger areas of the delta (Tulana and Goose Bay, areas 2 and 3), altering the typical outmigration pathway of larvae. Larval drift catches by the U.S. Geological Survey at Modoc Point Bridge, roughly 2 km upstream of Riverbend on the Williamson River, did not decrease from 2007 to 2009; but instead, catches in 2009 were roughly 3 times higher than catches in 2007 (Craig Ellsworth, U.S. Geological Survey, personal communication). Thus, the decline in catches at the reference site was not likely caused by a postrestoration decrease in larval sucker production.

Because the 2 pilot sites, Riverbend and South Marsh, did not experience discernible declines in catches from pre- to postrestoration, decreased abundance at the reference sites in 2009 and 2010 was most likely due to the reconfiguration of the landscape at the mouth of the Williamson River and not to interannual variability in larval production. Furthermore, larvae are no longer forced to enter Upper Klamath Lake at the mouth of the Williamson River and transport southeast along the Goose Bay shoreline but instead may exit the delta and enter the lake at numerous points (Tammy Wood, U.S. Geological Survey, personal communication). As a result of these new postrestoration dispersal pathways, accumulation of larvae along the Goose Bay shoreline is not as prolific as it was prior to 2008. Most importantly however, catches of larvae in restored wetlands in 2009 and 2010 indicate that these areas are successful in retaining larval suckers in habitat that is shallow, vegetated, or in close proximity to vegetation.

While larval suckers were significantly larger in the pilot areas than in the reference site prior to restoration, this trend was not witnessed postrestoration in 2009 and 2010. This finding differs from past studies focusing on pilot and reference wetland use by larval suckers (Crandall et al. 2008). Additionally, larger larvae were captured in the reference site than in the restored sites after restoration. Two logical explanations exist for this disparity: (1) the sample size of larval suckers captured in 2009 and 2010 at the reference site is small ($n = 133$) and might not accurately reflect the length composition of larval suckers at this site; and (2) a portion of the larvae captured at the reference site could have been retained in the pilot or restored wetlands for a period of time prior to being caught. The second is more plausible given that an ontogenetic transition in Lost River and shortnose sucker feeding occurs between 20 mm and 30 mm (Markle and Clauson 2006)—a shift that could be associated with a migration to more lacustrine habitats. Therefore, larger fish at the reference site could be a manifestation of the migration of suckers that were retained in the restored and pilot wetlands of Upper Klamath Lake during this ontogenetic shift.

Because of their strong advection properties, restored wetlands are able to retain larvae longer than sites in other areas of Upper Klamath Lake. Riverbend retained shortnose sucker larvae up

to 19 days longer than open water sites located in the lower Williamson River, and South Marsh only had a 42% 28-day emigration rate from the lake compared to a rate of 76% for sites located in the lake (Markle et al. 2009). If larvae are retained longer in restored wetlands and if emigration from the lake to areas of low survivability (Ewauna–Keno impoundment) is less likely, the opportunity for increased larval growth and survival is plausible in the restored and pilot restoration sites.

Better-fed larvae could result from a greater presence of wetland vegetation at the pilot and restored sites at the delta. Cooperman and Markle (2004) discovered that larger larvae with full guts were associated with emergent macrophytes rather than with submergent macrophytes or open water, suggesting that the recently created wetland habitat at the delta with its emergent macrophytes provides quality feeding areas for larval suckers. The greater amount of emergent macrophytic habitat available at the restored and pilot restoration sites compared to the reference sites could be manifested in the greater gut fullness levels in these areas in all 4 years of the study. Emergent macrophytes are important for foraging success and reduced predation (Cooperman and Markle 2004). Additionally, Chipps et al. (2006) found that undisturbed wetland sites, which generally have increased plant species richness and fewer exotic species, had greater chironomid abundance. Chironomidae are a main prey for larval and juvenile suckers (Markle and Clauson 2006).

Finally, warmer water temperatures could lead to larger larvae as warm water refugia are associated with increased larval development rates (Vondracek et al. 1989, Bestgen 2008). During May and June 2008 and 2009, we witnessed continuous *in situ* water temperatures in the transitional and emergent wetlands at the delta that were about 1–2 °C higher than in the Williamson River (Wong et al. 2010). Warmer water temperatures in the restored and pilot restoration sites could be positively impacting growth and feeding.

Although it is possible that reduced intraspecific competition resulted in better-fed larvae during a year of decreased larvae production, we do not suspect this to be a contributing factor to disparity in gut fullness among sites. Better-fed larvae were observed in 2006 and 2007 in the pilot wetlands, when larval catches were higher. Other researchers have not experienced

density-dependent effects (Cooperman and Markle 2004). Furthermore, prey availability does not seem to be a limiting factor for suckers in the system, as productivity in Upper Klamath Lake is very high (Markle and Clauson 2006). Regardless of the exact cause of better-fed larvae in the restored and pilot wetlands pre- and postrestoration, it is likely that these fish would have a greater chance of survival, since natural mortality is thought to be inversely proportional to body size and larger larvae are less vulnerable to predation (Miller et al. 1988, Bronte et al. 2006).

With dispersal of larvae into restored wetlands postrestoration and the association of better-fed larvae with the pilot and restored areas, increased young-of-year survival and subsequently greater recruitment into the adult spawning population could result. Whether or not the additional rearing habitat at the delta will equate to successful recruitment is yet to be seen; however, our results indicate that shallow water habitat (<1 m deep) in the restored areas of the delta provides improved rearing conditions for larval shortnose and Lost River suckers.

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LITERATURE CITED

- ANDERSON, D.R. 2008. Model based inference in the life sciences; a primer on evidence. Springer, New York, NY. 184 pp.
- ANDERSON, G.O., A.X. WILKENS, S.B. BURDICK, AND S.P. VANDERKOOI. 2009. Seasonal distribution and abundance of larval and juvenile Lost River and shortnose suckers in Hanks Marsh, Upper Klamath National Wildlife Refuge, Upper Klamath Lake, Oregon: 2007 Annual Report. U.S. Geological Survey Open-File Report 2009-1014. 36 pp.
- BARRY, P.M., E.C. JANNEY, D.A. HEWITT, B.S. HAYES, AND A.C. SCOTT. 2009. Population dynamics of adult Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) suckers in Clear Lake Reservoir, California, 2006-08. U.S. Geological Survey Open-File Report 2009-1109. 18 pp.
- BESTGEN, K.R. 2008. Effects of water temperature on growth of razorback sucker larvae. *Western North American Naturalist* 68:15-20.
- BOLKER, B.M., M.E. BROOKS, C.J. CLARK, S.W. GEANGE, J.R. POULSEN, M.H.H. STEVENS, AND J.S. WHITE. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127-135.
- BRONTE, C.R., P.C. MCKEE, M.E. HOLEY, M.L. TONEYS, AND P.E. HAVER. 2006. Relative survival of lake trout stocked at different sizes and quality in Lake Michigan. *Journal of Great Lakes Research* 32:386-394.
- BUETTNER, M., AND G. SCOPPETTONE. 1990. Life history and status of Catostomids in Upper Klamath Lake, Oregon. Oregon Department of Fish and Wildlife, Klamath Tribe, and National Fisheries Research Center, Reno, Nevada.
- CHENG, R., J. GARTNER, AND T. WOOD. 2005. Modeling and validation of wind-driven circulation in Upper Klamath Lake, Oregon. In: R. Walton, editor, Proceedings of the 2005 World Water and Environmental Resources Congress, 15-19 May 2005. EWRI/ASCE, Anchorage, AK.
- CHIPPS, S.R., D.E. HUBBARD, K.B. WERLIN, N.J. HAUGERUD, K.A. POWELL, J. THOMPSON, AND T. JOHNSON. 2006. Association between wetland disturbance and biological attributes in floodplain wetlands. *Wetlands* 26:497-508.
- COOPERMAN, M.S., AND D.F. MARKLE. 2003. Rapid out-migration of Lost River and shortnose sucker larvae from in-river spawning beds to in-lake rearing grounds. *Transactions of the American Fisheries Society* 132: 1138-1153.
- _____. 2004. Abundance, size, and feeding success of larval shortnose suckers and Lost River suckers from different habitats of the littoral zone of Upper Klamath Lake. *Environmental Biology of Fishes* 71:365-377.
- COOPERMAN, M.S., D.F. MARKLE, M. TERWILLIGER, AND D. SIMON. 2010. A production estimate approach to analyze habitat and weather effects on recruitment of two endangered freshwater fish. *Canadian Journal of Fisheries and Aquatic Science* 67:28-41.
- CRANDALL, J.C., L.B. BACH, N. RUDD, M. STERN, AND M. BARRY. 2008. Response of larval Lost River and shortnose suckers to wetland restoration at the Williamson River Delta, Oregon. *Transactions of the American Fisheries Society* 137:402-416.
- ELLSWORTH, C.M., T.J. TYLER, S.P. VANDERKOOI, AND D.F. MARKLE. 2009. Patterns of larval sucker emigration from the Sprague and lower Williamson Rivers of the Upper Klamath Basin, Oregon, prior to the removal of Chiloquin Dam—2006 annual report. U.S. Geological Survey Open-File Report 2009-1027. 32 pp.
- ELSEROAD, A., A. ALDOUS, C. STEVENS, AND L. BACH. 2006. Williamson River Delta Preserve wetland vegetation monitoring 2000-2004. The Nature Conservancy, Portland, OR. Available from: http://conserveonline.org/library/WRDP%20Vegetation%20monitoring%2000-04_final.doc/view.html
- ELSEROAD, A., N. RUDD, AND H. HENDRIXSON. 2010. Williamson River Delta Preserve vegetation monitoring: Goose Bay first-year post-breaching results. The Nature Conservancy, Portland, OR. Available from:

- <http://conserveonline.org/library/williamson-river-delta-preserve-vegetation-1/view.html>
- FALK, D.A. 1990. Restoration of endangered species: a strategy for conservation. Pages 328–334 in J.J. Berger, editor, *Environmental restoration: science and strategies for restoring the earth*. Island Press, Washington, DC.
- GEARHART, R.A., J.K. ANDERSON, M.G. FORBES, M. OSBURN, AND D. OROS. 1995. Watershed strategies for improving water quality: Upper Klamath Lake, Oregon. Volume 2. Humboldt State University, Arcata, CA.
- HARVEY, C.J., N. TOLMIERI, AND P.S. LEVIN. 2006. Changes in body size, abundance, and energy allocation in rockfish assemblages of the Northeast Pacific. *Ecological Applications* 16:1502–1515.
- HENDRIXSON, H. 2008. Non-native fish species and Lost River and shortnose suckers use of restoration and undisturbed wetlands at the Williamson River Delta: Final report for activities conducted in 2006 and 2007. Submitted to USFWS Ecosystem Restoration Office, 2008.
- HOUDE, E.D. 2002. Mortality. Pages 67–87 in L.A. Fuiman and R.G. Werner, editors, *Fishery science: the unique contributions of early life stages*. Blackwell Publishing Co., Osney Mead, Oxford, United Kingdom.
- JANEY, E.C., R.S. SHIVELY, B.S. HAYES, P.M. BARRY, AND D. PERKINS. 2008. Demographic analysis of Lost River sucker and shorinose sucker populations in Upper Klamath Lake, Oregon. *Transactions of the American Fisheries Society* 137:1812–1824.
- KAUSHAL, S.S., P.M. GROFFMAN, P.M. MAYER, E. STRIZ, AND A.J. GOLD. 2008. Effects of stream restoration on denitrification in an urbanizing watershed. *Ecological Applications* 18:789–804.
- MARKLE, D.F., AND K. CLAUSON. 2006. Ontogenetic and habitat-related changes in diet of late larval and juvenile suckers (Catostomidae) in Upper Klamath Lake, Oregon. *Western North American Naturalist* 66:492–501.
- MARKLE, D.F., M.R. CAVALLUZZI, AND D.C. SIMON. 2005. Morphology and taxonomy of Klamath Basin suckers (Catostomidae). *Western North American Naturalist* 65:473–489.
- MARKLE, D.F., AND L.K. DUNSMOOR. 2007. Effects of habitat volume and fathead minnow introduction on larval survival of two endangered sucker species in Upper Klamath Lake, Oregon. *Transactions of the American Fisheries Society* 136:567–579.
- MARKLE, D.F., S.A. REITHEL, J. CRANDALL, T. WOOD, T.J. TYLER, M. TERWILLIGER, AND D.C. SIMON. 2009. Larval fish transport and retention and the importance of location for juvenile fish recruitment in Upper Klamath Lake, Oregon. *Transactions of the American Fisheries Society* 138:328–347.
- MILLER, T.J., L.B. CROWDER, J.A. RICE, AND E.A. MARSCHALL. 1988. Larval size and recruitment mechanism in fishes: towards a conceptual framework. *Canadian Journal of Fisheries Aquatic Science* 45:1657–1670.
- MITSCH, W.J., AND R.F. WILSON. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. *Ecological Applications* 6:77–83.
- NATIONAL RESEARCH COUNCIL. 2004. *Endangered and threatened fishes in the Klamath River Basin*. National Academies Press, Washington, DC.
- PALMER, M.A., E.S. BERNHARDT, J.D. ALLAN, P.S. LAKE, G. ALEXANDER, S. BROOKS, J. CARR, S. CLAYTON, C.N. DAHM, J. FOLLSTAD SHAH, ET AL. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* 42:208–217.
- RICKER, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1636–1656.
- SCOPPETTONE, G.G., AND G. VINYARD. 1991. Life history and management of four endangered lacustrine suckers. Pages 359–377 in W.L. Minckley and J.E. Deacon, editors, *Battle against extinction: native fish management in the American West*. University of Arizona Press, Tucson, AZ.
- TERWILLIGER, M.D., T. REECE, AND D.F. MARKLE. 2010. Historic and recent age structure and growth of endangered Lost River and shortnose suckers in Upper Klamath Lake, Oregon. *Environmental Biology of Fishes* 89:239–252.
- [USFWS] U.S. FISH AND WILDLIFE SERVICE. 1993. *Lost River (Deltistes luxatus) and Shortnose (Chasmistes brevirostris) Sucker Recovery Plan*. U.S. Fish and Wildlife Service, Portland, OR. 108 pp.
- VONDRACEK, B., J.J. CECH, AND R.K. BUDDINGTON. 1989. Growth, growth efficiency, and assimilation efficiency of the Tahoe sucker in cyclic and constant temperature. *Environmental Biology of Fishes* 24:151–156.
- WONG, S., H. HENDRIXSON, AND C. DOEHRING. 2010. Post-restoration water quality conditions at the Williamson River Delta, Upper Klamath Basin, Oregon: 2007–2009. The Nature Conservancy. Available from: <http://conserveonline.org/library/post-restoration-water-quality-conditions-at-the-/@/view.html>
- ZEDLER, J.B. 1996. Ecological issues in wetland mitigation: an introduction to the forum. *Ecological Applications* 6:33–37.

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