

Response of Larval Lost River and Shortnose Suckers to Wetland Restoration at the Williamson River Delta, Oregon

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Abstract.—Population declines of the federally endangered Lost River sucker *Deltistes luxatus* and shortnose sucker *Chasmistes brevirostris* have been linked to several factors, including the loss of larval nursery habitat associated with lake fringe and riparian wetlands. Restoration of deltaic wetlands in the Williamson River delta, Oregon, is regarded as one strategy that may increase larval nursery habitat and survival. This study examined larval sucker presence, growth, development, and feeding in pilot restoration wetlands at the Williamson River delta to determine whether wetland restoration provides habitat that is conducive to larval rearing. We compared results from the restoration wetlands to those in riparian and lacustrine wetland reference sites during 2003 and 2004. The seasonal timing of larval Lost River and shortnose suckers captured in the restoration wetlands was similar to that in reference sites during the April–July study period. The frequency of occurrence in the restoration wetlands was comparable to that in reference sites; larvae were collected in 90–100% of transects during periods of peak abundance. These data are an indication that restored wetlands provide critical habitat for larval suckers. Larval sucker length, developmental phase, and gut fullness in the restoration wetlands indicated that larvae were feeding, growing, and hence, rearing, in those areas. Water temperatures in the restoration wetlands were 3–4°C higher than those in reference sites, especially early in the season, which may have increased the restoration sites' suitability for larval rearing compared with reference sites. Our results indicate that initial wetland restoration efforts at the Williamson River delta have successfully created suitable rearing habitat for larval Lost River and shortnose suckers and suggest that further large-scale wetland restoration in the delta will increase larval rearing opportunities and contribute to the recovery of these two endangered species.

Freshwater fish are becoming threatened or extinct at an alarming rate, both regionally and worldwide (Moyle and Leidy 1992; Richter et al. 1997; Ricciardi and Rasmussen 1999). A common cause of these declines is the loss of critical habitat for one or more life stages (Poff and Allan 1997; Fuiman and Werner 2002). In some cases, there may be so little habitat remaining that habitat restoration becomes essential to the recovery of the at-risk species (Allan and Flecker 1993; Cook et al. 2005). However, habitat restoration is often costly and potential benefits are, at times, uncertain. To determine how well the restored habitat functions, it is practical to examine the abundance and condition of the target species occupying the restored habitat.

In this study, we used field observations to quantify larval responses of two endangered catostomids, the

Lost River sucker *Deltistes luxatus* and shortnose sucker *Chasmistes brevirostris*, to wetland restoration. Both species are large, long-lived, highly fecund lacustrine suckers that are endemic to the upper Klamath River basin of Oregon and California (Scopetone and Vinyard 1991; Moyle 2002). Historically, these species were abundant throughout their range (Cope 1879; Gilbert 1898; Coots 1965), but over the past century they have declined to such a degree as to warrant listing as endangered species (Andreassen 1975; Bienz and Ziller 1987; USFWS 1988). Several factors—including overfishing, degraded water quality, water diversions, competition with and predation by exotic species, and habitat loss and modification—have been linked to these declines (USFWS 1988, 1993, 2001).

The largest remaining adult populations of these species reside in Upper Klamath Lake, Oregon. While some individuals spawn at in-lake springs, most migrate upstream to spawn in the Williamson River, Oregon, and its largest tributary, the Sprague River

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(USFWS 1993; Markle and Cooperman 2002). Currently, larval suckers rapidly emigrate from riverine natal grounds and exhibit only limited in-river growth (Buettner and Scopettone 1990; Klamath Tribes Natural Resources Department 1996; Cooperman and Markle 2003). Thus, they are believed to use the channelized lower Williamson River only as a transit corridor to access nursery habitat located in the vegetated littoral zones of Upper Klamath Lake (Cooperman and Markle 2003, 2004). Presumably, larval suckers would have historically used the extensive (~2,600-ha) riparian, slough, and emergent-marsh wetlands associated with the Williamson River delta (WRD) for rearing. However, alteration of the WRD has virtually eliminated these habitats.

Recruitment and larval survival in Lost River and shortnose suckers is highly variable (Simon et al. 2000; Markle and Duns Moor 2007), and there have been extensive periods when it was low (Coleman et al. 1988; Markle and Cooperman 2002), possibly due to excessively high larval mortality associated with the loss of emergent-wetland nursery habitat (NRC 2004). Restoration of riparian and lake fringe wetlands is recognized as an important strategy that may improve larval survival, thereby potentially aiding in the recovery of Lost River and shortnose sucker populations (USFWS 1993, 2001; IMST 2003; NRC 2004).

In 2000 and 2003, The Nature Conservancy and its partners completed two small-scale (<75-ha), pilot wetland restoration projects at the WRD (USDA 2005); these projects were aimed at increasing nursery habitat for larval suckers while providing baseline information for a proposed large-scale wetland restoration effort at the WRD. Preliminary fish surveys in the pilot restoration wetlands revealed that larval suckers were present (J.D.C., unpublished data), but the seasonal timing and extent of their presence and condition remained unclear.

We investigated the response to these restoration wetlands by larval Lost River and shortnose suckers to determine whether wetland restoration effectively provides larval nursery habitat. Specific study objectives were to (1) assess the seasonal timing and relative abundance of larval suckers in the restoration wetlands and (2) determine whether larvae are rearing (i.e., feeding and growing) within the restoration wetlands. To understand the potential benefits of these pilot efforts and future large-scale wetland restoration efforts at the WRD, larval growth and feeding and environmental conditions (specifically, water temperature) in the restoration wetlands were compared with those in adjacent reference sites in Upper Klamath Lake and the lower Williamson River.

Study Area

This study was conducted at The Nature Conservancy's 3,035-ha Williamson River Delta Preserve (WRDP), which encompasses the majority of area occupied historically by the WRD, located along the terminal 6.4 km of the Williamson River and adjacent to Upper Klamath and Agency lakes (Figure 1). Prior to the early 20th century, the WRD was an expansive, diverse deltaic marsh ecosystem that formed where the Williamson River entered Upper Klamath Lake (Gearheart et al. 1997). Between the 1920s and 1950s, the WRD was diked with more than 40 km of levees and drained for agriculture, while the lower 6 km of the Williamson River was straightened and channelized (Matthews 1999). The levees isolated the WRD from the surrounding waters, resulting in the loss of approximately 2,600 ha of emergent-marsh habitat. The modifications to the river and surrounding delta floodplain also altered nearshore topography, changed distribution of vegetation, and significantly reduced the extent of riparian and lake fringe wetlands that were exterior to the levees (Gearheart et al. 1997; Duns Moor et al. 2000). Combined, these modifications probably reduced the extent and availability of larval sucker nursery habitat at the WRD.

The study area consisted of two pilot restoration sites (Riverbend and South Marsh) and two reference wetland sites (Upper Klamath Lake and Williamson River) at the WRDP. Restoration at the Riverbend site occurred in the fall of 2000 at an interior point bar on the north bank of the Williamson River, 5 km upstream from the mouth (Figure 1). Approximately 1,300 m of levee was mechanically leveled at this location, reconnecting 11 ha of former deltaic wetland with the Williamson River after over 50 years of isolation. The South Marsh restoration site is located near the southern extent of the historical WRD and is adjacent to Upper Klamath Lake. Restoration began in 1997, when the area was allowed to flood via seepage through the levees. In the fall of 2003, the levees were breached in two locations, reconnecting 70 ha to Upper Klamath Lake. In general, vegetative composition in both Riverbend and South Marsh after restoration was similar to that at reference sites and consisted primarily of mixed emergent and woody species, including hardstem bulrush *Scirpus acutus*, needle spikerush *Eleocharis acicularis*, and common spikerush *E. palustris*, and willows *Salix* spp.

The two reference sites (Figure 1) were selected to coincide with larval sucker habitats studied prior to restoration at the WRD (Klamath Tribes Natural Resources Department 1996; Cooperman and Markle 2003). Both reference sites had been previously

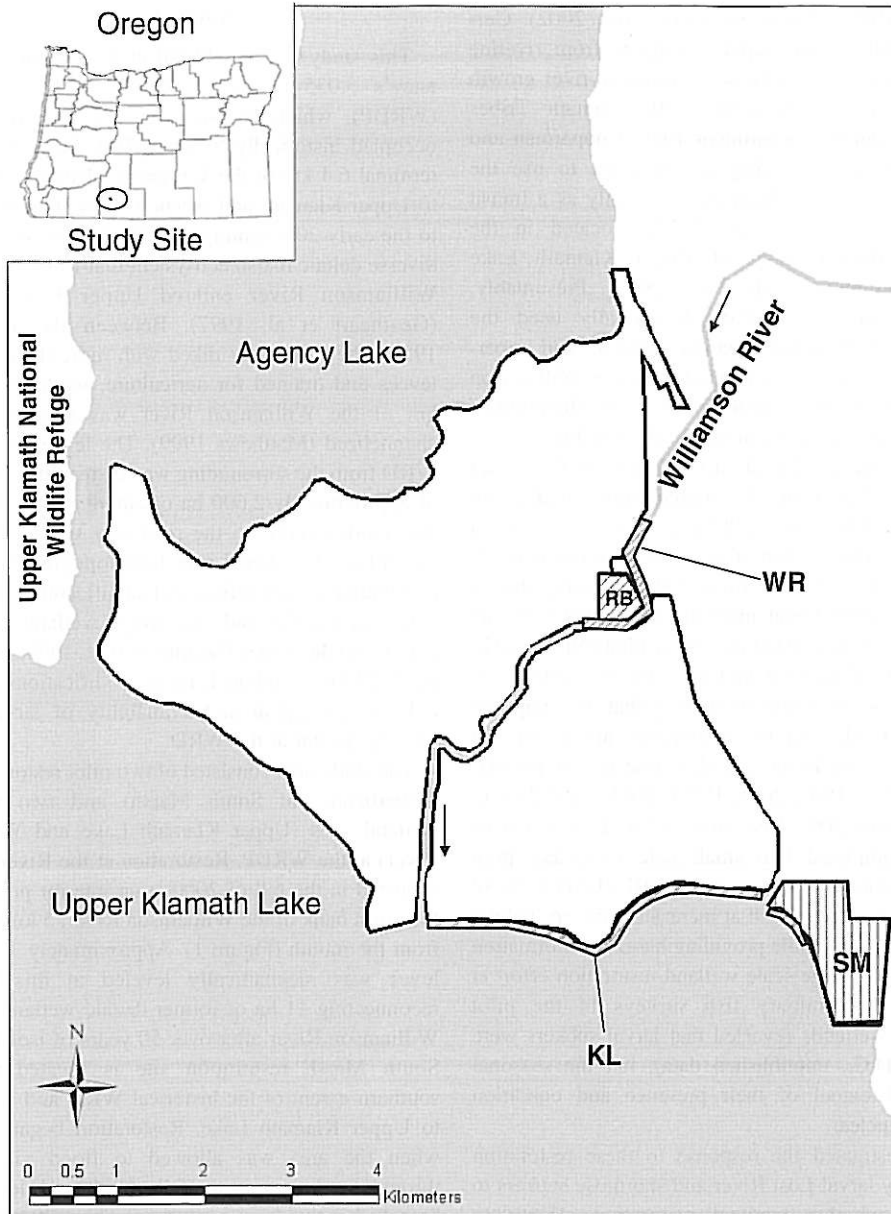


FIGURE 1.—Map of the Williamson River Delta Preserve, Oregon, study area, showing the Riverbend (RB) and South Marsh (SM) restoration wetlands and Upper Klamath Lake (KL) and Williamson River (WR) reference sites, where larval suckers were sampled in 2003 and 2004. Arrows denote direction of flow in the river.

modified during levee construction and channelization activities at the WRD, but since that time they have existed in a relatively undisturbed state. The Upper Klamath Lake site included the lake's shoreline extending from 200 m east of the Williamson River mouth to the northwest corner of South Marsh. This area has been identified as primary nursery habitat for larval suckers spawned in the Williamson and Sprague

streams (Markle and Cooperman 2002). It is vegetated with small stands of hardstem bulrush, giant bur-reed *Sparganium eurycarpum*, and swamp smartweed *Polygonum coccineum* interspersed with willows and areas devoid of vegetation (Dunsmoor et al. 2000; Cooperman and Markle 2004). The Williamson River site included a section proximate to Riverbend in an area previously described as transitory (nonrearing) habitat

for larval suckers (Cooperman and Markle 2003, 2004). Vegetation primarily included willows, spikerushes, and reed canarygrass *Phalaris arundinacea*.

Methods

Larval suckers were sampled from the two restoration and two reference sites and were evaluated for seasonal presence and relative abundance, growth, and feeding. In conjunction with the larval sampling, water temperature measurements were collected in all four sites throughout the study period.

Larval sampling.—Larval suckers were sampled at Riverbend, Upper Klamath Lake, and Williamson River in 2003 and 2004. In 2004, we also sampled the newly restored South Marsh. We restricted sampling to vegetated nearshore zones (<1 m deep) in each site because previous research on larval Lost River and shortnose suckers indicated that these fish inhabit vegetated shoreline areas during the day (Buettner and Scopetone 1990; Klamath Tribes Natural Resources Department 1996; Cooperman and Markle 2003).

Larval suckers were sampled with time-restricted strip (belt) transects similar to those used in reef fish surveys (Brock 1954; Terry and Stephens 1976; Thresher and Gunn 1986). At each site, we randomly selected five to eight transect starting points from a baseline, excluding reaches void of vegetation. Transects ran parallel to the shoreline for 15 min. Observers wearing polarized glasses moved at a constant pace and used fine-mesh aquarium dip nets to collect all larvae observed at depths less than 20 cm within 0.5 m on both sides of the transect. Captured larvae were quickly transferred to a 1-L plastic bucket filled with 250–400 mL of water and were held there for the duration of the sampling period. Upon completion of the sample, larvae were sieved back through the dip net, rinsed into 250-mL jars with a spray bottle, and fixed in a 7% solution of formalin. Within 96 h, larvae were sorted from collected debris, transferred to 10-mL glass vials, labeled, and preserved in a 70% solution of ethanol.

All portions of the study area are influenced by Upper Klamath Lake water surface elevation, and during each year declining water elevation caused desiccation of the transects. Thus, it was impossible to sample the same transect repeatedly over the course of the study period and transect locations were moved to follow the receding shoreline.

Several factors can affect the accuracy of visual surveys, including water clarity and current, ambient light level, substrate, fish behavior, and observer bias (Sale and Sharp 1983; Watson et al. 1995; Thresher and Gunn 1986). However, if conducted in a consistent fashion, strip transects can yield comparable estimates

of relative abundance (Sale and Sharp 1983; Stephens et al. 2006). We took several measures to minimize sampling bias. All transects were located in slack water with no discernable water current and were only conducted in daylight (0800–1600 hours) under qualitatively assessed clear and calm water conditions. To minimize among-collector differences in fish detection and capture abilities, we restricted the number of collectors to one in 2003 and two in 2004. We did not observe ontogenetic changes in larval behavior or habitat use during our study; therefore, we assume that all larval suckers were sampled equally. Lost River and shortnose sucker larvae are neustonic, and we believe they were effectively sampled with dip nets to a depth of 20 cm. If water depth at a sampling location was greater than 20 cm, we limited sampling to the upper 20 cm of the water column and thus may have missed any larvae inhabiting deeper portions of the water column.

Larval sampling began within 1 week after sucker larvae were visually observed in at least two sites. All sites were sampled once every 7–12 d throughout both years. During each sampling interval, all transects were sampled within a 3-d period; however, poor water visibility and field logistics prevented the sampling of all transects during each interval. Sampling was terminated when larval catch at all sites declined to levels near zero.

All sucker larvae were viewed under a variable-power (7–30×) dissecting microscope and assessed for (1) standard length (SL; nearest 0.1 mm), (2) developmental phase, and (3) gut fullness. Although the Klamath largescale sucker *Catostomus snyderi* co-occurs with Lost River and shortnose suckers, we assumed that the majority of captured larvae were the latter two species because (1) the study area is proximate to Upper Klamath Lake, a primary habitat for juvenile and adult Lost River and shortnose suckers (Buettner and Scopetone 1990; Markle and Cooperman 2002; Moyle 2002) and (2) juvenile Klamath largescale suckers are extremely rare in the vicinity of Upper Klamath Lake (Simon et al. 2000; Cooperman and Markle 2004). Therefore, larval Klamath largescale suckers may have been included in the samples, but if so they probably comprised a very small percentage of the overall sample.

We assumed that any differences in species autecology were negligible relative to our study objectives, and we analyzed all larvae as a single group for each site. Due to a behavioral shift to a more benthic orientation (Simon et al. 1996), increased ability to avoid capture in dip nets (J.D.C., personal observation), and rarity, all juveniles and 20-mm or larger larvae were excluded from analysis (2003: $N = 9$;

2004; $N = 39$). To increase evenness of sampling effort and larval catch across sites and time, we grouped sampling effort for each year into four roughly equal time intervals. A time interval contained three rounds of sampling; when combined, the four time intervals encompassed the majority of the annual study period (~14 weeks). We analyzed means per transect location and time interval for determining site differences in larval capture rate and length.

Seasonal presence and relative abundance.—The seasonal presence of larval suckers within sites was determined by examining the frequency of larval occurrence across time intervals. Occurrence was defined as the collection of at least one larval sucker during a sample. Due to the small sample sizes at sites during several time intervals, data analysis was limited to a visual inspection of the data.

Larval catch rate (catch per unit effort [CPUE]), defined as the number of larvae captured per minute, was compared across sites and time intervals in each year to investigate the relative abundance of sucker larvae in the restoration and reference sites. We used PROC MIXED in the Statistical Analysis System (SAS) for Windows (SAS Institute 2004) to run a mixed-model analysis of variance (ANOVA) on $\log_e(x + 0.01)$ transformed CPUE for examining the main effects of site (Upper Klamath Lake, Williamson River, Riverbend, or South Marsh) and time interval (1–4) and the interaction between site and time interval. Transects with zero catches of sucker larvae were included, and transects nested within sites were included in the model as a random effect. Levene's test and graphical analysis of studentized residuals indicated heterogeneous variances across sites or time intervals even for log-transformed data. We therefore fitted models that allowed unequal variances, and we used the KR option for adjusting degrees of freedom to account for complex covariances and correlated errors (Littell et al. 2006). Site and time interval interacted in their effects on CPUE in 2003, leading us to compare sites within each time interval. We used the SIMULATE adjustment in the LSMEANS statement for simple and main effect comparisons. This procedure is recommended over Tukey's test for unbalanced designs with unequal variances (Edwards and Berry 1987). The control-variate-adjustment technique (CVADJUST) was specified to obtain accurate estimates of the q -distribution.

Larval rearing.—The degree to which sucker larvae reared (i.e., fed and grew) within restoration and reference sites was assessed by examining SL, developmental phase, and gut fullness. Developmental phase was categorized using the Snyder and Muth (1990) protocols as modified by Cooperman and

Markle (2003). With this protocol, six phase designations are defined based on the degree and progression of fin formation, including (from least to most developmentally advanced) preflexion protolarvae, flexion mesolarvae (divided into early, middle, and late), postflexion mesolarvae, and metalarvae. Gut fullness was categorized by estimating the percent of visible material occupying the digestive tract, and categories followed those of Cooperman and Markle (2003). Categories included empty (no visible material) and low (>0–20%), medium (21–50%), medium-high (51–75%), and high fullness (>75%). Larvae that were damaged or that lacked visible guts were excluded from the analysis. For all sites, gut fullness was not correlated to time of day (2003: Pearson's product-moment correlation coefficient $r = 0.128$, $N = 131$, $P = 0.144$; 2004: $r = 0.138$, $N = 167$, $P = 0.076$), so data were grouped for all transects within sites.

We used a mixed-model ANOVA to determine how larval length varied across sites and time intervals for each year. The model was the same as that for CPUE and allowed for unequal variances over time based on analysis of residuals. Results obtained with log and square-root transformations did not differ from those obtained with untransformed data, so we report the latter for ease of interpretation. The site \times time interaction was significant in both years, so we used the SIMULATE adjustment in SAS to compare site means within each time interval. Lengths from Riverbend and Williamson River at time interval 4 in 2003 were analyzed separately since almost no fish were collected from upper Klamath Lake during this sampling interval. The ANOVA model for this analysis allowed variances to differ across sites.

We used hierarchical log-linear modeling to test for dependence between developmental phase or gut fullness and site or time interval. For fitting the models, the iterative proportional fitting algorithm in PROC CATMOD of SAS was used (SAS Institute 2004). We applied the backward selection procedure as demonstrated by Quinn and Keough (2002), first comparing the saturated model to one without the three-way interaction. Our reduced model had a significantly poorer fit for both developmental phase and gut fullness in both years, so we applied two-way contingency table analysis within each time interval to examine how dependence between either developmental phase or gut fullness and site changed over time. We report deviations from expected, percent of site total, and cell chi-square values to illustrate the nature of these three-way interactions. Under the null model of complete independence, expected values are the product of the probabilities of being at a particular site and in a particular developmental phase or gut

TABLE 1.—Year, time interval, range of sampling dates, number of transect locations (*L*), total number of transect visits (*V*), frequency of occurrence of Lost River and shortnose sucker larvae (%), and numbers of sucker larvae captured in dip-nets (*N*) at four sites in the Williamson River Delta Preserve, Oregon, 2003 and 2004. Asterisks denote restored wetlands.

Year	Time interval	Dates (day of year)	Upper Klamath Lake				Riverbend*				Williamson River				South Marsh*			
			<i>L</i>	<i>V</i>	%	<i>N</i>	<i>L</i>	<i>V</i>	%	<i>N</i>	<i>L</i>	<i>V</i>	%	<i>N</i>	<i>L</i>	<i>V</i>	%	<i>N</i>
2003	1	30 Apr–14 May (120–134)	5	5	100	229	6	15	100	567	6	16	88	74				
	2	26 May–11 Jun (146–162)	5	11	100	712	10	19	100	1,602	6	12	100	1,539				
	3	18 Jun–2 Jul (169–183)	5	13	83	71	10	17	88	827	6	14	100	1,235				
	4	15 Jul–5 Aug (196–218)	4	7	14	1	8	17	82	70	6	14	64	70				
		Total		19	36		1,013	34	68		3,061	24	56		2,900			
2004	1	27 Apr–13 May (118–134)	4	10	100	72	6	16	100	461	5	13	92	256	4	7	86	38
	2	19 May–2 Jun (140–154)	5	14	85	326	6	18	100	2,416	5	15	100	894	4	12	90	476
	3	7–24 Jun (159–176)	4	11	82	179	5	13	100	1,255	5	13	100	2,365	4	9	66	184
	4	28 Jun–13 Jul (180–195)	4	11	55	70	6	13	69	708	5	13	100	673	4	10	20	12
		Total		17	46		647	23	60		4,840	20	54		4,188	16	38	

fullness category (i.e., site total \times [category total/grand total]). We had insufficient data for the Upper Klamath Lake site at time interval 4 in 2003, so we compared frequency of developmental phase and gut fullness between Riverbend and Williamson River using a separate two-way contingency table analysis.

Temperature.—Nearshore water temperature was measured during late April through early August in both 2003 and 2004. A submersible temperature logger (Onset Stowaway; Onset Computer Corporation, Bourne, Massachusetts) programmed to record temperature every 30 min was located at the starting point of a randomly selected transect in each site. Loggers were secured to 6.35-mm rebar tripods and deployed in open water within 2 m of the shore at areas deep enough to measure temperature approximately 5 cm below the water's surface. As water surface elevation declined during the study period, loggers were visually inspected every 7–10 d; if necessary, they were moved to deeper areas to keep them consistently 5 cm under the water surface. If a logger became stranded above the water surface between inspections, an estimation of days stranded was made and the data for this time period were omitted from analysis. We used the daily mean temperature in each site to examine seasonal trends.

Results

Seasonal Presence and Relative Abundance

Frequency of occurrence within restoration and reference sites was similar in time intervals 1 and 2 in both years, and sucker larvae were present in more than 85% of all transects (Table 1). Frequency of occurrence remained above 80% for all sites in time interval 3 except South Marsh in 2004, when larvae were captured in only six of nine transects (66%). By time interval 4, frequency of occurrence declined to 14–55% in Upper Klamath Lake and South Marsh and remained between 69% and 100% in Riverbend and Williamson River. Larvae were still present in all Williamson River

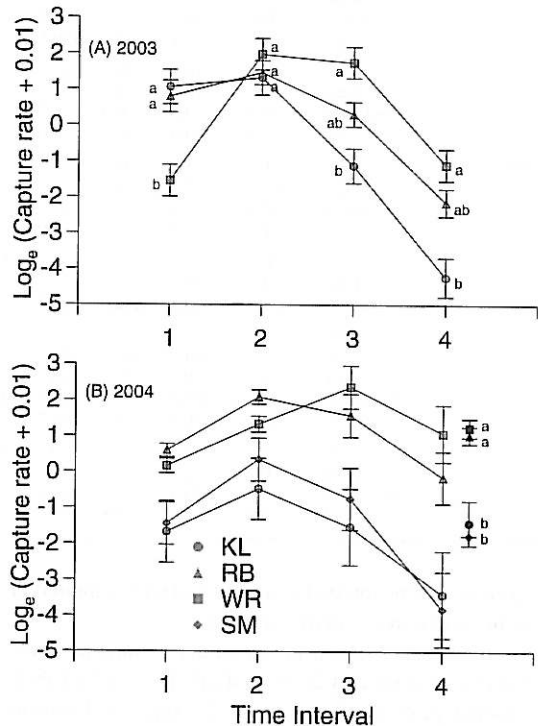


FIGURE 2.—Least-squares mean (\pm SE) catch per unit effort (capture rate; $\log_e[x + 0.01]$) of larval Lost River and shortnose suckers at wetland restoration sites (Riverbend [RB] and South Marsh [SM]) and reference sites (Upper Klamath Lake [KL] and Williamson River [WR]) in the Williamson River delta, Oregon, during (A) 2003 (site means were compared within each of four time intervals [defined in text] because of a significant site \times time interaction) and (B) 2004 (site means were compared across all time intervals [solid black symbols]). South Marsh was not sampled in 2003. Means followed by the same letter were not different at the 0.05 level.

TABLE 2.—Larval Lost River and shortnose suckers cross-classified by developmental stage, site, and time interval at two restored sites (Riverband [RB] and South Marsh [SM]) and two reference sites (Williamson River [WR] and Upper Klamath Lake [KL]) at the Williamson River Delta Preserve, 2003 and 2004. Number (*N*) and percent of larvae in each stage are presented along with deviation from expected and cell chi-square values for two-way contingency table analyses by time interval. South Marsh was not sampled in 2003. Only RB and WR were compared at interval 4 in 2003 since almost no larvae were encountered in KL. Asterisks by time intervals denote significant chi-square ($P < 0.001$). Test of independence for interval 4 in 2003 was not significant ($\chi^2 = 1.19$; $df = 4$, $P = 0.8791$). Developmental stages are: (1) preflexion protolarvae, (2) early flexion mesolarvae, (3) midflexion mesolarvae, (4) late-flexion mesolarvae, (5) postflexion mesolarvae, and (6) metalarvae.

Year	Time interval	Variable	RB larval stage						WR larval stage					
			1	2	3	4	5	6	1	2	3	4	5	6
2003	1*	<i>N</i>	120	244	133	60	8	0	45	29	0	0	0	0
		% total	21	43	24	11	1	0	61	39	0	0	0	0
		Deviation	-24.2	-24.8	26.0	20.2	2.8	0.0	26.1	-6.2	-14.0	-5.2	-0.7	0.0
		χ^2	4.1	2.3	6.3	10.3	1.5	0.0	36.1	1.1	14.0	5.2	0.7	0.0
	2*	<i>N</i>	276	763	230	265	52	1	711	788	20	14	3	0
		% total	17	48	14	17	3	0	46	51	1	1	0	0
		Deviation	-142.6	1.6	91.2	84.7	-33.4	-1.5	305.8	51.1	-114.4	-160.5	-79.6	-2.4
		χ^2	48.6	0.0	59.8	39.8	13.1	0.9	230.9	3.5	97.4	147.6	76.7	2.4
	3*	<i>N</i>	13	158	241	306	99	5	98	704	274	122	33	0
		% total	2	19	29	37	12	1	8	57	22	10	3	0
		Deviation	-30.0	-176.5	37.9	132.0	37.4	-0.8	33.6	203.1	-30.1	-138.6	-59.3	-8.7
		χ^2	20.9	93.1	7.1	100.1	22.7	0.1	17.5	82.4	3.0	73.7	38.1	8.7
4	<i>N</i>	0	12	16	13	19	6	0	9	11	9	15	8	
	% total	0	18	24	20	29	9	0	17	21	17	29	15	
	Deviation	0.0	0.3	0.9	0.7	0.0	-1.8	0.0	-0.3	-0.9	-0.7	0.0	1.8	
	χ^2	0.0	0.0	0.1	0.0	0.0	0.4	0.0	0.0	0.1	0.0	0.0	0.5	
2004	1*	<i>N</i>	81	141	95	86	54	1	124	121	6	3	0	1
		% total	18	31	21	19	12	0	49	47	2	1	0	0
		Deviation	-37.3	-36.4	32.5	21.3	20.0	-0.1	58.2	22.2	-28.8	-33.0	-18.9	0.4
		χ^2	11.7	7.5	16.9	7.0	11.7	0.0	51.4	5.0	23.8	30.3	18.9	0.2
	2*	<i>N</i>	66	957	778	496	107	4	139	729	24	1	1	0
		% total	3	40	32	21	4	0	16	82	3	0	0	0
		Deviation	-56.4	-95.8	172.5	25.8	-40.7	-5.4	93.6	338.1	-200.8	-173.6	-53.8	-3.5
		χ^2	26.0	8.7	49.1	1.4	11.2	3.1	192.6	292.6	179.4	172.6	52.9	3.5
	3*	<i>N</i>	2	114	347	493	271	18	47	1538	631	104	33	0
		% total	0	9	28	40	22	1	2	65	27	4	1	0
		Deviation	-13.4	-409.8	27.3	279.5	113.2	3.2	17.8	548.1	26.8	-299.6	-265.2	-28.0
		χ^2	11.7	320.6	2.3	365.7	81.2	0.7	10.9	303.5	1.2	222.4	235.9	28.0
4*	<i>N</i>	0	12	123	329	228	7	2	164	270	100	119	14	
	% total	0	2	18	47	33	1	0.3	25	40	15	18	2	
	Deviation	-1.0	-73.1	-70.4	116.8	41.4	-13.8	1.1	82.6	84.9	-103.1	-59.6	-5.9	
	χ^2	1.0	62.8	25.6	64.3	9.2	9.1	1.2	83.7	39.0	52.3	19.9	1.7	

transects at time interval 4 in 2004 and were captured in all but one transect during that year.

Larval sucker CPUE increased across time intervals 1 and 2 in 2003 and 2004, and all sites reached their seasonal peak in time interval 2 except Williamson River in 2004 (Figure 2). Regardless of restoration status, peak CPUE in the riverine sites was higher than in the lake sites. This was especially apparent in 2004, when CPUE in South Marsh and Upper Klamath Lake was relatively low. By time interval 4, CPUE declined in all sites and few larvae were captured at any site beyond this time (J.D.C., unpublished data). In 2003, the interaction between time interval and site was significant ($F_{6,19.5} = 18.15$, $P < 0.0001$). At time interval 1, larvae were scarce in Williamson River relative to the other sites but subsequently increased

and remained significantly more abundant there than in Upper Klamath Lake for the duration of the study period (Figure 2). The interaction between time interval and site in 2004 was not significant ($F_{9,30.8} = 1.81$, $P = 0.1056$), but main effects were highly significant (site: $F_{3,10.6} = 7.56$, $P = 0.0055$; time: $F_{9,25.3} = 29.89$, $P < 0.0001$). Catch rate was higher in Williamson River and Riverbend than at the other sites, and such differences became greater after time interval 2 (Figure 2). Other than a small peak in South Marsh at time interval 2, catch rate in the lake sites never exceeded more than 1 larva/min.

Larval Rearing

Temporal trends in SL varied among sites in both years (site \times time interaction, 2003: $F_{4,32.6} = 16.23$, P

TABLE 2.—Extended.

Year	KL larval stage						SM larval stage						
	1	2	3	4	5	6	1	2	3	4	5	6	
2003	56	139	31	1	0	0							
	25	61	14	0	0	0							
	-1.9	31.0	-12.0	-15.0	-2.1	0.0							
	0.1	8.9	3.3	14.1	2.1	0.0							
	23	286	85	156	151	5							
	3	41	12	22	21	1							
	-163.2	-52.7	23.2	75.8	113.0	3.9							
	143.1	8.2	8.7	71.6	336.3	13.7							
	0	1	9	21	27	10							
	0	1	13	31	40	15							
	-3.6	-26.7	-7.8	6.6	21.9	9.5							
	3.6	25.7	3.6	3.0	94.1	188.4							
	2004	7	51	7	6	1	0	0	5	4	21	6	0
		10	71	10	8	1	0	0	14	11	58	17	0
-11.6		23.1	-2.8	-4.2	-4.3	-0.2	-9.3	-8.9	-0.9	15.9	3.3	-0.1	
7.2		19.2	0.8	1.7	3.5	0.2	9.3	5.7	0.2	49.8	4.1	0.1	
2		76	120	91	29	4	1	27	107	211	114	8	
1		24	37	28	9	1	0	6	23	45	24	2	
-14.4		-64.8	39.0	28.1	9.2	2.7	-22.8	-177.6	-10.7	119.6	85.3	6.2	
12.6		29.8	18.8	12.6	4.3	6.0	21.8	154.2	1.0	156.6	253.4	20.8	
0		8	27	52	83	9	0	3	10	29	114	20	
0		4	15	29	46	5	0	2	6	16	65	11	
-2.2		-67.3	-19.0	21.3	60.3	6.9	-2.2	-71.0	-35.2	-1.2	91.7	17.9	
2.2		60.2	7.8	14.8	160.4	22.2	2.2	68.2	27.4	0.0	376.9	153.2	
0		0	7	10	34	17	0	0	0	0	5	5	
0		0	10	15	50	25	0	0	0	0	50	50	
-0.1		-8.3	-11.8	-10.6	15.8	15.0	0.0	-1.2	-2.8	-3.0	2.3	4.7	
0.1		8.3	7.4	5.5	13.8	110.9	0.0	1.2	2.8	3.0	2.0	74.4	

< 0.0001; 2004: $F_{9,31.1} = 4.43$, $P = 0.0009$). In 2003, mean SL increased over time at Upper Klamath Lake, becoming significantly greater than at the other sites by time interval 2 (simple effect test: $F_{2,29.6} = 40.14$, $P < 0.0001$). Length did not vary over time at Riverbend ($F_{2,29} = 2.07$, $P = 0.1439$) or Williamson River ($F_{2,29.6} = 0.2$, $P = 0.8169$; Figure 3). Williamson River fish had the smallest mean SL throughout 2003 but were statistically different from Riverbend only at interval 2. Statistical power was lowest at time interval 3 due to higher variances. Fish length in interval 4 did not differ for Williamson River and Riverbend ($F_{1,7.69} = 1.68$, $P = 0.2329$). In 2004, mean SL was highest in South Marsh and lowest in Williamson River. Fish grew larger at Upper Klamath Lake and South Marsh than at

the Williamson River, but SL did not significantly change over time at Riverbend (Figure 3B).

Developmental phase was completely dependent upon site and time interval in both 2003 and 2004, and the relationship varied significantly over time (2003: G^2 [likelihood ratio χ^2 statistic] = 163.77, $df = 22$, $P < 0.001$; 2004: $G^2 = 265.23$, $df = 45$, $P < 0.001$). In 2003, Riverbend and Upper Klamath Lake had more middle, late, and postflexion mesolarvae than expected under the null hypothesis of independence, and there were fewer protolarvae and early flexion mesolarvae than expected. Late and postflexion mesolarvae were more abundant in time interval 1 at Riverbend than at Upper Klamath Lake, but these phases were more equally represented at both sites during later time intervals (Table 2). By time interval 3, middle, late,

TABLE 3.—Larval Lost River and shortnose suckers cross-classified by gut fullness, site, and time interval at two restored sites (Riverbend [RB] and South Marsh [SM]) and two reference sites (Williamson River [WR] and Upper Klamath Lake [KL]) in the Williamson River Delta Preserve, 2003 and 2004. Number (*N*) and percent of larvae in each gut fullness class are presented along with deviation from expected and cell chi-square values for two-way contingency table analyses by time interval. South Marsh was not sampled in 2003. Only RB and WR were compared at interval 4 in 2003 since almost no larvae were encountered in KL. Asterisks by time intervals denote significant chi-square ($P < 0.001$). Test of independence for interval 4 in 2003 was not significant ($\chi^2 = 4.53$; $df = 4$; $P = 0.330$). Gut fullness classes are: (1) empty, (2) low, (3) medium, (4) medium-high, and (5) high.

Year	Time interval	Variable	RB gut fullness					WR gut fullness				
			1	2	3	4	5	1	2	3	4	5
2003	1*	<i>N</i>	5	82	91	126	257	6	43	14	7	4
		% total	1	15	16	22	46	8	58	19	9	5
		Deviation	-4.1	-24.2	-6.7	9.4	25.7	4.8	29	1.1	-8.4	-26.5
	2*	χ^2	1.9	5.5	0.5	0.8	2.9	19.1	60	0.1	4.6	23
		<i>N</i>	84	375	282	226	527	337	578	117	69	78
		% total	6	25	19	15	35	29	49	10	6	7
	3*	Deviation	-4.1	-67	-44.2	-2.1	117.3	5.1	75.6	47.9	2.4	-130.9
		χ^2	1	26.2	12.4	>0.1	46.4	1	21.6	9.4	>0.1	37.3
		<i>N</i>	12	104	113	147	414	30	340	291	233	328
	4	% total	2	13	14	19	52	2	28	24	19	27
		Deviation	-0.6	1.6	-0.9	-0.1	>0.1	0.6	-1.6	0.9	0.1	>-0.1
		χ^2	0.6	1	0.1	>0.1	>0.1	1	1.6	0.2	>0.1	0
2004	1*	<i>N</i>	4	57	65	90	219	26	75	5	4	8
		% total	1	13	15	21	50	22	64	4	3	7
		Deviation	-16.6	-58.7	4.5	13.5	57.4	20.4	43.6	-11.4	-16.8	-35.8
	2	χ^2	13.4	29.8	0.3	2.4	20.4	74.5	60.6	7.9	13.5	29.3
		<i>N</i>	75	610	545	439	716	90	527	144	59	40
		% total	3	26	23	18	30	10	61	17	7	5
	3	Deviation	-45.4	-170.6	53.9	61.8	100.3	46.6	245.5	-33.1	-77	-182
		χ^2	17.1	37.3	5.9	10.1	16.3	50	214.2	6.2	43.6	149.2
		<i>N</i>	40	287	216	191	489	99	632	689	541	373
	4	% total	3	23	18	16	40	4	27	30	23	16
		Deviation	-6.6	-17.8	-77.2	-52.5	154.2	10	50.3	129.4	76.4	-266
		χ^2	0.9	1	20.3	11.3	71	1.1	4.3	29.9	12.5	110.8
4	<i>N</i>	30	163	89	77	327	72	171	145	111	164	
	% total	4	24	13	11	48	11	26	22	17	25	
	Deviation	-19.8	-2.5	-29	-18.8	70.1	23.8	11.1	30.9	18.4	-84.3	
4	χ^2	7.9	>0.1	7.1	3.7	19.1	11.8	0.8	8.4	3.7	28.6	

and postflexion mesolarvae and metalarvae comprised more than 80% of the catch from these sites. Conversely, protolarvae and early flexion mesolarvae dominated the Williamson River catch, comprising 100, 98, and 65% in time intervals 1–3, respectively. Frequency of middle, late, and postflexion mesolarvae and metalarvae increased at the Williamson River site in time interval 4, coinciding with declines in larval CPUE; thus, the distribution of developmental phases was equal at Williamson River and Riverbend (Pearson's $\chi^2 = 1.19$, $df = 4$, $P = 0.8791$).

In 2004, developmental phase distribution was similar to that in 2003, as Riverbend, Upper Klamath Lake, and South Marsh generally had more middle, late, and postflexion mesolarvae and metalarvae than expected. Late and postflexion mesolarvae and metalarvae were most prevalent at South Marsh in time interval 2

and became dominant in both Upper Klamath Lake and Riverbend by time interval 3. In these sites, the combined proportion of these four phases increased over the study period to more than 90% by time intervals 3 and 4. As in 2003, Williamson River larvae were primarily protolarvae and early flexion mesolarvae, comprising 96, 97, and 67% of the catch in time intervals 1–3, respectively. The frequency of more-advanced phases of larvae increased at Williamson River in time interval 4.

Gut fullness was also dependent upon site and time interval during both years (2003: $G^2 = 79.76$, $df = 16$, $P < 0.0001$; 2004: $G^2 = 519.91$, $df = 36$, $P < 0.0001$). Larvae with medium-high and high gut fullness dominated the catch in Riverbend and Upper Klamath Lake in 2003; this distribution was particularly evident at Riverbend (Table 3). Only in time interval 2 did

TABLE 3.—Extended.

Year	KL gut fullness					SM gut fullness					
	1	2	3	4	5	1	2	3	4	5	
2003	3	38	45	46	94						
	1	17	20	20	42						
	-0.7	-4.8	5.6	-1	-0.8						
	0.1	0.5	0.8	>0.1	>0.1						
	39	216	120	117	195						
	6	31	17	17	28						
	-55.1	-23	13.9	32.8	31.4						
	32.2	2.2	1.8	12.7	6						
	0	2	6	9	32						
	0	4	12	18	65						
	-1	-8.6	-3.7	-0.2	13.6						
	1	7	1.4	>0.1	10						
	2004	1	25	15	17	12	0	17	6	4	4
		1	36	21	24	17	0	55	19	13	13
-2.3		6.4	5.3	4.7	-14	-1.5	8.8	1.7	-1.5	-7.5	
1.6		2.2	2.8	1.8	7.5	1.5	9.3	0.7	0.4	4.9	
11		95	83	56	73	27	84	56	82	209	
3		30	26	18	23	6	18	12	18	46	
-5.1		-9.1	17.5	5.7	-9.1	3.9	-65.9	-38.3	9.6	90.8	
1.6		0.8	4.7	0.6	1	0.6	29	15.6	1.3	69.7	
1		25	17	24	109	9	30	15	22	99	
1		14	10	14	62	5	17	9	13	57	
-5.7		-18.9	-25.2	-11	60.8	2.3	-13.6	-27	-12.8	51.1	
4.9		8.1	15	3.5	76.7	0.8	4.3	17.3	4.7	54.5	
1		8	7	8	35	0	0	3	2	5	
2		14	12	14	59	0	0	30	20	50	
-3.3		-6.2	-3.2	-0.2	12.9	-0.7	-2.4	1.3	0.6	1.3	
2.5		2.7	1	>0.1	7.5	0.7	2.4	1	0.3	0.4	

empty and low-fullness categories constitute more than 25% of the total catch for each of these sites. Empty and low-fullness guts were much more common than expected in larvae sampled in Williamson River during time intervals 1 and 2 in 2003 (66–78% of the total). However, the distribution trended toward fuller guts by time interval 3 in Williamson River. At time interval 4, larval catch declined dramatically and the distribution of gut fullness was nearly identical between Riverbend and Williamson River (Pearson's $\chi^2 = 4.53$, $df = 4$, $P = 0.330$): 84% of larvae had medium-high and high gut fullness.

The pattern of gut fullness was similar in 2004; fuller guts were prevalent at Riverbend throughout all four time intervals. Larvae sampled in South Marsh had medium-high and high gut fullness (>63%) in time intervals 2 and 3, while sample size was low in time

intervals 1 and 4. Larvae from Upper Klamath Lake had medium-high and high gut fullness (76%) in time interval 3, but deviations from expected values were relatively small during the other time intervals. Empty guts and low fullness were again most common in the Williamson River larvae in time intervals 1 and 2, while high fullness remained underrepresented throughout the sampling period.

Temperature

In 2003 and 2004, daily mean nearshore water temperature in the restoration wetlands of Riverbend and South Marsh was generally higher than that at reference sites in Upper Klamath Lake and, especially, the Williamson River (Figure 4). Temperature profiles from all sites exhibited similar seasonal trends and frequently varied by 3–5°C within several days.

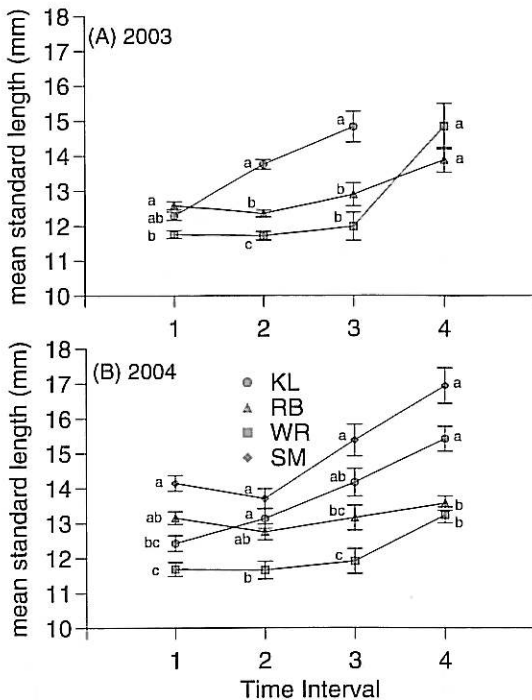


FIGURE 3.—Least-squares mean (\pm SE) standard length of larval Lost River and shortnose suckers at wetland restoration sites (Riverbend [RB] and South Marsh [SM]) and reference sites (Upper Klamath Lake [KL] and Williamson River [WR]) in the Williamson River delta, Oregon, during four time intervals (defined in text) in (A) 2003 and (B) 2004. Letters denote results of comparisons among sites within each interval. Sites with the same letter are not different at the 0.05 level.

Temperatures at all sites were coolest in May, increased to summertime highs in June and July, and declined in early August. Temperatures were higher in the restoration sites than at Upper Klamath Lake during the initial 6 weeks of the study period in both years; at times, the temperature differed as much as 3–4°C. During the first 4 weeks of the study period in each year, temperatures in the Williamson River were similar and occasionally warmer than those in Upper Klamath Lake, but after the third week in June Williamson River temperatures remained consistently 4–5°C below those of the other sites and rarely exceeded 20°C.

Discussion

Sucker larvae were consistently captured in newly restored deltaic wetlands at the WRD during both years of our study, indicating that restored deltaic wetlands can provide habitat conditions that are suitable for larval suckers. Other studies have shown that flood-

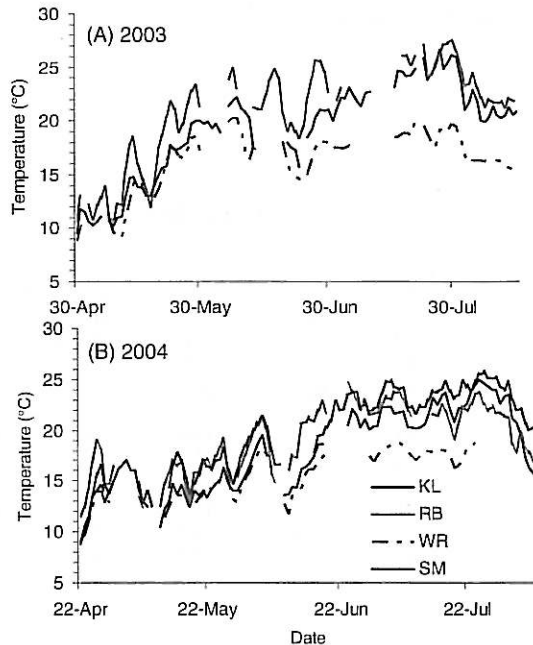


FIGURE 4.—Mean daily nearshore water temperature measured at wetland restoration sites (Riverbend [RB] and South Marsh [SM]) and reference sites (Williamson River [WR] and Upper Klamath Lake [KL]) in the Williamson River Delta, Oregon, during (A) 2003 and (B) 2004.

plain wetlands similar to the restored WRD deltaic wetlands are biologically productive and complex and, as a result, provide excellent rearing habitat for fish (Bayley 1995; Sparks 1995; Modde et al. 2001; Sommer et al. 2002; Ribeiro et al. 2004).

Analysis of SL, developmental phase, and gut fullness of sucker larvae captured in the restoration wetlands of Riverbend and South Marsh strongly suggests that these fish were feeding and growing (hence, rearing) in these locations. Rapid onset of exogenous feeding by larvae is critical for survival (Welker et al. 1994; Werner 2002); the Klamath Tribes Natural Resources Department (1996) observed that Lost River and shortnose sucker larvae must begin feeding soon after initiating flexion to avoid starvation. The presence of numerous late and postflexion mesolarvae and metalarvae with medium-high and high gut fullness within Riverbend and South Marsh is strong evidence that these larvae had successfully initiated exogenous feeding and subsequently grew in the restoration wetlands. Larval feeding, growth, and development in the restoration wetlands may have benefited their condition, which is critically important to larval survival as larvae in better condition are

presumably less likely to suffer mortality from starvation or predation (Suthers 2000).

The length, developmental phase, gut fullness, and temperature data also indicated that conditions in the restoration wetlands during early intervals within each study year were especially conducive to larval rearing, perhaps more so than existing nursery habitat in Upper Klamath Lake. At time interval 1 in 2003, Riverbend had the largest larvae and the highest frequencies of middle, late, and postflexion mesolarvae with medium-high and high gut fullness. At time interval 1 in 2004, both Riverbend and South Marsh had larger larvae than Upper Klamath Lake, and late and postflexion mesolarvae were over seven times more frequent in South Marsh than in Upper Klamath Lake. Water temperature regimes in Riverbend and South Marsh probably contributed to beneficial early season conditions that promoted larval growth and development in the restoration wetlands. Throughout both years, water temperature in the restoration wetlands was frequently several degrees warmer than that in the Williamson River and Upper Klamath Lake reference sites, especially early in the study period. Water temperature is an extremely important variable for exothermic fish through its governing of metabolism and growth (Clady 1976; Werner 2002; Meise et al. 2003), and warmer water in the restoration wetlands may have benefited larvae by increasing developmental rates and decreasing mortality (Werner 2002).

Our findings support previous results indicating that the Williamson River currently serves primarily as a transit corridor for larvae as they emigrate to nursery habitats in Upper Klamath Lake (Cooperman and Markle 2003, 2004). Through late June (time interval 3) in 2003 and 2004, larvae captured in Williamson River were shorter, exhibited earlier phases of development, and possessed lower degrees of gut fullness (primarily empty and low fullness) than those captured at other sites. Contrarily, larvae in Upper Klamath Lake (including South Marsh) were consistently larger, were more developmentally advanced, and had fuller guts than larvae in Williamson River. These data, coupled with the presence of protolarvae in Upper Klamath Lake and South Marsh, indicate that larvae can rapidly emigrate from natal areas to Upper Klamath Lake and do not grow appreciably in the lower Williamson River.

However, while the patterns of site presence, CPUE, and SL in Riverbend were similar to those in the Williamson River (suggestive of similar functionality), larvae inhabiting the Riverbend site were more developmentally advanced and had higher gut fullness. We believe this reflects an important difference between the two sites in their ability to retain

emigrating larvae based on the suitability of conditions for feeding and growth. Warmer water and (potentially) elevated food resources (J.D.C., unpublished data) are features of Riverbend that probably function to retain larvae in the restoration wetlands. Retention and growth in Riverbend may elevate the larvae's chances of survival after entering Upper Klamath Lake, because their increased swimming ability and condition may allow them to access nursery habitats instead of being transported out of the lake by wind-driven currents and into unfavorable habitat associated with sink populations (Cheng et al. 2005; D. F. Markle, Oregon State University, unpublished data).

Although the presence of some early flexion mesolarvae in South Marsh highlights the potential for rapid site entry and subsequent within-site growth, it is likely that some developmentally advanced larvae did move from Upper Klamath Lake into South Marsh, as (1) these sites are in close proximity to one another; (2) all larvae must first pass through Upper Klamath Lake to reach South Marsh, and shoreline distribution and movement of larvae exiting the Williamson River may be influenced by prevailing winds that blow toward South Marsh (Klamath Tribes Natural Resources Department 1996; Cheng et al. 2005); and (3) distributions of developmental phase and gut fullness between the two sites was similar. Overall, South Marsh appears to be functioning similarly to portions of Upper Klamath Lake that were identified by Cooperman and Markle (2003, 2004) as being suitable larval sucker nursery habitat.

The functionality of different larval habitats, regardless of restoration status, may be based partly on their location, including their proximity to natal grounds. Larval catch in Riverbend and Williamson River was higher and more persistent than that in South Marsh and Upper Klamath Lake, but growth was generally greater in the latter sites. The presence of higher larval numbers at sites closer to spawning grounds is expected because, by necessity, all larvae that are spawned upstream of the WRD must travel through the lower Williamson River to access nursery areas. High rates of larval mortality are well documented (Houde 1987, 2002; Markle and Cooperman 2002), and many larvae probably perish before entering Upper Klamath Lake, resulting in reduced catch at those sites. Additionally, the overall habitat area in the lower Williamson River is relatively small and confined compared with expansive (~360-km²) Upper Klamath Lake. Thus, larvae are likely to be concentrated in the Williamson River, serving to increase CPUE in those sites.

Overall, results of our 2-year study reveal that restoration of deltaic wetlands at the WRD can provide

suitable habitat conditions for larval Lost River and shortnose suckers and that, if presented with the opportunity, larvae will rapidly colonize and rear in these habitats. The growth and feeding patterns of larvae inhabiting Riverbend and South Marsh were similar to those observed in Upper Klamath Lake (a site with a documented history of larval rearing) yet dissimilar to those in the Williamson River (a site believed to serve as a transit corridor for emigrating larvae). The potential benefits of deltaic wetland rearing may be especially great early in the season, when temperatures in Williamson River and Upper Klamath Lake are cooler. During the early part of the season, restored habitats may better support larvae by offering a warmwater refuge at a time when other habitats may be less productive.

Low recruitment associated with the loss of larval nursery habitat has been implicated as a factor contributing to population declines in Lost River and shortnose suckers (USFWS 1993; NRC 2004), and our results indicate that wetland restoration as recommended by the NRC (2004) and the Oregon Independent Multidisciplinary Science Team (2003) is a viable strategy for increasing larval nursery habitat and potentially improving larval survival and recruitment. Restoration has successfully diversified the rearing options for larval suckers; future large-scale restoration of the WRD is likely to significantly increase the habitat area that is suitable for larval rearing. For larval fish, locating suitable rearing habitat at the necessary time is critical to survival (Werner 2002); thus, the restoration of deltaic wetlands—a habitat type that was once abundant but that is now largely missing—provides a tool to potentially increase larval survival and contribute to the recovery of these two endangered species.

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