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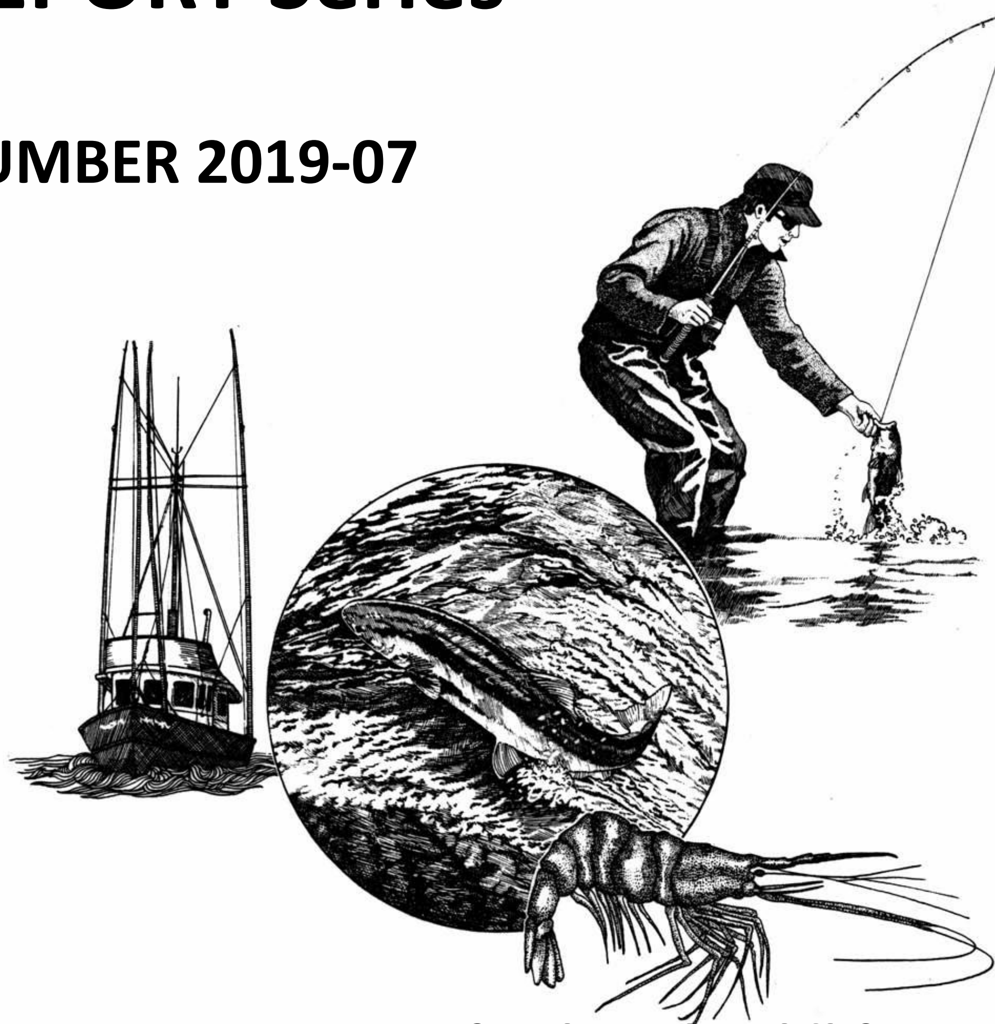

Oregon Department of Fish and Wildlife

Warner Sucker Life History: A Review

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Introduction

The Warner Sucker *Catostomus warnerensis* is endemic the Warner Basin, a semi-arid endorheic basin that encompasses 6,858 km^2 in southeastern Oregon, northwestern Nevada, and extreme northeastern California (Figure 1). As a result of the horst and graben topography that typifies the Great Basin, the Warner Basin has a north-south orientation bounded by Hart Mountain and Poker Jim Ridge on the east and the Abert Rim (Warner Rim) on the west. Three major tributaries streams (Honey, Deep, and Twentymile creeks) flow from the Warner Mountains into a chain of shallow ephemeral lakes and marshlands on the valley floor that are the remnants of pluvial Lake Warner. Hart and Crump lakes comprise the largest lakes in the valley. Between these lakes, a ridge extends from the west, constricting the valley in an area known as “the Narrows” (Figure 1), and separates the valley into two regions commonly referred to as the South Warner Valley and the North Warner Valley.

The Warner Sucker was first described by Snyder (1908) from specimens collected in Deep and Honey creeks during surveys of the Warner Basin in 1897 and 1904. The presumed historical range of the Warner Sucker consists of the low- to moderate-gradient reaches of the tributaries, the three relatively permanent lakes (Hart, Crump, and Pelican lakes), and several ephemeral lakes during periods of abundant precipitation (U.S. Fish and Wildlife Service 1985; Williams et al. 1990).

Following its initial description, there was little study of the Warner Sucker until the 1970s when efforts were carried out to provide information on the status and distribution of the species; these studies also provided insights into the species’ life history. It became quickly evident from these studies that self-sustaining populations of suckers reside in the tributaries (Hayes 1978). Warner Suckers express two life history types: stream-residents and lake-residents. The stream-resident populations complete their entire life-cycle in the tributaries, with the exception of occasional migrants to the lakes. Lake-resident suckers express an adfluvial strategy in which they reside in lakes most the year but return to the tributaries each spring to spawn. Lake-residents have also been observed spawning in Hart Lake (White et al. 1990). Because of this, lake-residents have been described as exhibiting facultative-potamodromy (Berg 1991): during normal to wet water years, adults ascend the tributaries to spawn, but they will attempt to spawn in the lakes when low tributary flows are insufficient for upstream migration. The lake population has been frequently extirpated by prolonged droughts that desiccated the lakes. Over the last century desiccation of Hart Lake has occurred roughly once every thirty years (1934, 1961, 1992, and 2015). After refilling, the lakes are recolonized by downstream migrants from the stream populations (Allen et al. 1994; Scheerer et al. 2016).

Bond (1966) was the first authority to suggest that Warner Sucker were endangered, due to their limited range and the negative effects of drought. Some of the studies in the 1970’s suggested that the range and abundance of suckers had decreased, likely due to the numerous irrigation diversions that fragmented its habitat (Andreasen 1975; Kobetich 1977; Coombs et al. 1979). The species was listed as threatened under the federal Endangered Species Act in 1985, with habitat fragmentation and the proliferation of piscivorous nonnative game fishes in the lakes identified as the primary threats to its persistence (U.S. Fish and Wildlife Service 1985).

Since the time of listing, several studies have been conducted on the Warner Sucker, significantly increasing the available information regarding the species’ biology. This report reviews information on the distribution, abundance, genetic structure, age and growth, early life history, and spawning of the Warner Sucker based on investigations conducted from the 1970s to the present.

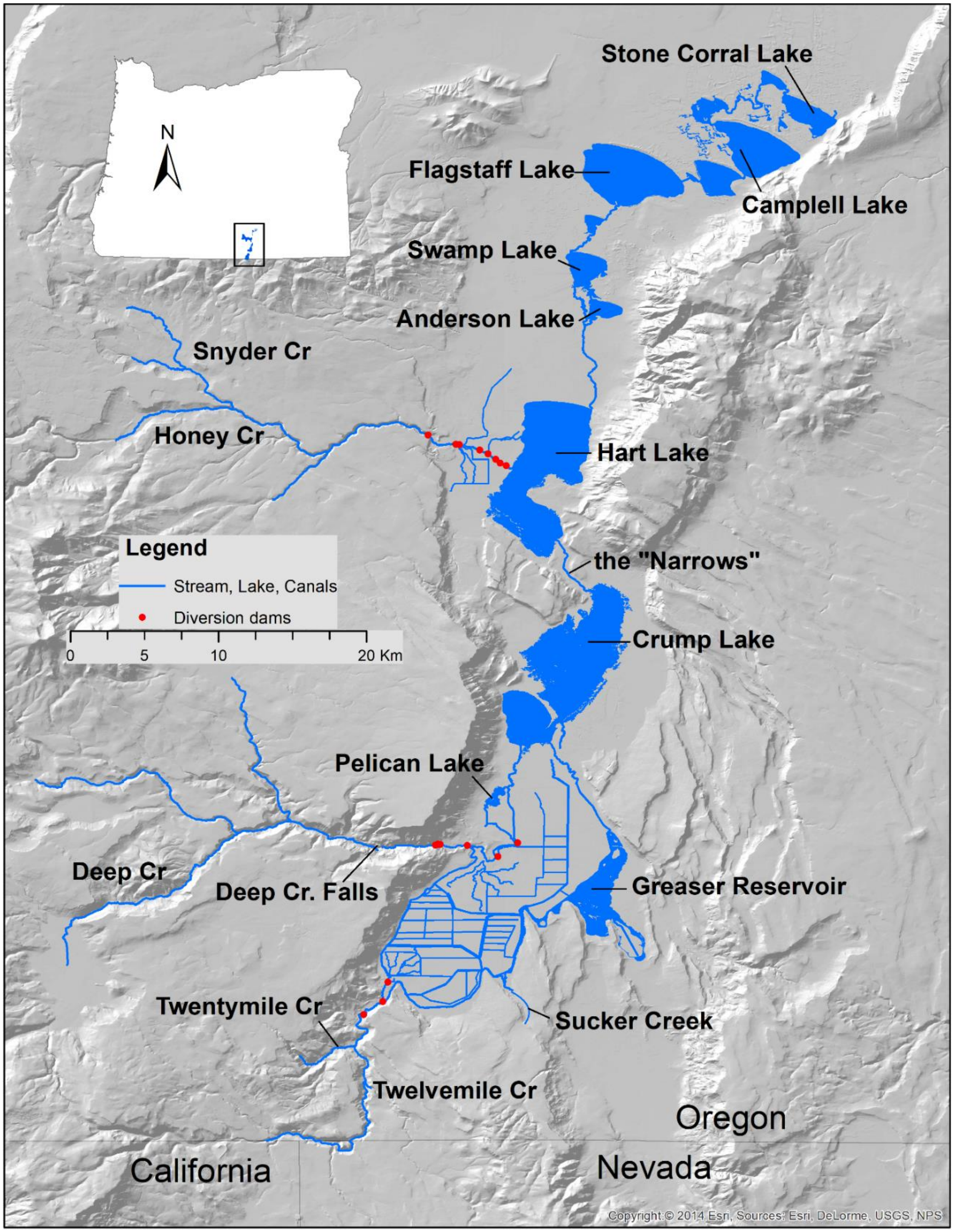

Figure 1. Map of the Warner Basin showing lakes, canals, streams, and irrigation diversion dams**.** Not shown is Bluejoint Lake, the northern-most lake in the basin.

Natural Aquatic Environment and Water Development History

The Warner Sucker has become highly adapted to the semi-arid landscape of the Warner Valley since the drying of pluvial Lake Warner at the end of the Pleistocene Epoch over 10,000 years ago. The life history of the species was shaped by the aquatic environment that existed before irrigation development altered the landscape, and an understanding of the natural aquatic conditions is necessary to inform a discussion of Warner Sucker life history. White settlement of the Warner Valley began in 1867 (Hunt 1964) with minor alteration to water courses for irrigation occurring soon after; major irrigation alterations to improve the land for hay and cattle production did not begin until the late 1930's (Hunt 1964). Little information is available describing the aquatic habitats of the Warner Valley prior to settlement, but a general sense of conditions can be discerned from reports by Whistler and Lewis (1916) and Stricklin and Perry (1923) that describe water use in the valley in the early 1900's, when irrigation development was still little changed from natural conditions.

South Warner Valley – Twentymile Creek enters the Warner Valley at the southern-most end. Prior to major irrigation alterations, the creek spread out through several distributary channels into the low-lying marshland upon entering the valley floor and annually flooded a large area in the spring (Figure 2; Appendix Figure 1). A small, shallow lake was located in a tule marsh to the east of the distributary channels of Twentymile Creek, close to where Sucker Creek enters the valley floor (Figure 1 and 2). The lake was about half the size of Pelican Lake when surveyed in the summer of 1921.

Deep Creek enters the valley from the west near the town of Adel and turns south to form a large alluvial fan a short distance downstream. From here the creek spreads out into a large area of low-lying marshland with no well-defined channel (Figure 3; Appendix Figure 1). Remnants of the distributary channels from both creeks are still evident on the valley floor (Appendix Figure 2). During spring high-flow periods, Deep Creek water merged with water from Twentymile Creek to follow the gradual slope of the valley floor north through the marshland to Crump and Pelican lakes (Whistler and Lewis 1916; Stricklin and Perry 1923; Hunt 1964). No well-defined channels connected the creek water to the lakes, but Whistler and Lewis (1916) reported that Pelican and Crump lakes were connected by a deep, meandering slough.

There were limited attempts to control water flow in the valley prior to the 1920's. Where Deep Creek turned south, a large ditch was constructed, known as the Reclamation Ditch, that carried water a short distance to the northeast and drained into the marshland to the east of Adel. Erosive forces enlarged the ditch so that it resembled a natural stream by the 1920's and carried most of the flow during high flow periods (Stricklin and Perry 1923). Other irrigation developments in the South Warner Valley were initially limited to a few canals that diverted creek water to clover and alfalfa fields on land above the annually flooded marshlands. The long periods of saturated soil in the marshlands limited crop production in these areas to native grasses that were cut for hay in the summer. As water receded from the marshland in late spring, a few small check dams comprised of earthen material or hay bales were constructed to spread and hold the water (Stricklin and Perry 1923).

North Warner Valley – Before substantial irrigation development occurred on Honey Creek, the creek spread out into numerous channels to form an alluvial fan once it emerged from the canyon (Stricklin and Perry 1923). The water was well distributed over a wild grass meadowland of approximately 2,000 acres by both natural channels and artificial spur ditches before eventually flowing into Hart Lake. The meadowland sloped from the canyon to the western shore of Hart Lake and was separate from the lower-lying marshland.

Direct connection of the streams to the lakes appeared to only occur during high water periods. Streamflow from the three major tributaries reaches a minimum by late summer (Figure 4). Stricklin and Perry (1923) reported that by September and October of 1921 water from the streams disappeared a short distance after reaching the valley marshland, suggesting that stream connectivity to the lakes was regularly lost by late summer.

Irrigation Development – Beginning in the late-1930's through the 1950's, substantial alterations to the tributaries and valley floor, in the form of irrigation dams, canals, and dykes, improved the land for hay and alfalfa production (Hunt 1964). The most substantial alterations occurred in the South Warner Valley. A 15-mile dike system was constructed along the eastern side of the southern valley, forcing Twentymile Creek flood waters to bypass the marshlands and flow north to Greaser Reservoir (Figure 1). At the head of the flood ditch, a low-head dam (MC Dam) and headworks were constructed to control flow into an irrigation canal that carried water along the west side of the valley (Hunt 1964)(Appendix Figure 3). The valley marshlands were drained by cutting large canals from west to east and then extending them north towards Crump Lake (Hunt 1964) (Figure 1).

In the North Warner Valley, streamflow through the numerous distributary channels of Honey Creek has been confined to a single channel that drains to Hart Lake. To better control flood irrigation of the meadowland, several low-head dams and headworks have been constructed along the length of the channel to divert water into irrigation canals (Appendix Figure 4). The other major alteration to Honey Creek was the construction of a flood ditch in the 1950s that conveyed flood water to marshland north of Hart Lake (Campbell-Craven Environmental Consultants 1994). This ditch was constructed to prevent the lower fields in the meadow from flooding as the level of Hart Lake rose, a phenomenon that occurred more frequently following efforts by the U.S. Army Corps of Engineers in the 1940's to increase water storage in the lake by raising the height of the natural berm and spillway along the north shore.

Prior to these developments, it is probable that Warner Suckers were periodically able to move between the lakes and streams during spring high water. This connectivity was likely greatest between Hart Lake and Honey Creek, where lake-resident fish would only need to navigate < 5 km of distributary channels before reaching the main creek channel. Connectivity was likely lowest for Twentymile Creek, where fish from Crump Lake would need to navigate at least 13 km of meandering channels and flooded marshland before reaching the main creek channel (Figure 1). The end result of the irrigation development from 1930-1960 was the loss of connectivity between lakes and tributaries, primarily due to diversion dams that operate through the spring. These barriers fragmented the habitat and are presumed to have had a significant impact on the ability of Warner Suckers to carry out many aspects of their life history.

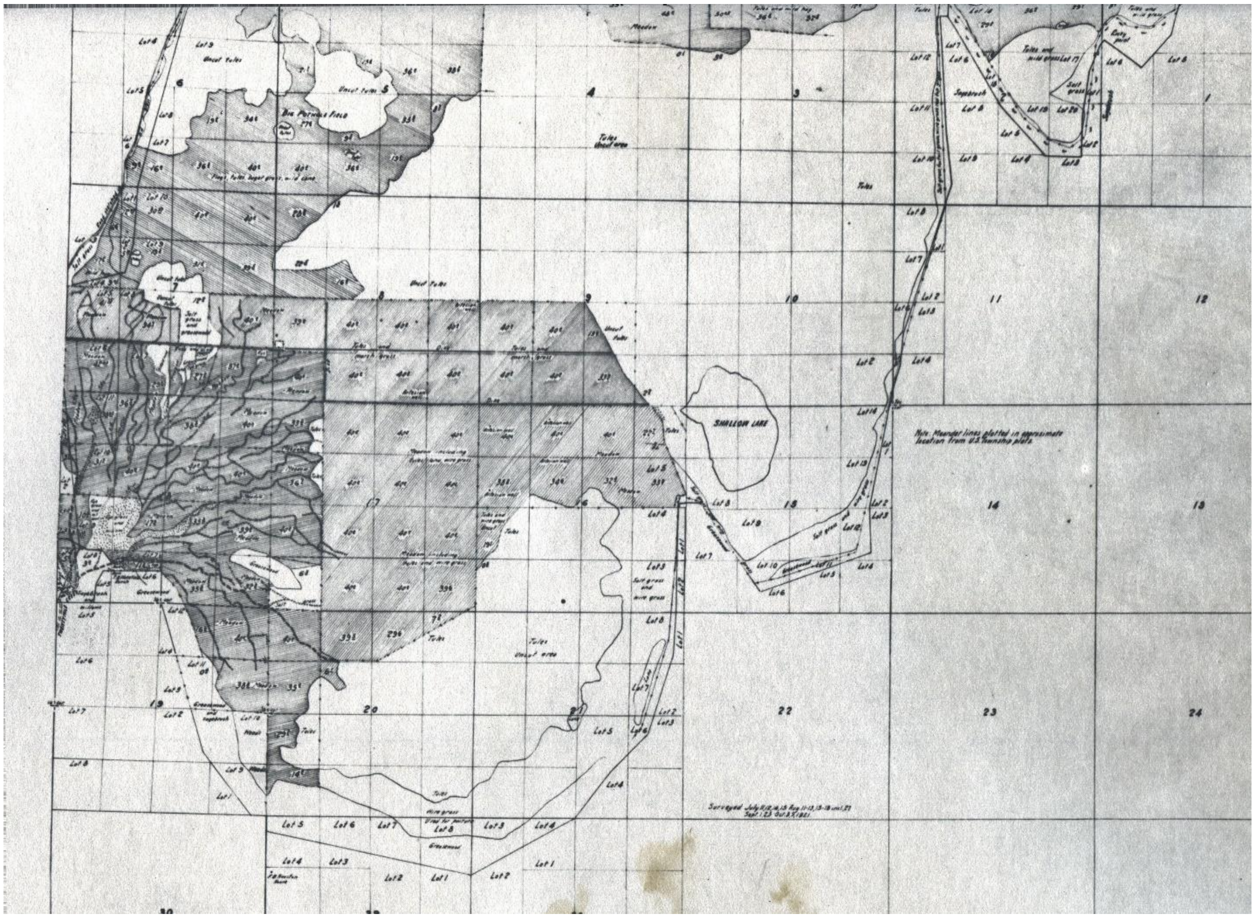

Figure 2. Map of South Warner Valley where Twentymile Creek enters valley floor from a survey conducted in the summer of 1921. Survey from Stricklin and Perry 1923.

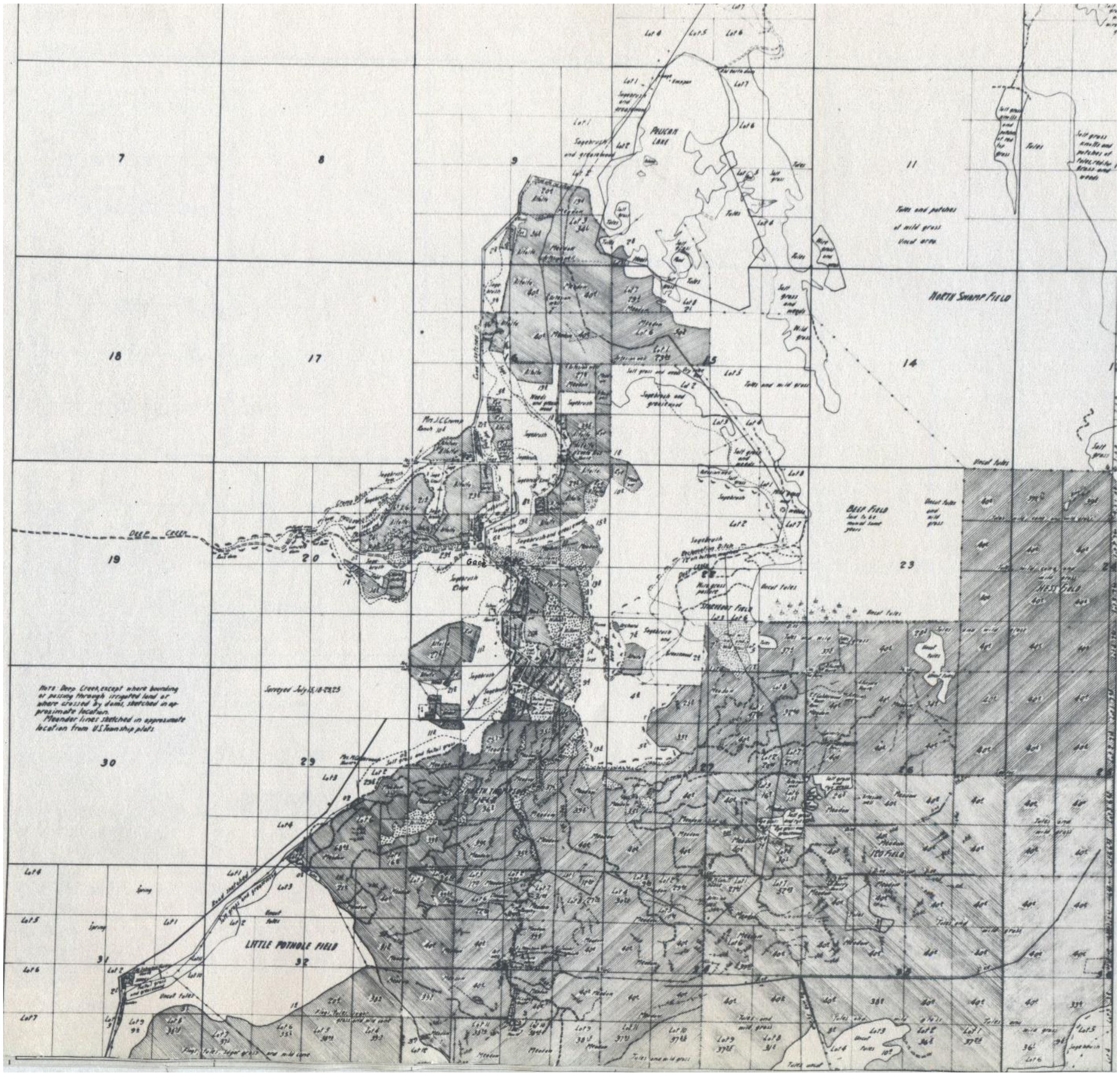

Figure 3. Map of South Warner Valley where Deep Creek enters valley floor from a survey conducted in the summer of 1921. Survey from Stricklin and Perry 1923.

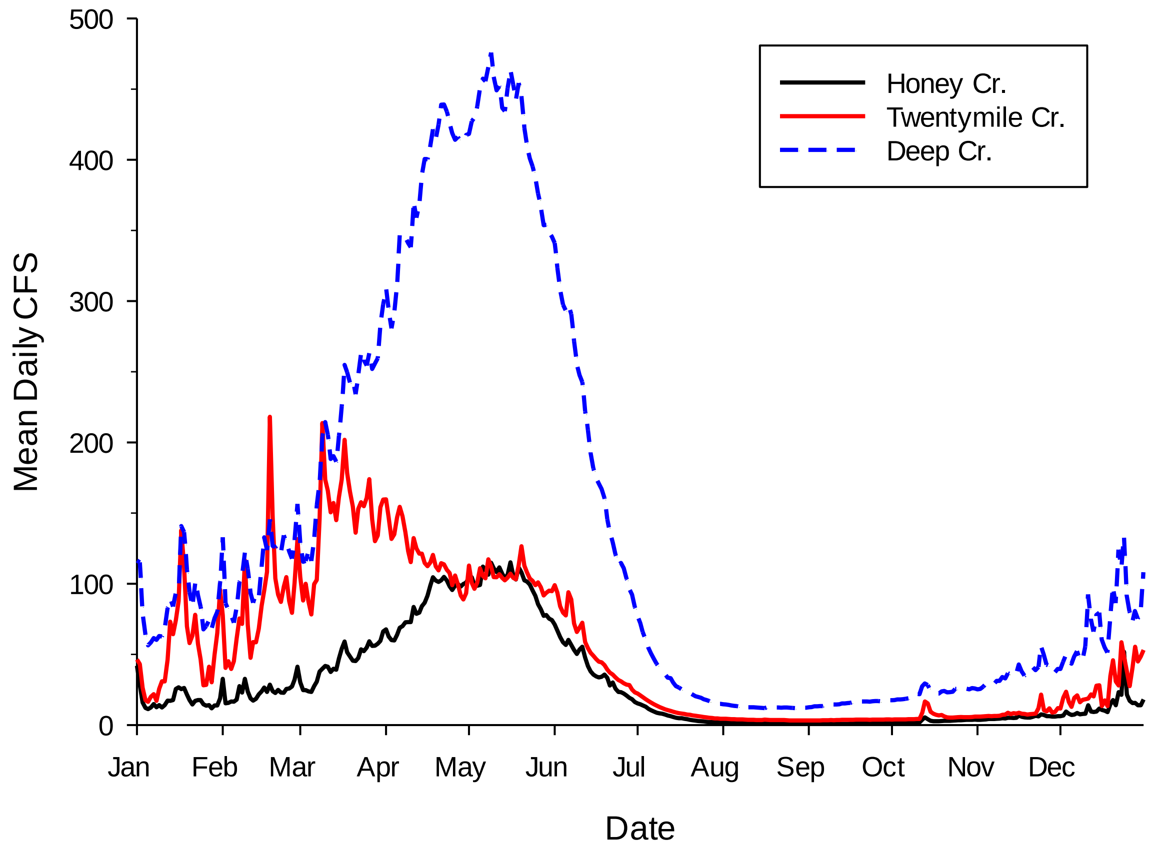

Figure 4. Mean daily streamflow in Honey, Twentymile, and Deep creeks. Streamflow based on average mean daily streamflow from Oregon Water Resources Department historic records from 1931-2018 for Honey Creek (Station ID 10378500) and Deep Creek (Station ID 10371500) or 1941-2018 for Twentymile Creek (Station ID 1036600). All gauging stations were upstream of irrigation diversions.

Distribution and Range

Twentymile Creek – In the Twentymile Creek subbasin, no Warner Suckers have been observed in the canal system between the distributary channels and Crump Lake (Coombs et al. 1979; Scheerer et al. 2007), with the exception of a few individuals collected <1 km downstream of the Cahill diversion (Scheerer et al. 2007)(Appendix Figure 3). The upstream-most occurrence recorded in the subbasin is in upper Twelvemile Creek downstream of the confluence with Cowhead Slough (Allen et al. 1994; Tait et al. 1995). However, there is a report of a single Warner Sucker (93 mm FL) captured in West Barrel Creek, a tributary of Cowhead Slough in northeastern California, approximately 9 km upstream from the Cowhead Slough confluence with Twelvemile Creek (Scoppettone and Rissler 2003).

The greatest density of Warner Suckers in the Twentymile Creek subbasin appears to be in lower Twelvemile Creek. Tait and Mulkey (1993b) surveyed several reaches in the Twentymile Creek subbasin and observed the greatest number of adult and juvenile suckers in a 1.6-km reach directly below the

O'Keefe Dam on Twelvemile Creek, located 2.5 km upstream from the confluence with Twentymile Creek (Appendix Figure 3). Tait et al. (1995) found a similar distribution of adults in 1994, but the greatest number of juveniles were found in the Nevada reach located 7 km upstream from the confluence. Richardson et al. (2009) evaluated the distribution of adult and juvenile suckers and found the majority of the population (86%) in the reach from the Dyke diversion on Twentymile Creek upstream to the old O'Keefe Dam on Twelvemile Creek. This low-gradient reach was characterized by a wide channel and deep pools, with abundant aquatic macrophytes and gravel-sized and smaller substrate.

In Twentymile Creek upstream of the confluence with Twelvemile Creek, Hayes (1978) collected adult suckers approximately 2 km upstream of the confluence (Appendix Figure 3). Juvenile suckers have been observed in the lower few hundred meters of stream upstream of the confluence (Coombs et al. 1979; Richardson et al. 2009).

Honey and Snyder Creeks – Swenson (1978) was the first to document adult suckers residing in the upper reaches of the Honey Creek subbasin with six fish (170-380 mm FL) collected from Snyder Creek. The upper extent of Warner Sucker distribution in Snyder Creek was documented the following year when postlarval suckers were found in a 100-m section of an unnamed tributary upstream of the "source" springs of the creek (Coombs et al. 1979). The authors report that the tributary, with snow melt as its major water source, was dry except for this 100-m section. Taylor's Meadows appears to be the upper extent of sucker distribution in Honey Creek (Coombs et al. 1979; White et al. 1990; Scheerer et al. 2007; 2011b). Warner Suckers have a somewhat discontinuous distribution in Honey Creek with higher numbers occurring upstream of the Twelvemile Creek confluence (not to be confused with Twelvemile Creek in the Twentymile Creek subbasin[1]) and lower numbers generally occurring in the 6-km canyon reach located directly upstream of the valley floor (Tait et al. 1995; Scheerer et al. 2007; 2011b). Lake-resident suckers are currently unable to migrate upstream past the 7th diversion (Plush-Town diversion) located 3.7 km upstream from the mouth of Honey Creek (Coombs et al. 1979)(Appendix Figure 4), so suckers residing downstream of the diversion are likely a mixture of fish from the lake population and downstream migrants from Honey and Snyder creeks. Few studies have investigated fish use of the irrigation canals in the lower Honey Creek system. Coombs et al. (1979) observed two larval suckers in an irrigation canal south of the fourth diversion but did not provide information on the spatial extent of surveys in the canal system. Scheerer et al. (2008) detected a radio-tagged adult in the canal system north of the same diversion. Overall, the extent that suckers occur in the canal system remains unknown.

Deep Creek – Nearly all suckers collected in Deep Creek, including all adults, have been in the lower 7.6-km reach from the mouth to Starveout diversion, the second diversion upstream from the mouth (White et al. 1990; Scheerer et al 2007). Historically, Deep Creek terminated in the marshland south of the town of Adel, but for the purpose of this report, the mouth of Deep Creek is considered to be located north of Pelican Lake where the meandering channel joins a short east-west ditch (UTM: 11T 0263158

[1] The numerical-distance naming convention of many creeks in the Warner Basin is based on the trail distance from various U.S. Army forts that were once located in the basin. Twentymile Creek was encountered 20 miles along the trail from Fort Bidwell. Twelvemile Creek in the Twentymile Creek subbasin was encountered 12 miles from the same fort whereas Twelvemile Creek in the Honey Creek subbasin was located 12 miles along a trial from Fort Warner.

E, 4678708 N). The only recent evidence of suckers occurring above Starveout diversion was a single sucker (116 mm FL) captured in 2007 in the pool formed by the diversion dam (Scheerer et al. 2007). The diversion dam appears to block upstream movement of lake-resident adults from Crump Lake based on radio-telemetry studies (Scheerer et al. 2006). Juvenile suckers residing below Starveout diversion are likely progeny of lake-resident spawners.

White et al. (1990) found no indication of a stream-resident population in Deep Creek during surveys in 1990. Warner Suckers have not been collected above the barrier falls located 15 km upstream from its mouth with Crump Lake (Snyder 1908; Andreasen 1975; White et al. 1990). Additionally, no adults were observed during snorkel surveys in the 2.9-km reach below the falls (O'Keefe diversion to Deep Creek Falls) in 1994 (Allen et al. 1994) or during electrofishing surveys in 2007 (Scheerer et al. 2007). Access to private land has not been granted in the reach from the Starvevout diversion upstream to the O'Keefe diversions, so the existence of a resident population in this reach is uncertain.

Warner Lakes – In the lake system Warner Suckers are most commonly found in Crump and Hart lakes, the two largest and more permanent lakes in the Warner Valley. When adequate water is present, Warner Suckers inhabit nearly all the lakes, sloughs, and potholes in the valley. The northern-most lake where suckers have been found was Stone Corral Lake (Hartzell et al. 2002)(Figure 1).

Distribution of suckers within Hart Lake appears to shift seasonally. Adult suckers congregate near the mouth of Honey Creek in the spring when there is sufficient creek flow (Allen et al. 1996; Bosse et al. 1997; Scheerer et al. 2012), presumably in preparation for a spawning run. Hartzell et al. (2002) noted that when creek flow was low in the spring, suckers were less congregated near the mouth but still present along the western shore. Scheerer et al. (2016) noted a similar distribution of suckers along the western shore in the spring and suggested that during dry years fish may be falsely attracted to irrigation return flow, thus limiting successful spawning migrations.

Considerable movement within the lakes occurs in the spring. Allen et al. (1996) noted that an adult sucker captured near the mouth of Honey Creek was recaptured the next day over 5 km away near the spillway and again near Honey Creek two weeks later. In the summer months, suckers are more widely dispersed in the lake (Allen et al. 1995) or near the east shore (Allen et al. 1994).

Abundance

Abundance of Warner Suckers has been estimated for the tributaries and Hart Lake (Table 1). Estimates in tributaries include fish as small as 60 mm FL (~age1) whereas only larger fish (~age 3 or greater) were collected during abundance estimates in the lakes.

Streams – Warner Sucker abundance in the tributaries has been evaluated by ODFW since 2007 using a variety of estimation techniques (Table 1). Estimates of Warner Suckers residing in the Honey Creek system have ranged from 2,202 fish in 2007 to 4,495 in 2011 (Table 1). These estimates do not include fish in the lower 3.7-km reach or most of Snyder Creek. A population assessment in the lower 3.7-km of Honey Creek in 2013 estimated 410 suckers (Scheerer et al. 2013). Scheerer et al. (2011b) reported that the highest density of suckers in Honey Creek were in the reach from Twelvemile Creek upstream to Snyder Creek.

Sucker populations in Twentymile Creek have been estimated at approximately 4,700 fish in both 2007 and 2009 (Table 1). Most suckers were observed in the reach from the Dyke diversion upstream to the old O'Keefe Dam on Twelvemile Creek, located 2.5 km upstream from the confluence with Twentymile Creek (Table 1). Based on the length of fish collected, the majority of fish in the population were age-1 or age-2 in 2007 and age-2 and older in 2009 (Figure 5)

Table 1. Warner Sucker population estimates in tributaries and Hart Lake.

Year	Reach	Population estimate	95% CI	Study
		Honey Creek		
2007	All except lower 3.7 km and most of Snyder Cr	2,202	81% [a]	Scheerer et al. 2007[b]
2011	All except lower 3.7 km and Snyder Cr	4,495	3,668 - 5,448	Scheerer et al. 2011b[d]
2013	Town diversion to mouth (lower 3.7 km)	410	169 - 721	Scheerer et al. 2013[e]
		Deep Creek		
2007	Relic Diversion to Starveout diversion (1.3 km)	150	192% [a]	Scheerer et al. 2007[b]
		Twentymile Creek		
2007	All	4,746	164%[a]	Scheerer et al. 2007[b]
2009	All	4,612	3,820 - 5,567	Richardson et al. 2009[c]
2009	Cahill wind deflector to Dyke diversion	677	299 - 1,334	Richardson et al. 2009[c]
2009	Upstream of Twelvemile Cr confluence	49	15 - 85	Richardson et al. 2009[c]
2009	Dyke diversion to O'Keefe Dam	3,779	3,112 - 4,603	Richardson et al. 2009[c]
2009	O'Keefe Dam to Cowhead Slough (Twelvemile Cr)	155	63 - 311	Richardson et al. 2009[c]
2014	Cahill wing deflector to Dyke diversion	482	368 - 638	Scheerer et al. 2014[f]
2015	MC diversion to Dyke diversion	813	761 - 861	Scheerer et al. 2015[f]
2016	Cahill diversion to MC diversion (MC canal)	963	860 - 999	Scheerer et al. 2017[f]
		Hart Lake		
1996	n/a	493	439 - 563	Allen et al. 2006[g]
2008	n/a	565	250 - 1,114	Scheerer et al. 2008[c]
2012	n/a	1,378	705 - 2,650	Scheerer et al. 2012[g]

[a] Relative confidence intervals.
[b] Multi-pass depletion sampling.
[c] Single-census mark-recapture technique.
[d] Bayesian logistic regression capture-recapture model.
[e] Bayesian closed-capture population estimator.
[f] Bayesian Jolly-Seber open-population model.
[g] Schnabel estimator.

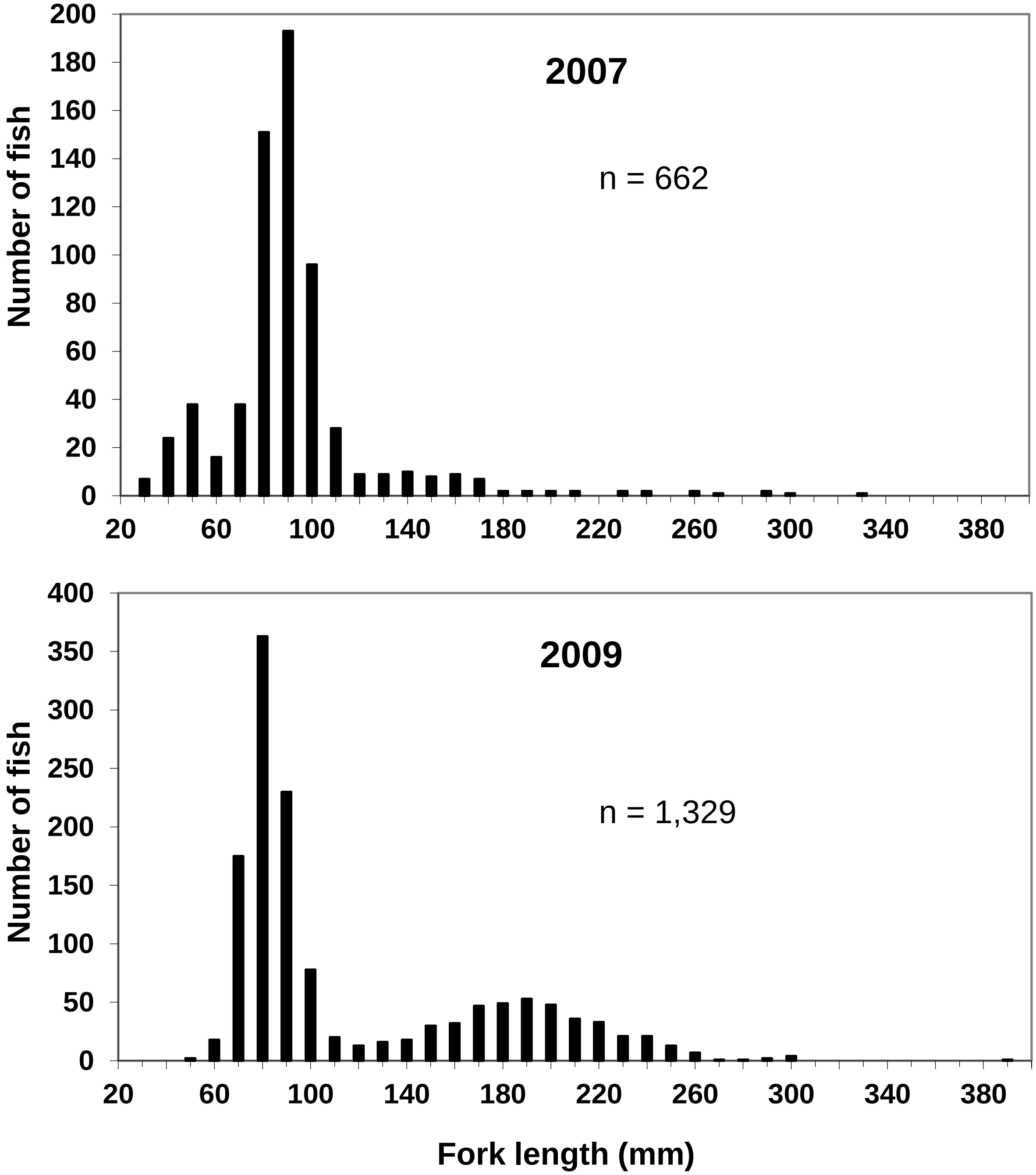

Figure 5. Length frequency distribution of suckers collected from Warner basin tributaries in 2007 (Scheerer et al.).

Lakes – Several studies have attempted to estimate Warner Sucker abundance in the lakes (Coombs et al. 1979; White et al. 1990; Allen et al. 1994; Allen et al. 1995; Allen et al. 1996; Bosse et al. 1997; Hartzell et al. 2001; Scheerer et al. 2006; Scheerer et al. 2008; Scheerer et al. 2012), but recapture rates were only sufficient to estimate abundance in 3 out of 10 years (1996, 2008, and 2012). Although quantitative abundance estimates were not always possible, Hart Lake typically produced greater catch rates of suckers than Crump Lake (Allen et al. 1994; Allen et al. 1995; Hartzell et al. 2002; Scheerer et al 2012).

Allen et al. (1996) estimated 493 (95% CI: 439-563) suckers in Hart Lake in 1996, four years after the lake was completely desiccated (Table 1). The smallest sucker captured was 180 mm SL, or approximately age 4 (see Figure 7). Scheerer et al. (2008) estimated 565 suckers (95% CI: 250-1,114) larger than 155 mm FL based on recaptured fish initially tagged in 2006, with an estimated mortality rate of tagged fish of 33%. In 2012, Scheerer et al. (2012) estimated 1,378 suckers (95%CI: 705-2,650) in Hart Lake with the smallest fish around 125 mm FL. The only other population estimate for fish residing in the lake system was an estimate of 1,316 suckers (95%CI: 666-66,667) in the spillway canal north of Hart Lake (Coombs et al. 1979). The authors caught 198 suckers in the canal over the course of their study, with several appearing spawned out in May.

Genetic Structure

DeHaan and coauthors (2012; 2017) conducted an analysis of genetic variation among Warner Suckers residing in the tributaries by genotyping 164 fish from the three tributaries at 16 microsatellite loci. There was evidence of significant genetic structure among tributary populations (DeHaan and VonBargen 2012; DeHaan et al. 2017). Tests of the genetic fixation index (F_{ST}), genetic assignment tests, and patterns of allele frequency heterogeneity all suggested that each tributary contains a genetically distinct spawning population. Interestingly, suckers residing in Snyder Creek likely represented a genetically distinct population from Honey Creek fish, despite their close geographic proximity and the apparent connectivity of their habitat. Overall, the authors concluded that gene flow among populations was low.

All of the tributary populations had high levels of genetic diversity. The Deep Creek population had the highest level of genetic diversity among the tributary populations, while Honey Creek had the lowest level of genetic diversity, but these differences were not substantial. In one population, Twentymile Creek, a statistically significant excess of heterozygotes suggested that this population may have experienced a recent bottleneck.

The same suite of nuclear microsatellite markers was used to determine the genetic origins of suckers residing in Hart and Crump lakes (DeHaan and VonBargen 2012; DeHaan et al. 2017). Of the 92 fish collected in Crump Lake, all but two were assigned to Deep Creek (the remaining two fish assigned to Honey and Snyder creeks). Nearly two-thirds of the suckers collected in Hart Lake (n=232) were also assigned to Deep Creek with the remainder assigning to Honey Creek, although the proportion was variable among collection years. Overall, their study indicated that Deep Creek is the primary source for lake-resident individuals. The low assignment of lake-resident suckers from the Honey Creek subbasin (and Twentymile Creek) was presumably due to the limited connectivity between these populations and the lake.

Some of the results of the genetics study may be attributable to the sampling location of the tributary sites. Nearly all the Deep Creek genetic samples came from juveniles collected in the lower reach below Starveout diversion where lake-resident suckers purportedly spawn (Coombs and Bond 1980); it is possible that the Deep Creek samples in this study represent the lake population, rather than a distinct tributary population. The reach where the samples were collected, which has a direct connection to the lakes, may be the only reach in Deep Creek where suckers are extant, due to spawning by lake-resident suckers. Additional sampling throughout Deep Creek could clarify the relationship between populations in the lakes and this tributary.

DeHaan et al. also genotyped 68 individuals that were collected from the irrigation canal in the Summer Lake Basin (DeHaan and VonBargen 2012; DeHaan et al. 2017). These fish originated from the salvage of approximately 75 suckers from Hart Lake in 1991, when a drought caused the lake to desiccate. The fish were held temporarily at Summer Lake prior to being transferred to a hatchery. Before the transfer occurred the adult fish spawned in the canal, and their offspring persisted to form a new population. Surprisingly, given their origin, the genotype analysis suggests that the fish at Summer Lake are genetically distinct from the populations found in the tributaries, although more genetically similar to Deep Creek fish than the other tributaries populations based on pairwise F_{ST} estimates. Although this population was founded by a small number of individuals, the genetic diversity of the population was not reduced (relative to tributary populations), did not show genetic evidence of a recent bottleneck, and did not show evidence of increased pairwise relatedness.

Age and Growth

Warner Sucker are thought to live for 20-25 years in the wild. The oldest Warner Suckers collected in the basin were lake-resident fish estimated to be 17 years old based on the aging of opercular bones (White et al 1991). Richardson et al. (2009) compared the precision of aging Warner Suckers with various hard structures and found that opercular bones underestimated age compared to otoliths, so it's likely these fish were actually older. White et al. (1991) suggested that the maximum life span of Warner Suckers may be in the low to mid-twenties. The Warner Sucker is considered to be a sister species of the Tahoe Sucker *Catostomus tahoensis* (Smith 1978), which has a longevity of 27 years based on the aging of otoliths (Scoppettone 1988).

Warner Sucker appear to grow quickly in the first several years of life, with growth continuing at a slower pace past the age of about 8 (Figure 6). Lake-residents attain a larger size compared to stream-residents, presumably due to a richer food source in the lakes, and possibly a longer lifespan.
White et al. (1991) noted considerable variability in growth rate based on the overlap in size between age 17 (320-400 mm FL) and age 10 suckers (310-390 mm FL). The authors attributed the variability to differential growth rates between the faster growing females compared to males, but also likely due to differences in the amount of time fish spent rearing in lakes versus streams. Coombs et al. (1979) also showed growth variability in suckers age 7-8 but not younger fish, based on back-calculated length-at-age derived from scale analysis (Figure 7). This same study noted that sucker growth seems fairly constant at 30-50 mm/yr for fish up to age 8 (Figure 7). Growth rates derived from recaptures of tagged fish show older fish grow at a slower rate. Richardson et al. (2009) reported two suckers in Twelvemile Creek (a Twentymile Creek tributary) were 120-121 mm FL when tagged and grew 90-94 mm after nearly two complete growing seasons, consistent with growth rates reported by Coombs et al. (1979) for age 2-3 year old suckers. A reanalysis of PIT-tag recapture data from Scheerer et al. (2006) found that two suckers that were 323-326 mm FL when tagged grew 52-55 mm over five years, while Scheerer et al. (2008) reported 300-405 FL fish caught in Hart Lake grew only between 0-15 mm over 1.8 to 2.2

years. Slower annual growth rates for older age Warner Suckers is consistent with other western sucker species (Scoppettone et al. 1988).

Warner Sucker likely become reproductively mature at age 3-5. Coombs et al. (1979) reported the presence of spawning checks on scales indicated suckers mature at age 3 to 4. Richardson et al. (2009) cautioned against using scales to age Warner Suckers since they can highly underestimate age compared to otoliths. Scales become more unreliable for aging suckers about the time fish become sexually mature (Scoppettone 1988), so the age at maturity reported by Coombs et al. (1979) may be a slight underestimate.

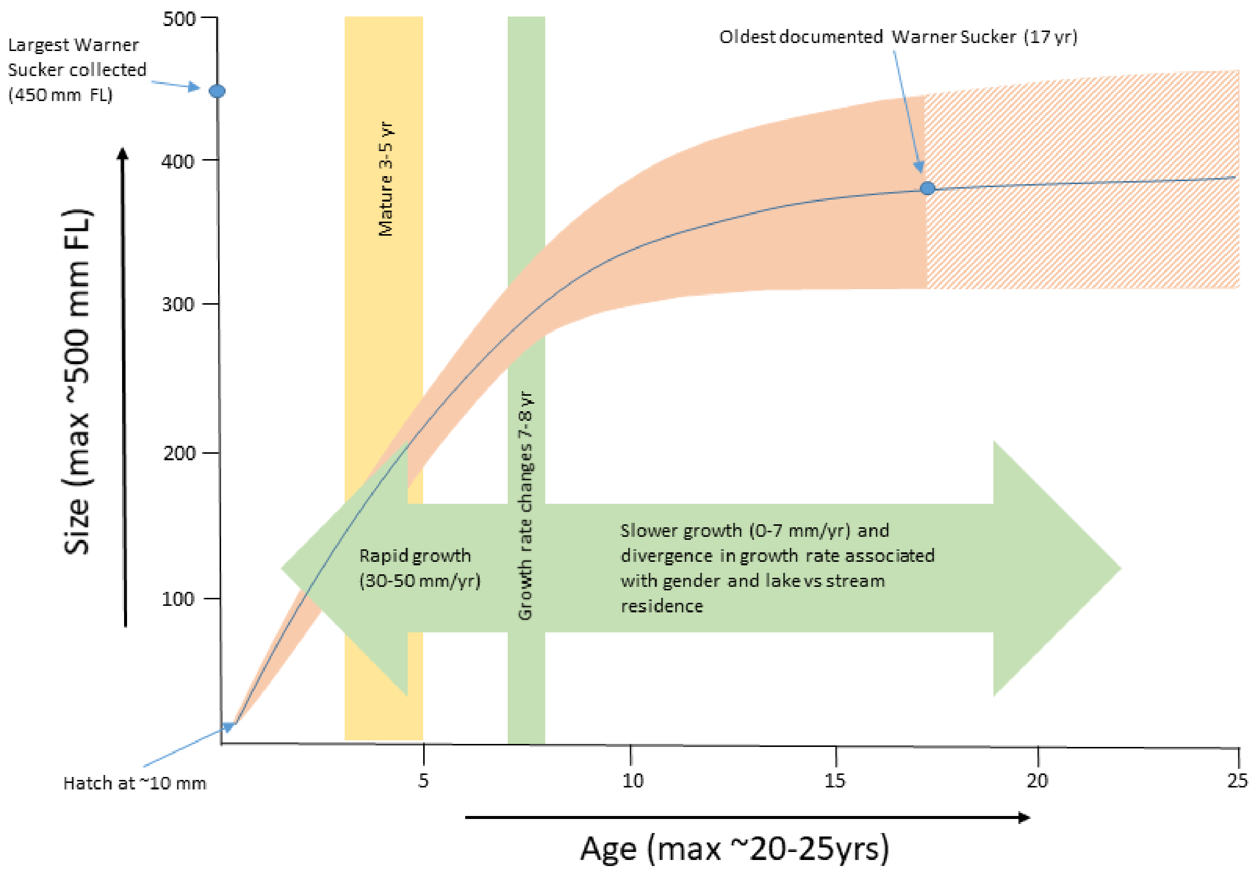

Figure 6. Conceptual model of Warner Sucker age and growth. Growth trajectory based on data presented by Coombs et al. (1979) and White et al. (1991) for lake-resident suckers. Largest sucker collected was from Hart Lake (Scheerer et al. 2006).

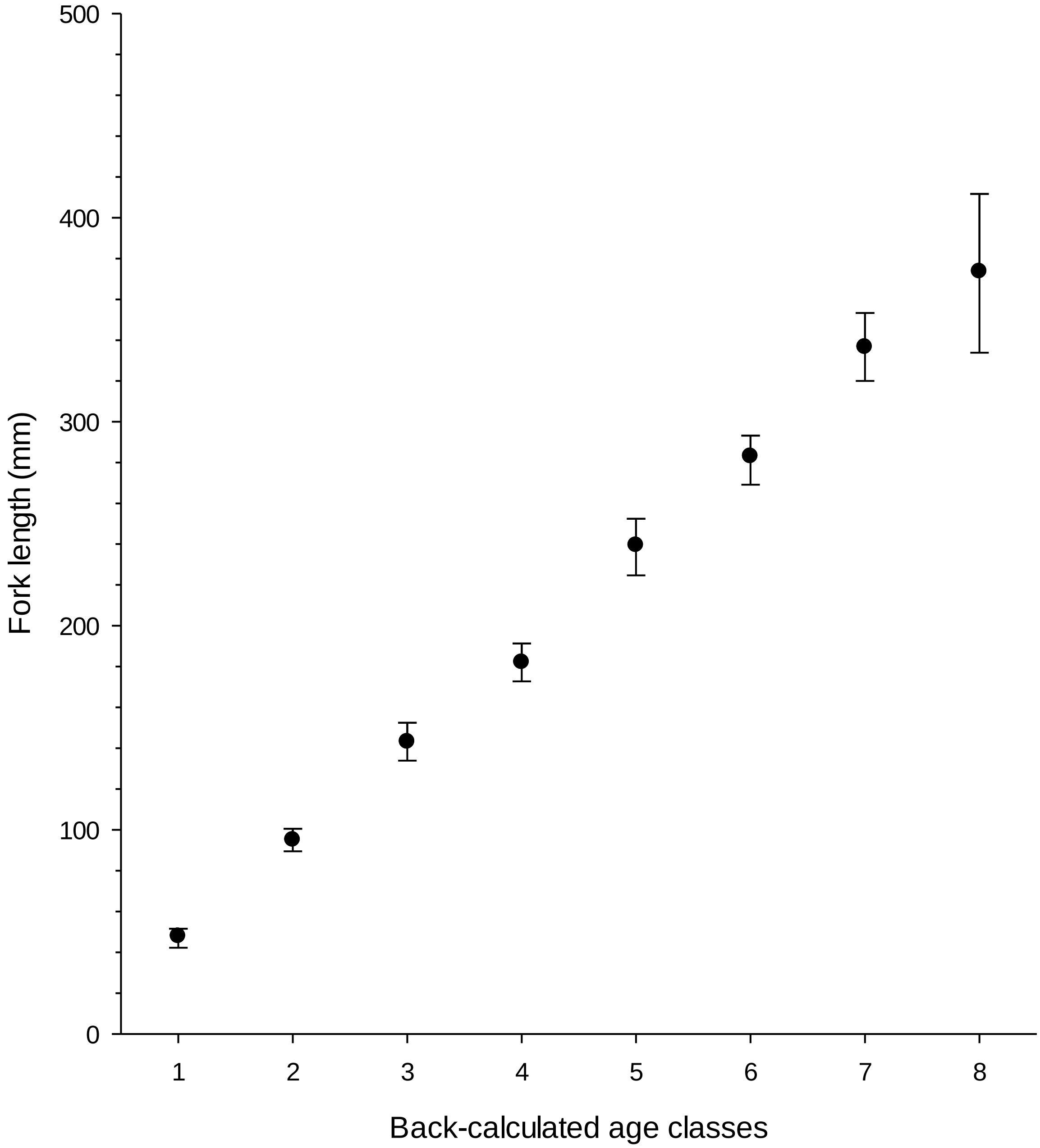

Figure 7. The mean values and 95 percent confidence intervals for back-calculated fork length at the time of each annulus formation (age class) of *Catostomus warnerensis* based on scales (n=50). Figure adapted from Coombs et al. (1979) using the author's reported standard length to fork length conversion. Fish used for aging were captured throughout the Warner Basin with most captured in the spring, so size at age would be prior to expected annual growth.

Early Life history

Larval Warner Suckers emerge from the gravel at a total length of around 10 mm in late spring and early summer (Kennedy and Vinyard 1997). In streams, larvae occupy vegetated areas with low to moderate flow and relatively shallow depths along stream margins or backwater areas during the first few months after hatching (~10-17 mm TL)(Coombs et al. 1979; Kennedy and Vinyard 2006). As the larvae grow in size, they move into mid-water habitats with moderate flows (Coombs et al. 1979; Kennedy and Vinyard 2006). Larvae select microhabitats with focal point velocities (FPV) between 3-6 cm/s and avoided areas with FPV >15 cm/s (Kennedy and Vinyard 2006). They feed on invertebrates in the upper half of the water column with planktonic cladocerans dominating the diet (Coombs et al. 1979; Tait and Mulkey 1993a). They also appear to segregate from larval Speckled Dace *Rhinichthys osculus* by feeding higher in the water column (Coombs et al. 1979). At night larvae move closer to shore, presumably to avoid entrainment into swift currents when visual orientation in the stream is lost (Kennedy and North 1993; Kennedy and Vinyard 1997).

Larval suckers are rarely collected in drift samples (Coombs et al. 1979; Kennedy and Vinyard 1997; Kennedy and North 1993; Bosse et al. 1997; Richardson 2009) and express a distinct drift avoidance behavior. Kennedy and Vinyard (1997) measured the response of larval suckers to artificial entrainment in mid-channel current and found larvae of all sizes (16-30 mm TL) resisted downstream displacement. Once released into the current, fish would immediately seek current refugia behind rocks and vegetation. The farthest downstream displacement was <3 m by the smallest size group studied. The authors speculate that this drift avoidance behavior may have evolved because of the unreliability of downstream lake habitat that periodically desiccate. The natural disappearance of the streamflow into the shallow marshland during the low-flow summer months may also be a selective pressure influencing this behavior. Warner Suckers are unique from other western suckers in that larvae do not drift downstream after hatching in streams (Cooperman and Markle 2011, Kennedy and Vinyard 1997).

As larvae develop into juveniles they become more bottom orientated. During the day juveniles associate with macrophyte beds, while at night they move into riffles and open areas to feed (Tait and Mulkey 1993a). Several other studies have noted that movements of both juvenile and adult Warner Suckers are primarily nocturnal (Richardson et al. 2009; Scheerer et al. 2015; Scheerer et al. 2016). Most juvenile foraging time (75%) occurs over large gravel or boulders, where they likely feed on diatoms, filamentous algae, and detritus (Tait and Mulkey 1993a).

Lake Emigration – The length of time suckers spend in streams before migrating to the lakes is uncertain. Based on the drift avoidance of young-of-year suckers, it is plausible that suckers do not migrate in their first year of life. Coombs et al. (1979) speculated that suckers spend 2-3 years in streams before migrating to the lakes. This would mean they begin to enter the lakes about the time they become sexually mature at age 3 or 4 (130-210 mm FL). Several studies have measured the size of suckers in Hart and Crump lakes to assess recruitment into the lake population (Table 2). The youngest suckers collected among the studies ranged from 1-6 years with age 3 and 4 suckers occurring at the highest frequency (Table 2). Age-1 suckers are particularly rare in lakes; in years when age-1 suckers were collected, only a single individual was recorded in each lake (Table 2). Several studies attributed the lack of smaller fish to reproduction or recruitment failure due to predation by invasive species (White et al 1990; Allen et al. 1995; Bosse et al. 1997; Hartzell et al 2002; Scheerer et al. 2006). An alternative hypothesis is that Warner Suckers do not generally enter lakes until they are age 3 or 4, or in years when densities are high in the streams. In this respect, the lakes may act as a repository for adult fish that increases the overall population size in the basin beyond the carrying capacity of the stream alone.

Table 2. Minimum size and age of Warner Suckers collected in nets from lakes in the Warner Basin. Age determined from length at age data from Coombs et al. (1979) unless otherwise stated. Numbers in parentheses are number of nets deployed by mesh size.

	Hart Lake		Crump Lake			
Year	Minimum size (mm)	Age	Minimum size (mm)	Age	Net mesh size (mm)	Study
1990	275 SL	6	136 SL	3	14; 22	White et al. 1990
1991	264 SL	5[a]			14; 22	White et al. 1991
1994	136 SL	3			14; 22	Allen et al. 1994
1995	215 SL	5	202 SL	5	6; 22	Allen et al. 1995
1996	180 SL	4	70 SL	2	6; 22	Allen et al. 1996
1997	103 SL	3	160 SL	4	6 (41); 22(1)	Bosse et al. 1997
2001	169 SL	4	154 SL	4	6 (1); 22 (5)	Hartzell et al. 2002
2006	~45 FL	1[b]	55 FL	1[b]	6 (1); 13 (5); 19 (6)	Scheerer et al. 2006
2008	241 FL	5	155 FL	3	6 (1); 13 (5); 19 (12)	Scheerer et al. 2008
2012	69 FL	1[b]	155 FL	3	13 (2); 19 (22)	Scheerer et al. 2012
2017	130 FL	3			19 (18)	Scheerer and Meeuwig 2017

[a] Age provided by White et al. 1991.

[b] Only one age-1 individual collected. Next largest suckers were age 4 in Crump Lake in 2006; age 6 in Hart Lake in 2006; age 3 in Hart Lake in 2012.

Spawning

Warner Sucker spawning typically occurs in the tributaries during spring, similar to many sucker species in the western North America (Harris 1962; Scoppettone and Vinyard 1991; Weiss et al. 1998). Many lacustrine suckers are obligate stream spawners (Scoppettone and Vinyard 1991), but some, like the Tahoe Sucker, have been observed spawning in both streams and lakes (Kennedy and Kucera 1978). In normal to wet water years, adult Warner Suckers that are rearing in the lakes ascend the tributaries to spawn, but will attempt to spawn in the lakes when low tributary flows do not allow for upstream migration (White et al. 1990). The frequency of lake spawning prior to irrigation development is unknown, but has likely increased since diversion dams block tributary access and irrigation withdrawals result in more years of low tributary flows.

Lake Spawning – The only direct observation of lake spawning was by White et al. (1990) in Hart Lake in the spring of 1990. Flow from Honey Creek (measured at the gauge above the diversions) was <40 cfs throughout the spring, with irrigation withdrawals likely resulting in little flow at the mouth. During the course of sampling lake-resident fish, the authors reported the following:

> On 9 April 1990, we noticed spawning activity in the shallow water along the east shore of Hart Lake. We first noticed the splashing and thrashing about of what appeared to be small groups of fish digging nest in the substrate gravels. Spawning was observed until the 18th of April, at points all along the east shore of Hart Lake as far south as the rock jetty.

The authors reported that spawning appeared to cease following a cold snap on 18 April and no spawning was observed after water temperatures returned to levels previously recorded during the spawning event (14.4-21.1 °C). The timing of the spawning event was about a month earlier than any other observation of spawning or spawned-out adults in the basin. The only other indication of spawning in April was from Coombs et al. (1979), who reported collecting spawned-out adults in the spillway canal north of Hart Lake from 29 April through 24 June. The early spawning in 1990 may have been the result of unseasonably warm weather that occurred for several days prior to and during the spawning (R. White –personal communication), resulting in lake temperatures reaching levels suitable for spawning.

Direct observation of lake-spawning has not been observed since 1990. The following year (1991) was another dry year and White et al. (1991) did not observe spawning in the lake during sampling from March through June; lake levels had receded to the point that the shoreline was comprised of the muddy substrate that made up the lake bed. The only other direct observation of spawning by lake-resident suckers were of the Hart Lake fish that were translocated to the Summer Lake Wildlife Management Area (SLWMA) in early May 1991. They were first observed spawning on 14 May, with spawning continuing until June. The first larval fish was observed on 17 June. Water temperature in the spring-fed ditch was 17°C. Although lake spawning has not been observed since 1990, other studies have reported catch of adults in Hart Lake that suggest spawning may have occurred along the east shore in other years. Hartzell et al. (2002) sampled Hart Lake in the spring of 2001 when lake elevations and flows from Honey Creek were similar to conditions reported during the 1990 spawning event. They did not observe suckers congregating near the mouth of Honey Creek as in previous years, but reported their largest net catch occurred on 14 May along the east shore where spawning was observed in 1990, with ripe adults comprising much of the catch. Based on these observations, we hypothesize that lake spawning may only occur under the rare environmental conditions where tributary flow is too low for migration upstream, but lake levels are high enough to inundate the cobble along the shoreline.

Lake-resident suckers are often found in the spillway canal of Hart Lake during the spawning season when the lake level is high enough to facilitate spill. Coombs et al. (1979) captured 198 suckers in the canal with many appearing to be ripe or spawned out. Williams et al. (1990) reported suckers entering the canal after water began spilling in mid-May 1989 and collected seven 'spawners' in the canal in June. Two suckers collected from the spillway canal in the spring of 1995 were thin, with eroded anal and caudal fins, indicative of spawned-out fish (Allen et al. 1995). The origin of the suckers captured in the canal is unknown: they may be from Hart Lake or the smaller lakes to the north.

It is unclear whether spawning is actually occurring in the canal or if suckers are attracted to the area for other reasons. Coombs et al. (1979) did not observe sucker larvae in the turbid canal water but visibility was poor. Appropriate spawning substrate may not be present in the canal. Coombs et al (1979) described the substrate as mud-silt with some boulders near the spillway and mainly a hardpan bottom with a thin layering of silt elsewhere. Capture data from Allen et al. (1996) showed 16 adult suckers, many of them ripe, moving between the mouth of Honey Creek and the spillway area in the spring of

1996 (Figure 7). Flow from Honey Creek was relatively low all spring, except for a brief pulse from 17-24 May. Interestingly, several of the suckers originally captured near the spillway were recaptured at the mouth of Honey Creek during or immediately after the flood pulse with some of these fish returning to the vicinity of the spillway in early June (Figure 8). A similar pattern of movement from the north of Hart Lake to Honey Creek and back to the north end of the lake was observed with radio-tagged suckers by Scheerer et al (2008). These observations are consistent with increased streamflow acting as a cue for spawning migration, as occurs in other sucker species (Tyus and Karp 1990; Modde and Irving 1998).

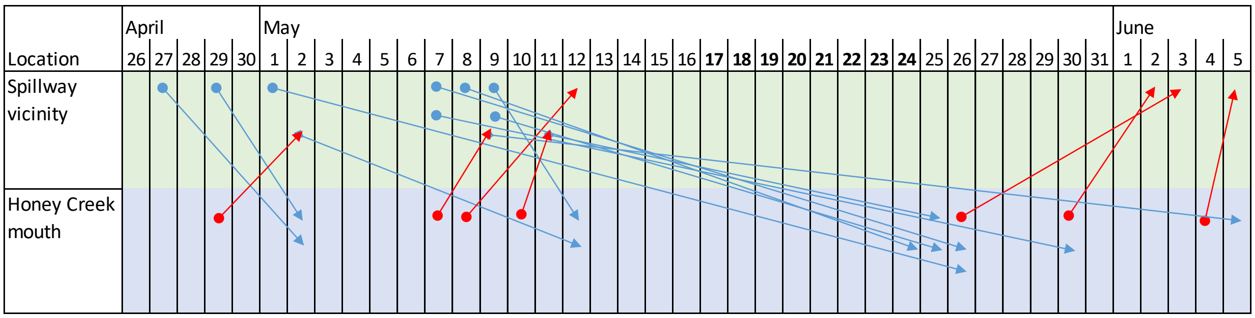

Figure 8. Movement of adult Warner Suckers in Hart Lake between the mouth of Honey Creek and the spillway vicinity based on capture data from Allen et al. (1996). Dots indicate location and date of initial capture and triangles indicate location and date of recapture. The bold dates indicate the period when Honey Creek flows were over 200 cfs. Most suckers were captured within 100 m of the spillway.

Typically, spawning by lake-resident suckers is thought to occur in tributaries when flows are sufficiently high to allow upstream migration. Adult suckers from Hart Lake tend to congregate near the mouth of Honey Creek during the spring, presumably in preparation of a spawning run into the creek (Williams et al. 1990; Allen et al. 1995; Allen et al. 1996; Scheerer et al. 2006; Scheerer et al. 2012). Several reports document lake-resident suckers entering Honey Creek in the spring. Swenson (1978) collected an adult below the 7th diversion from the mouth (Plush-Town diversion) on 02 May, 1978 and speculated that it must have entered Honey Creek sometime in April before stoplogs were added to downstream diversion dams (Appendix Figure 4). Scheerer et al. (2006) detected a radio-tagged adult from Hart Lake just downstream of the Plush-Town diversion in mid-May of 2006. Coombs and Bond (1980) caught an adult sucker ascending the mouth of Honey Creek on 09 April, 1980 and caught another sucker below the 4th diversion (East Field diversion) on 29 April. Scheerer et al. (2006) collected a spawned-out female on 11 May in a screw trap located at the mouth of Honey Creek, presumably reentering the lake after spawning. Passive integrated transponder (PIT) antennas located at the mouth of Honey Creek detected PIT-tagged suckers entering the creek from 25 April to 26 May, 2009 (Richardson et al. 2009) and from 30 April to 18 June, 2012 (Scheerer et al. 2012). Based on these studies, it appears suckers enter Honey Creek in April and May but are unable to ascend farther than the Plush-Town diversion. Spawning likely occurs somewhere in the 3.7 km reach below the Plush-Town diversion, depending on the timing of the spawning run and when stoplogs are installed at the various diversions.

The lower 2 km of the Honey Creek contains poor quality spawning habitat with sparse areas of gravel that are mostly covered with silt (Scheerer et al. 2013), so productivity in this reach may be low. Williams et al. (1990) noted only two riffles between Hart Lake and the first diversion (Rookery diversion) with suitable gravel for spawning (Appendix Figure 4). A fish ladder was installed at the Rookery diversion in 2015, but prior to that year the two riffles were likely the only spawning areas accessible to lake-resident suckers after stoplogs were installed in the spring. Williams et al. (1990) reported collecting a few larval suckers below the diversion in 1989. Scheerer et al. (2006) observed larval suckers in Hart Lake near the mouth of Honey Creek in early-June 2006.

Before the construction of Priday Reservoir, suckers from Hart Lake would spawn in Fish Creek (Coombs and Bond 1980). The authors report that several local ranchers described the creek as having had large runs of spawning suckers. Given that the small creek dries up relatively early in the year, the authors speculated that spawning must have occurred in the lower few miles. It is unclear how much Priday Reservoir and irrigation diversions have altered flows to the lower creek, but it's possible that in wet water years, spawning is still attempted in the creek. Although the literature does not mention other small creeks as potential spawning streams for lake suckers, the intriguingly-named Sucker Creek that currently flows into upper Greaser Reservoir near the southern end of the valley (Figure 1) may be worth further investigation. The lower 1.5 km of the creek is low-gradient with suitable spawning substrate.

Suckers residing in Crump Lake appear to spawn in lower Deep Creek. Scheerer et al. (2006) detected a radio-tagged adult from Crump Lake that had migrated up Deep Creek to a point just downstream of Starveout diversion by mid-May 2006. Coombs and Bond (1980) collected spawned out adults in Deep Creek near Pelican Lake, but none above Starveout diversion, and speculated that spawning is occurring below this diversion. It appears that all spawning by lake-resident suckers in Deep Creek occurs below the impassable Starveout diversion located 7.6 km from the mouth.

There is some evidence that adults from Crump Lake may also spawn in the slough between the lake and Greaser Dam. Young-of-year suckers were collected in the slough in 1989 (Williams et al 1990) and 1990 (White et al. 1990). Allen et al. (1996) captured a 270 mm adult sucker from the base of the dam and suggested that spawning may occur between the impassible dam and Crump Lake.

Besides suitable habitat, increases in water temperature and streamflow can both influence spawning in western sucker species (Tyus and Karp 1990; Modde and Irving 1998). The variability in the timing and location of spawning by lake-resident Warner Suckers may be due to the interannual variability in these cues. For example, in years when water temperatures and substrate are suitable in the lake before streams flows increase to levels sufficient to permit migration, some suckers may attempt to spawn in the lake. It is unknown whether a portion of the lake-resident Warner Sucker population will skip spawning in years when spawning conditions are not favorable in the basin (i.e., when lake levels do not inundate cobble shoreline and tributary flows are low). Skipped spawning by a proportion of the adult population can occur in western lacustrine sucker species when drought conditions prevent upstream migration or reduces lake spawning habitat (Scoppettone et al. 2000; Burdick et al. 2015: Scoppettone et al. 2015). Although Warner Suckers are not considered true lacustrine suckers, lake populations may be operating as such since diversion dams and irrigation water withdraws have reduced stream flows and lake levels.

Stream Spawning – Direct observations of Warner Suckers spawning in tributaries are rare. White et al. (1991) observed spawning on 02 June 1991 below the former O'Keefe Dam in Twelvemile Creek, approximately 2.5 km upstream from the confluence with Twentymile Creek. The authors observed a group of adults swimming in 25 cm of water near the shore directly below the outflow of the dam in well oxygenated, 17°C water. A brightly-colored sucker was observed stirring up gravel and silt, and four more fish moved in and further stirred up the sediment. Although egg and milt disposition could not be observed through the suspended sediments, the authors did collect eggs in the area afterwards. Kennedy and North (1993) observed spawning in the same pool the following year on 19 May, 1992. Five males and two female suckers ranging in size from 130-200 mm TL were observed spawning repeatedly in the area. Water temperature was 20.5°C, depth was 46-77 cm, and substrate was gravel covered by detritus. There was no noticeable flow in the area of spawning.

Observed spawning behavior in suckers involves two males approaching each side of a female that is at rest on the substrate. The males spread their fins and press against the female. All three members of the spawning trio arch their backs and vibrate rapidly, releasing eggs and milt. Simultaneously, all three fish dig into the substrate with their anal and caudal fins, partially burying the fertilized eggs (Reighard 1920; Page and Johnson 1990). Additional males in the area may attempt to sneak in to fertilize eggs. The trio spawning behavior was observed in Warner Suckers held in captivity at the High Desert Museum in Bend, Oregon (Jon Nelson–High Desert Museum, pers. comm.; https://www.youtube.com/watch?v=4Ntp9dfObYo).

Although direct observations of stream spawning events are rare, information on the general location of Warner Sucker spawning can be inferred from the presence of postlarval suckers (the stage immediately after yolk sac absorption, 11-17 mm SL). Postlarval Warner Suckers actively avoid drifting downstream (see section on early-life history), therefore the location of fry aggregations may provide an approximate location of spawning. Kennedy and North (1993) did not observe larvae in the pool below the O'Keefe Dam in 1992, but they did observe a distinct concentration of postlarvae approximately 100 m downstream. Another aggregation was observed approximately 200 m upstream of the O'Keefe Dam, suggesting spawning occurs above the old dam site as well. Additional fry aggregations were observed at the confluence of Twentymile and Twelvemile creeks and upstream of the MC diversion in a boulder-strewn pool near an alfalfa field. Coombs et al. (1979) observed postlarvae in Twentymile Creek 50 m upstream of the confluence with Twelvemile Creek, suggesting suckers use this reach to spawn. Tait and Mulkey (1993b) conducted snorkel surveys in 1-mile reaches in the Twentymile Creek system in 1993 and reported the highest concentration of young-of-year (YOY) in the reach that extended from the Twentymile-Twelvemile creeks confluence to one mile downstream. In 1994, the highest snorkel counts of YOY were in a 1.8-mile reach extending downstream from the O'Keefe Dam (Tait et al. 1995). Coombs and Bond (1980) reported larval suckers at the confluence of Twentymile and Twelvemile creeks. These observations suggest spawning occurs in multiple locations in the creek system with most spawning occurring in the lower Twelvemile Creek reach.

In Honey Creek, no direct observations of spawning has been reported. Longtime local residents of the Warner Valley reported that in the late 1930's large numbers of suckers from the lakes would ascend the creek in the spring and travel far up into the canyon to spawn (Andreasen 1975). Information on the spawning locations of the stream population can be inferred from observation of postlarval suckers. Coombs et al. (1979) reported a few postlarval suckers between the eighth diversion (JJ diversion) and the mouth of Honey Creek, none in the 8 km canyon reach between the eighth diversion and Deppy Creek, and a fairly continuous distribution upstream of Deppy Creek to the Taylor Meadows. Although no larval suckers were observed in the canyon reach in 1979, larvae were observed in the reach by Tait and Mulkey (1993) and Tait et al. (1995), with the greatest density just below Deppy Creek. In Snyder Creek, postlarval suckers were observed in the reach directly below the 'source' springs and in an unnamed tributary upstream of the springs, but no larvae were found in the lower 8 km of the creek. This suggests spawning in Snyder Creek occurs within the vicinity of the springs.

Sexual Differences. – Sexual dimorphism in the shape of the anal fin is common in Catostomids (Reighard 1920; Page and Johnston 1990) and is true of Warner Suckers as well. The distal end of the anal fin on male Warner Suckers is very broad and rounded whereas females have narrower fins and the distal edge is angular (Coombs et al. 1979). During the spawning season, tubercles also develop on the anal and caudal fins of male fish. A colored lateral band usually develops during the spawning season ranging in intensity from pink to bright red on both males and females, but more frequently on males (Coombs et al. 1979).

Several studies have documented that females outnumber males in the lakes (White et al 1991; Allen et al. 1994, 1996; Bosse et al. 1997; Hartzell et al. 2002; Scheerer et al. 2006, 2008, 2011a, 2012). The percentage of females in the lakes population has ranged from a low of 52% (Allen et al. 1994; Scheerer et al. 2012) to as high as 73% (White et al. 1991). A greater proportion of females appears to hold for stream populations as well with the percentage of females in Twentymile Creek ranging from 54-60% (Scheerer et al. 2008; Richardson et al. 2009). Females of several sucker species outlive males (Harris 1962; Hauser 1969), which may account for the greater proportion of females in the Warner Sucker population.

Life History Considerations and the Future of the Warner Sucker

Warner Suckers are uniquely adapted to life in the semi-arid landscape of the Warner Basin. The avoidance of downstream drift by larval suckers is an example of a life history characteristic that likely evolved as the landscape became drier. When pluvial Lake Warner existed in the Pleistocene, the ancestral suckers inhabiting the basin likely had an adfluvial life history similar to many western lacustrine sucker species, with larvae immediately drifting downstream into lakes. This strategy would have become less favorable as Lake Warner gradually dried and streams terminated in the shallow marshlands during the period of larval outmigration in the summer.

The plasticity in spawning behavior would also seem to benefit the Warner Sucker in the semi-arid basin that experiences considerable variability in streamflow and lake levels between wet and dry years. Both lake and stream spawning behaviors by lake-resident suckers may be alternate strategies to deal with interannual variability among water years. Each spawning strategy would have a different level of reproductive success depending on the water year and environmental conditions that together would act as an evolutionarily stable adaptation for this long-lived, iteroparous species. The interannual frequency of lake spawning is currently not known. Although occurring rarely at present, these environmental conditions may become more common in the future. Most climate projections predict increased winter runoff and reduced spring and summer streamflows in the western United States (Maurer et al. 2007; Chambers 2008; Hidalgo et al. 2009). This would likely result in an increased frequency of years when the lakes are full but streamflows are insufficient to allow successful upstream spawning migrations in the Warner Basin.

Warner Suckers have been able to adapt over thousands of years to the effects of a drying climate in the Warner Basin. However, recent changes to the aquatic environment, specifically irrigation development and the introduction of invasive species to the lakes, are thought to have reduced the species' range and abundance (U.S. Fish and Wildlife Service 1985). Prior to irrigation development in the basin, there were undoubtedly drought years when low streamflows limited or prevented successful upstream spawning migrations of lake-resident suckers. However, the construction of diversion dams in the lower stream systems has exacerbated the problem by limiting or preventing successful spawning migrations by lake-resident fish. It appears that some diversion dams (i.e., Plush-Town diversion on Honey Creek and Starveout diversion on Deep Creek) are complete barriers to upstream passage, while others are partial or intermittent barriers. Diversion dam operations usually begin in the spring and coincide with upstream spawning migrations, so all the dams have the potential to block upstream migration, depending on when stoplogs are put in place to divert water. If managers desire to improve spawning success of lake-resident suckers then it will be important to address any barriers to upstream movement.

The other major change to the aquatic environment of the Warner Basin has been the introduction of invasive predatory fish species in the lakes. Crappie *Pomoxis* spp. and brown bullhead *Ameiurus nebulosus* are now common in the lakes and are purported to have a negative impact on suckers via predation on juveniles, although actual predation has not been directly observed. The extent that predation impacts suckers depends on the frequency of juvenile production in the lakes and the size of stream-resident suckers that migrate to the lakes. If Warner Suckers typically rear in streams for 2-3 years and enter the lakes at a larger size, then their vulnerability to predation would be limited because they would exceed the gape size of most predators. Understanding the recruitment dynamics of the lake population would help clarify whether predation by invasive species is a threat; however, recruitment dynamics may change as dam modifications increase access by lake suckers to spawning habitat farther upstream.

In summary, Warner Suckers have adapted to thrive in the geographically limited range and harsh semi-arid conditions of the Warner Basin. Relatively recent anthropomorphic alterations to the aquatic environment in the valley presents challenges to the species' ability to express the full suite of its life history characteristics. Recently, there has been a concerted effort among management agencies and landowners to provide fish passage through the numerous diversion dams and to screen irrigation canals in the valley. These changes, along with other habitat improvements, should help Warner Suckers better carry out all aspects of their life history.

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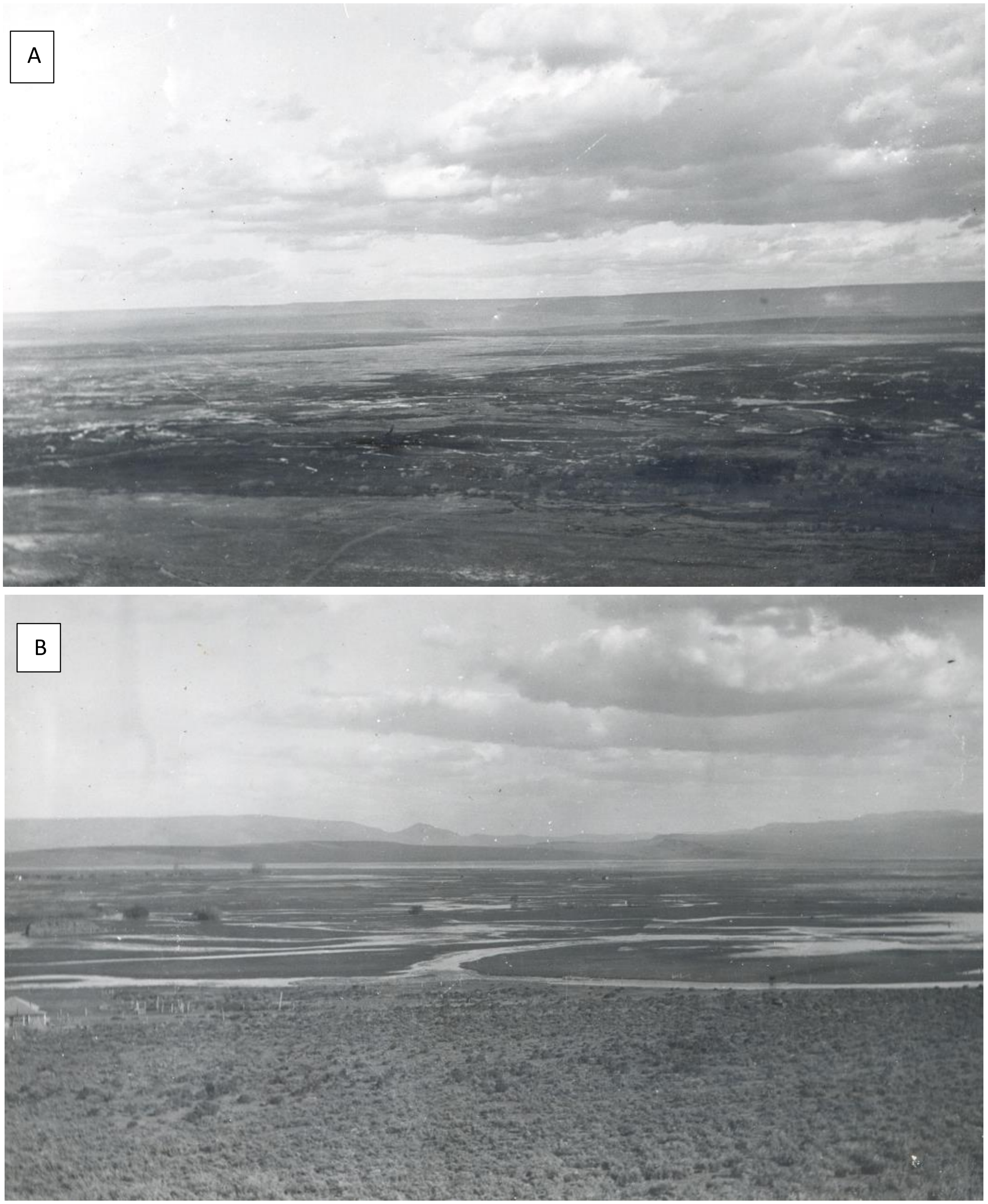
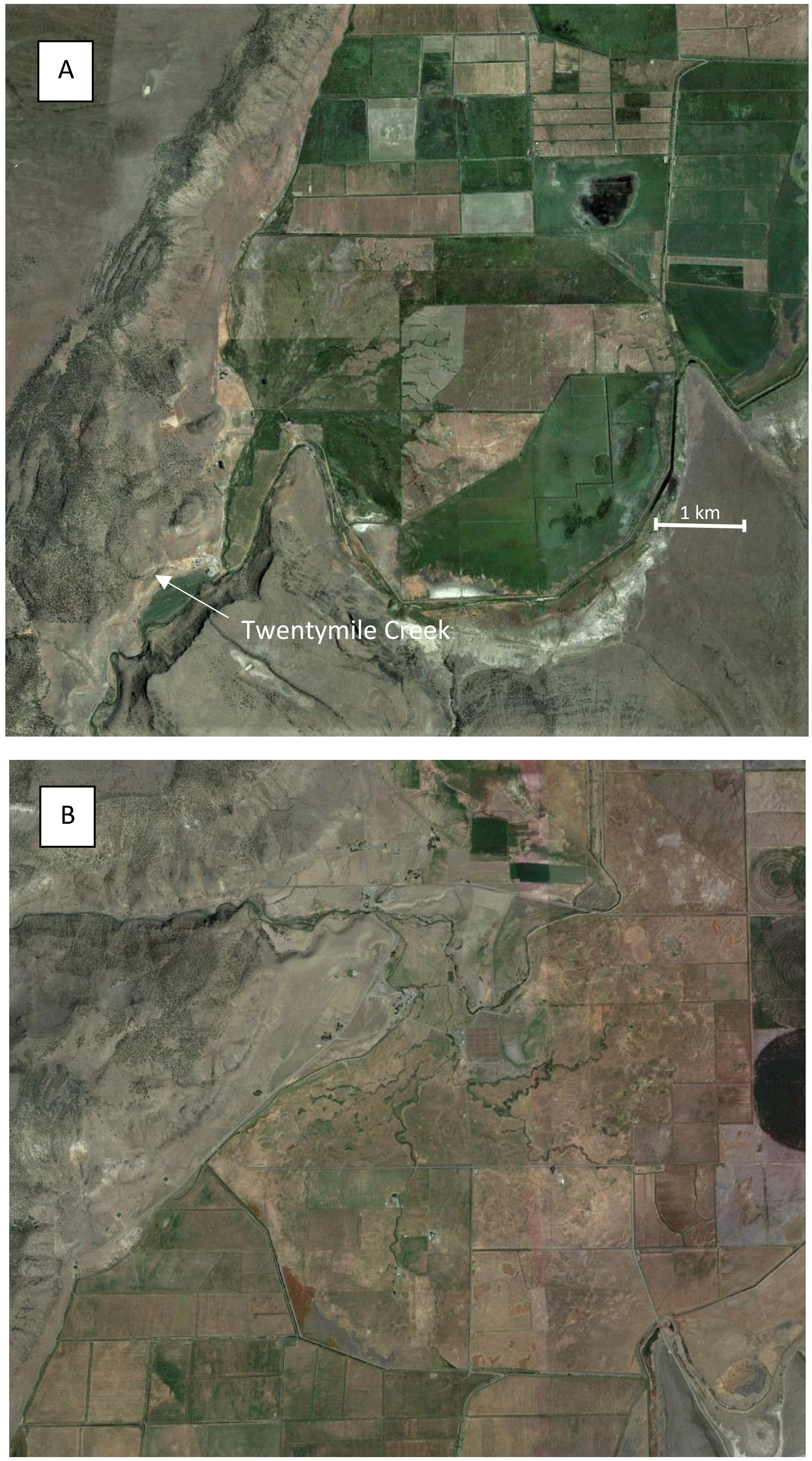
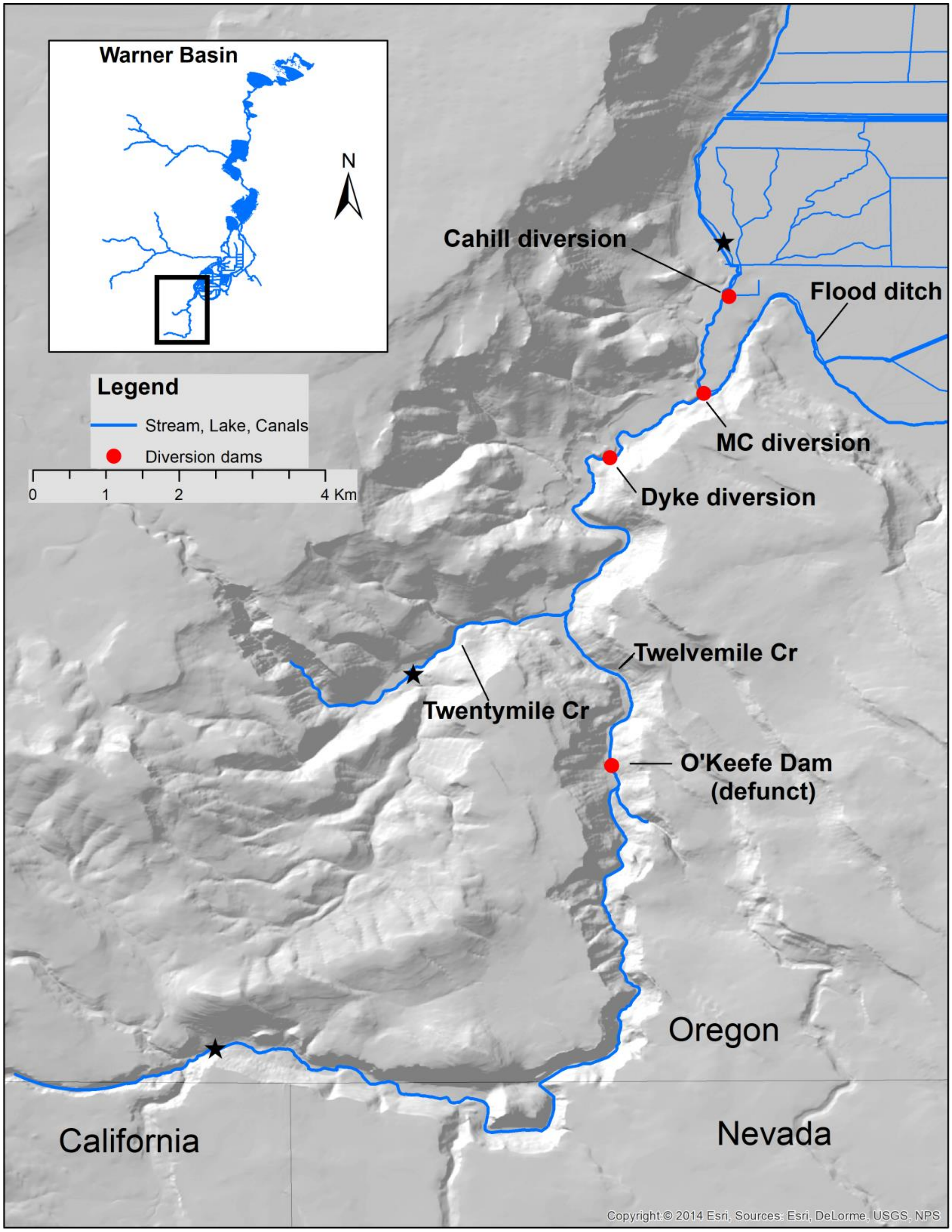
Appendix



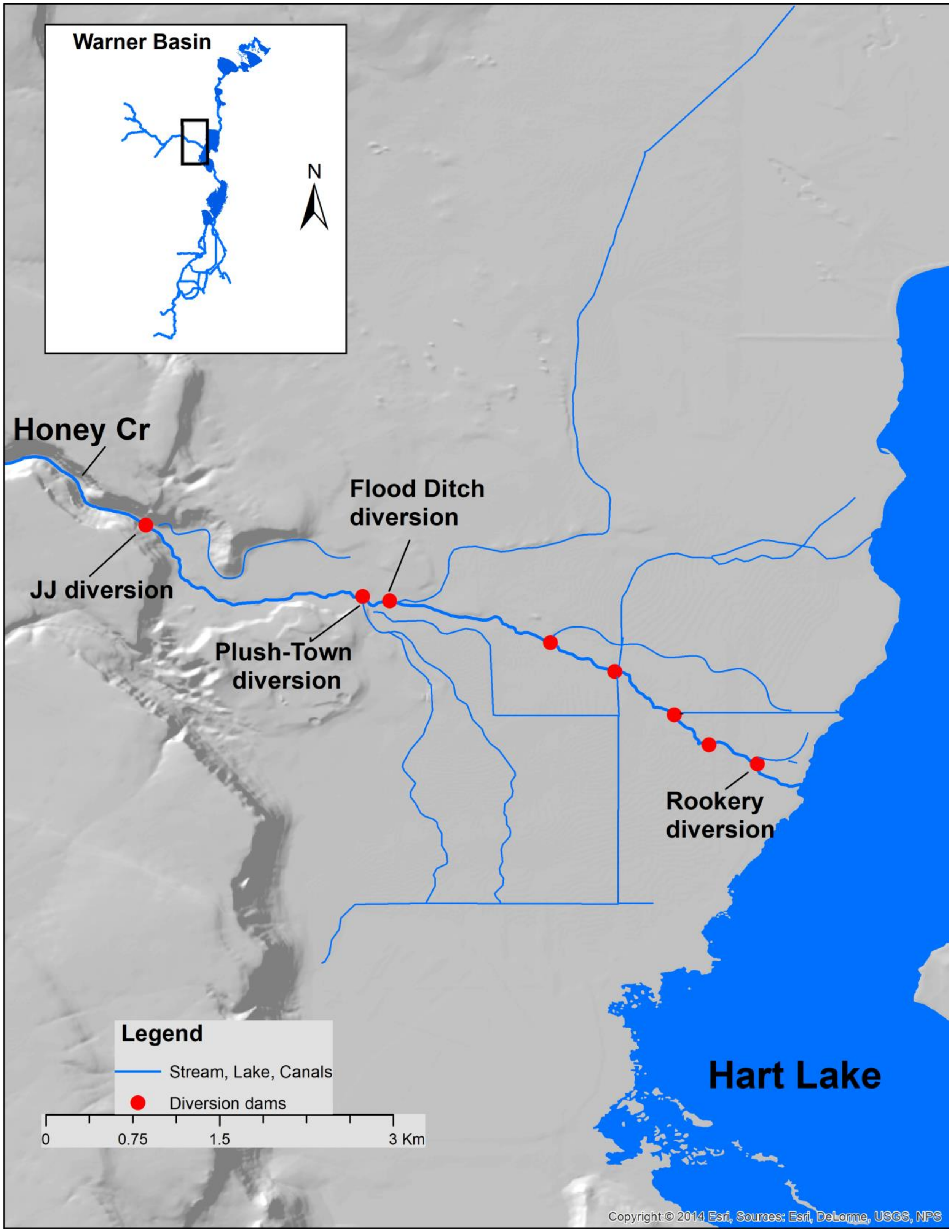
Appendix Figure 1. Photos of South Warner Valley overlooking flooded marshland near Twentymile Creek (A) and Deep Creek (B) taken in the spring of 1921. Twentymile Creek photo taken on 27 April, 1921 looking north-easterly from a point on the hill above Cressler Ranch house with location of photo given as Section 13, Township 40S, Range 23E. Deep Creek photo taken on 07 May, 1921 looking east over part of MC Ranch south of Adel with location given as NW1/4-SE1/4 Section 29, Township 39S, Range 24E. Photos from Stricklin and Perry 1923.



Appendix Figure 2. Satellite imagery showing remnant channels terminating in the marshland on the valley floor for Twentymile Creek (A) and Deep Creek (B). Imagery from Google Earth.



Appendix Figure 3. Map of Twentymile Creek subbasin showing canals, streams, irrigation diversion dams, and upper- and lower-most distribution on Warner Sucker**.** Star symbols denote lower- and upper-most locations of Warner Sucker observed in the subbasin, not including the reported observation in West Barrel Creek in the Cowhead Slough subbasin.



Appendix Figure 4. Map of lower Honey Creek showing canals, stream, and irrigation diversion dams.