

AN ABSTRACT OF THE THESIS OF

Susan A. Reithel for the degree Master of Science in Fisheries Science presented on August 18, 2006.

Title: Patterns of Retention and Vagrancy in Larval Lost River and Shortnose Suckers from Upper Klamath Lake, Oregon.

Abstract approved:

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Larval transport and retention of two endangered suckers were studied in a highly altered lacustrine/riverine complex. The endangered populations of Lost River sucker, *Deltistes luxatus*, and shortnose sucker, *Chasmistes brevirostris*, in Upper Klamath Lake (UKL), Oregon are the largest remnant populations of these suckers. Downstream of UKL, the Keno Impoundment is a seasonally lethal, anoxic habitat. We investigated species densities and hatch date differences between larvae retained in Upper Klamath Lake and those transported below the Link River Dam into the Keno Impoundment. In 2004, larval and juvenile Lost River suckers were captured in greater densities below the dam. Larval shortnose suckers were captured in greater densities in UKL while juveniles were captured in equal densities above and below the dam. Lost River suckers had earlier hatch dates than shortnose suckers and individuals below the dam had earlier average hatch dates for both species. These patterns suggest that, in 2004, early spawned fish, especially Lost River suckers, were more likely to be transported from Upper Klamath Lake while shortnose suckers were more likely to be retained.

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Patterns of Retention and Vagrancy in Larval Lost River and Shortnose Suckers from
Upper Klamath Lake, Oregon.

by
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A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented August 18, 2006
Commencement June 2007

Master of Science thesis presented by Susan A. Reithel presented on August 18, 2006.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes the release of my thesis to any reader upon request.

Susan A. Reithel, Author

Acknowledgments

I am grateful to the U.S. Bureau of Reclamation for funding this work, providing storage space for boats and equipment, and for sharing data and resources, especially R.

Piaskowski for keeping us abreast of events affecting the water bodies of the basin and especially the suckers, and J. Cameron for hydrolab calibration and sharing water quality data. I am grateful to M. Buettner (USFWS) and L. Dunsmoor (Klamath Tribes) for sharing some of the insight they have gained during their long tenure in the basin and L. Dunsmoor for sharing Klamath Tribes Braymill hatchery data. I received much feedback from individuals with the U.S. Geologic Survey, especially B. Hayes, E. Janney, and R. Shively who provided 2004 adult sucker CPUE data. T. Wood contributed considerable time and energy helping us match the biological data with the hydrology of UKL and I really appreciate her efforts and enjoyed our dialogue.

I thank my coworkers at Oregon State University especially D. Simon, M. Terwilliger, S. Remple, M. Cooperman, M. Cunningham, M. Jansen, B. Alfonse, E. Snyder, A. Norris, M. Maier, and other members of the Markle lab. My thesis committee, R. Hughes and H. Li, provided valuable suggestions and guidance. My major advisor, D. Markle, shared remarkable insight into fish biology, ecology and science in general. I am also very grateful to my family and friends who helped me with this project by supporting my enthusiasm and listening to my small tales of triumph and woe.

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Patterns of Retention and Vagrancy in Larval Lost River and Shortnose Suckers from Upper Klamath Lake, Oregon.

Introduction

Klamath suckers

The Lost River sucker, *Deltistes luxatus*, and shortnose sucker, *Chasmistes brevirostris*, are long-lived, highly fecund, iteroparous species endemic to the Upper Klamath Basin of southern Oregon and northern California (Buettner and Scopettone 1990). Population declines led to federal listing as endangered species in 1988. Upper Klamath Lake is a refuge for the largest populations of both species (Stine 1982; Buettner and Scopettone 1990; USFWS 2002).

Abundances of Lost River and shortnose suckers have declined since pre-1900 estimates due to over-harvest of spawning adults, habitat loss and modification from dams and water diversions, potential negative interactions between suckers and non-native species, hybridization, lack of recruitment, and poor water quality (USFWS 1988, 1993, 2001; Buettner and Scopettone 1990; Simon and Markle 1997; Kann and Smith 1999; Markle and Cooperman 2002; Markle et al. 2005; Markle and Dunsmoore 2006, in press). Prior to listing, sucker populations were predominately comprised of older, larger individuals due to lack of recruitment. During a 13-year period, from 1984 to 1997, only one strong year class emerged (1991). This year class briefly augmented populations until repeated fish kills from 1995-1997 removed most adults of both species (Perkins et al. 2000). Loss of unique spawning groups throughout the basin has further reduced the reproductive potential of the species (Markle and Cooperman 2002).

Although there is no numeric estimate of the historical abundance of suckers, existing accounts suggest a dramatic decline. The Klamath and Modoc tribes annually captured and dried large quantities of suckers at as few as three localities in the basin (Cope 1879; Howe 1968; Klamath Republican 1900 cited by Golden 1969; Andreasen 1975). By the late 1890's, white settlers were also harvesting suckers for home and commercial purposes (Gilbert 1898; Howe 1968; Helfrich 1972). Harvesting occurred at very high rates at one time supporting a cannery and shipments by the barrel. Settlers harvested suckers by the wagonload along the eastern shore of Upper Klamath Lake and in the Lost River (Andreasen 1975; Helfrich 1972).

Immoderate harvest practices continued into the 20th century. During this time, little was done to monitor sucker populations or understand their life history. In 1959, suckers became a game fish in the State of Oregon. Ten years later, a bag limit of ten was imposed to alleviate over-harvest and wastage (Golden 1969). There was growing concern over the number of sucker carcasses discarded on shore after capture and other examples of excessive use, "Another common sight is a party of snaggers (fisherman) with the entire box of a pickup loaded with fish...catches of this size could have a detrimental effect on the overall fishery" (Golden 1969).

Declines were soon evident. In 1968, the snag fishery harvested approximately 10,000 suckers. By 1985, harvest had declined by 95% with only 687 suckers captured (Golden 1969; USFWS 1993; Markle and Cooperman 2002). The State of Oregon closed the fishery in 1987 (Scoppettone and Vinyard 1991) and both suckers were listed as federally endangered species the following year.

The Lost River and shortnose suckers are obligate lake dwellers but spawn in tributary rivers or lake springs (Buettner and Scoppettone 1990; USFWS 1993). These species, plus the June sucker, *Chasmistes liorus*, and Cui-ui, *Chasmistes cujus*, comprise a group of four lake dwelling sucker species, all of which are federally listed as endangered. The Lost River and shortnose suckers are the only two lake suckers to co-occur in the same basin (Scoppettone and Vinyard 1991).

Each lake species inhabits waters altered by extensive development projects. Species declines have been attributed to similar causes; intensive fishing, loss of spawning habitat, highly altered lacustrine and riverine environments and degraded water quality. In recent years, each species has undergone 10-20+ years of little or no recruitment. A fifth species, the Snake River sucker, *Chasmistes muriei*, described after its recent extinction, presumably occupied lakes of the upper Snake River basin (Scoppettone and Vinyard 1991). The imperiled status of these fish gives further impetus to study the dynamics of sucker recruitment in Upper Klamath Lake.

Lost River suckers have been aged to 43 years and shortnose suckers to 33 years. Females of both species mature at 7-9 years of age (Scoppettone 1988; Scoppettone and Vinyard 1991; Markle and Cooperman 2002; USFWS 2002). Lost River suckers grow up to 1 meter in length; shortnose suckers are smaller and stouter, typically, less than 50 cm SL (standard length) fully mature (Moyle 2002).

Both species spawn in spring, the majority migrate up the Williamson and Sprague rivers. A smaller number of fish, predominately Lost River suckers spawn at springs along the eastern shore of Upper Klamath Lake. There is spatial and temporal segregation within and between spawning localities. Lost River suckers prefer coarser

substrate and the majority of individuals spawn approximately one month before shortnose suckers (Buettner and Scoppettone 1990; Cunningham and Shively 2001; Hayes and Shively 2001). Run timing can vary from year to year, and is presumably influenced by annual variations in temperature and flow (Golden 1969; Andreasen 1975; Hayes and Shively 2001; Hayes et al. 2003; Hendrixson et al. 2003).

Typically, Lost River sucker spawning peaks in April. It may begin as early as February and extend into May. Shortnose sucker spawning typically peaks in May, but may begin as early as March and extend into June (Scoppettone and Buettner 1990; Cunningham and Shively 2001; Hayes and Shively 2001; Hayes et al. 2003). In 2003, in the Williamson River, the largest CPUE (catch per unit effort) value for Lost River suckers occurred on March 28 and for shortnose on April 29 (Hendrixson et al. 2003), suggesting that the temporal difference between the species remains even when spawning peaks shift (Andreasen 1975).

The river and springs group also differ in run timing. Both observational and CPUE data indicate that Lost River sucker spawning peaks earlier at the lakeshore springs than in the rivers (Andreasen 1975; Buettner and Scoppettone 1990; Klamath Tribe 1991, 1993; Perkins et al. 2000). Shortnose sucker behavior is slightly more difficult to assess as their presence at the springs is minimal, but CPUE values indicate earlier spawning at the springs (USGS, Klamath Falls office, 2004 unpublished data).

Earlier spawning at the springs is probably the result of warmer temperatures at the springs in winter. In February 1990, the springs were 4 to 14 degrees (C) warmer than surrounding waters in Upper Klamath Lake. Aerial photographs taken in the same

month show the springs were unfrozen and distinguishable in aerial photographs (Fletcher 1991).

Suckers exhibit a strong fidelity to spawning site. Mark/recapture studies indicate very little mixing between the river and springs groups and each is considered a discreet stock (Klamath Tribe 1993; Perkins et al. 2000; Hayes et al. 2003; Hendrixson et al. 2003). In 2003, of 405 tagged fish captured at the eastern shore springs, 98% were originally tagged at these springs and 2% were tagged in the Williamson River (Hayes et al. 2003).

Perhaps the greatest difference between spawning groups is that the shoreline springs group is predominately composed of Lost River suckers (Klamath Tribes 1991; Klamath Tribes 1993; USFWS 1993). Until the 1990's little or no mention was made of shortnose suckers spawning at the springs (Andreasen 1976; Fortune 1979; Klamath Tribe 1993). More recent information suggests they are present but in low numbers. For example, in 2000, 94% of suckers captured at the shoreline springs were Lost River suckers, 5% shortnose and 1% intermediate hybrids (Hayes and Shively 2001).

Historical loss of spawning stocks at Barkley, Odessa, and Harriman springs, has caused some concern (USBR 2001). Suckers were last observed at Barkley springs in the 1970's and at Harriman springs in 1974 (Andreasen 1975; Markle and Cooperman 2002). There may be additional, undetected springs groups that have disappeared. Fishing tackle, used to catch suckers, has been systematically collected and mapped at low water levels in Upper Klamath Lake. Tackle was found at four areas within the lake that also had flowing springs but are not known to be active spawning sites (Cooperman and Markle 2002). Although, shoreline spawners show movement between eastern shore

springs, recolonization has not yet occurred at Barkley springs (Perkins et al. 2000; USBR 2001; Hayes et al. 2003), or the western shore springs, Harriman and Odessa.

The larvae of both shortnose and Lost River suckers rear in Upper Klamath Lake. Larvae from the Williamson River and its tributaries begin nighttime, surface drift into Upper Klamath Lake immediately after swim up and can be transported from spawning beds into Upper Klamath Lake in one day (Scoppettone and Buettner 1990; Cooperman and Markle 2003). Drift behavior of the shoreline springs larvae is less understood.

Historically there was seasonal connectivity between Upper Klamath Lake, the Lost River and Lower Klamath Lake thru connections between Link River, the outlet of UKL and the Keno Impoundment section of the Klamath River. Suckers were once present in great numbers in the Lost River and in Lower Klamath Lake (Cope 1879; Coots 1965; Helfrich 1972; Stine 1982). Presumably, some suckers, particularly the offspring of spawning groups in Upper Klamath Lake and its tributaries, may have been able to use habitat downstream of UKL and return in the spring to spawn. Suckers have been observed moving up the Klamath River and into Link River, presumably spawning in the Link River or rejoining Upper Klamath Lake populations (Golden 1969; Stine 1982). The corridors that connected these water bodies are now managed waterways and not successfully traversed by suckers.

Although larvae and juveniles may have historically reared downstream of Upper Klamath Lake, the present water quality of the Keno Impoundment is such that entrained larvae and juveniles are expected to have poor survivorship, such that few would survive to navigate the recently installed fish ladder at the Link River Dam (Martin and Saiki 1999; Saiki et al. 1999; USFWS 2001). Excessive summer algal blooms in Upper

Klamath Lake generate poor water quality. The decay of the algae (*Aphanizomenon flos-aquae*) leads to high water column oxygen demand. When this water enters the Keno Impoundment, conditions become hypoxic (Doyle and Lynch 2005). By July, it is common for most of the Keno Impoundment to have dissolved oxygen levels < 1 mg/L, levels below the LC_{50} values for both species of suckers (Martin and Saiki 1999; Saiki et al. 1999; Jason Cameron USBR, personal communication).

Entrainment contributes to sucker recruitment failure (USFWS 2002). In 1996 and 1997, Gutermuth et al. (1998) estimated 3,300,000 and 1,700,000 larvae and juveniles < 74 mm were entrained in the A-Canal at the southern end of Upper Klamath Lake, just north of the Link River dam that regulates flow into the Keno Impoundment. In 2002 and 2003, larval trawl CPUE (catch per unit effort) values in the Keno Impoundment were 15-20% of those in Upper Klamath Lake (Terwilliger et al. 2003b). Suggesting that a substantial number of larval suckers are entrained into the impoundment.

Recruitment

Rises and falls of fish populations have concerned humans for centuries, as the magnitude of the fishery often dictated the welfare of the fishing communities. Between 1866 and 1909, the Norwegian herring fishery fluctuated up to four orders of magnitude. By this time, ichthyologists had established only a rudimentary understanding of the migration and spawning behaviors of a few species. Identifying and enumerating the mechanisms involved in fluctuating populations was and continues to be a difficult task (Hjort 1914; Cowan and Shaw 2002). Yet, thru the study of the Norwegian herring, a

fundamental discovery was made, that a single or very few year-classes can represent the majority of fishes present in a long-lived, multi-aged population (Hjort 1914).

Recruitment, or the addition of new members to the adult population, is a critical component of life history ecology (Everhart and Youngs 1981; Anderson 1988; Cowan and Shaw 2002). Fish commonly pass thru several stages before full maturity.

Typically, the mortality rates for each stage decreases with increasing size. Mortality rates during the larval stage, including those of the suckers, regularly exceed 90% (Houde 2002; Markle and Cooperman 2002).

Even small changes in mortality rates during the larval stage or shifts in the duration of the larval stage can result in substantially different abundances entering the juvenile stage. Yet, relationships between strong year-classes and larval abundance are difficult to establish. In part, because although zero larval survival will produce zero adult fish, it does not follow that high larval survival will result in an abundant year-class. Many factors, such as over winter mortality, affect survival after the larval stage and further influence the number of individuals achieving recruitment (Simon and Markle 2001; Cowan and Shaw 2002; Houde 2002). Even with these difficulties, many fishery biologists and managers consider understanding the recruitment process, especially those at early life stages, to be one of the most important aspects of managing commercial, recreational and endangered species (Anderson 1988; Rothschild 2000; Cowan and Shaw 2002; Fuiman 2002).

Many factors influence larval fish survival: predators, cannibalism, food availability, patterns of drift and swimming, currents, tides, flow, floods, drought, disease, temperature, wind, pollution, sediments, water quality and quantity, among

others (Ware 1975; Everhart and Youngs 1981; Martin et al. 1981; Cushing 1982; Anderson 1988; Fortier and Gagne 1990; Buettner and Scopettone 1990; Mion et al. 1998; Fuiman 2002). The number of influential factors and potential interactions has made the discovery of causal relationships between year-class success and recruitment difficult to quantify and describe (Everhart and Youngs 1981).

Many fish have temporally and spatially consistent spawning behavior. A spring spawning event is common and has the advantage of producing larvae in conjunction with the primary (spring) production so that larval feeding coincides with this annual event (Cushing 1969). The primary production cycle is annually variable and influenced by factors such as wind speed and strength, irradiance and heat (Cushing 1975; Anderson 1988). Fish whose larvae are dependant on the primary production cycle will therefore be vulnerable to the variability of the cycle (Cushing 1969). After hatch, many fish passively drift to downstream nursery grounds (Mantefeil et al. 1978; Pavlov 1994). Successful spawning grounds provide not only adequate spawning habitat but also a position in relation to nursery grounds where young can effectively emigrate from spawning grounds and immigrate into appropriate nursery grounds (Harden Jones 1968).

These principles of larval success are reflected in two of the most influential hypotheses concerning larval recruitment: Cushing's match/mismatch and Sinclair's member/vagrant hypotheses (transport/retention) (Cushing 1975; Sinclair 1988). The match/mismatch hypothesis relates larval survival to the overlap between spawning and production of food resources. This hypothesis assumes that the greater the overlap between the development period and peak production the greater the possibility for successful recruitment (Cushing 1975).

According to the transport/retention hypothesis, physical processes play the primary role in facilitating retention in or transport to suitable rearing habitat (Hjort 1914; Parrish et al. 1981; Iles and Sinclair 1982; Sinclair 1988). The hypothesis assumes that fish are adapted to spawn in certain areas and at certain times to ensure the integrity of the larval population by limiting dispersal into inappropriate areas, thereby ensuring that larvae remain within the reproductive pool of the species (Iles and Sinclair 1982; Sinclair 1988). Both of these hypotheses address marine systems and the inclusion of marine developed hypothesis with the freshwater environment has been lacking (Frank and Leggett 1994). Neither theory is considered individually adequate to explain larval survival and the processes affecting recruitment (Anderson 1988; Fortier and Gagne 1990; Cowan and Shaw 2002).

A broader application or an incorporation of both match/mismatch and member/vagrant hypotheses may be seen in a “bet-hedging” or a “spreading of risk” context. In this view, variation in a population and its environment helps spread (diminish) the risk of extinction (Den Boer 1968). For long-lived, iteroparous species, such as Lost River and shortnose suckers reproductive risk is spread out on both an intra- and inter-annual basis. Suckers consistently spawn in the spring of every year but there is variation in spawning time between the riverine and shoreline springs groups and between species. This variability in spawning locality and timing would spread risk within a year. Their iteroparous nature would be a buffer against a period of bad conditions such as severe drought and protect the species against an extended lack of recruitment (Den Boer 1968; Markle and Cooperman 2002).

Passive drift is common in many families of fish and the most prevalent type of fish movement at the larval life stage (Manteifel et al. 1978). Nursery areas are often distant from spawning grounds, thus requiring larvae to drift or travel to reach them (Harden Jones 1968; Manteifel et al. 1978; Pavlov 1994; Cowan and Shaw 2002). Drifting larval fish are transported or retained, both actively and passively, by features such as currents, advection fronts, gyres, circulation patterns, and vertical and lateral migrations. These features, in turn, are influenced by, or a product of, physical and seasonal factors such as wind and tides. Variation in the strength, duration, or direction of these transport mechanisms can affect larval success within and across years (Hjort 1914; Manteifel et al. 1978; Brown and Armstrong 1985; Peterman and Bradford 1987; Pavlov 1994; Mion et al. 1998; Hare et al. 1999; Reiss et al. 2000; Hare et al. 2002; Leis and McCormick 2003).

Seasonal and geographic factors influence growth and drift (Pavlov 1994). In the northern hemisphere, seasonal changes create different conditions for early and late hatched larvae. Days are longer and nights are shorter during the summer, so that the duration of diurnal drift should decrease (Manteifel et al. 1978). Experiments with cyprinids show that as larvae grow they tend to drift fewer hours each night (Manteifel et al. 1978). For larval roach, *Rutilus rutilus caspicus*, the light intensity threshold for rheotaxis (orientation to flow) decreased with increasing growth until the juvenile stage when the behavior ceased (Pavlov 1978). The seasonal increase in temperature from spring to summer positively affects growth rates. In most cases, as growth rates increase, larvae will transform to a juvenile life stage and an adult swimming type faster and cease

drifting sooner (Anderson 1988; Kaufman 1990; Pavlov 1994; Clarkson and Childs 2000).

The increased energetic costs of swimming at cooler temperatures during the larval stage may contribute to the temperature and growth relationship. Metabolic costs of swimming increased more rapidly at 15°C than at 20°C for another Cypriniformes fish, the Danube bleak, *Chalcalburnus chalcoides*. The potentially higher metabolic costs for active transport during cooler conditions could translate into higher metabolic costs to seek out habitat and search for food in early spring thus reducing the growth potential of early hatched larvae (Wieser and Kauffmann 1998)

We investigated larval sucker distribution in Upper Klamath Lake and the Keno Impoundment. The primary questions of interest were whether there were species or age differences in larval catch per unit effort above and below Link River Dam. A species or spawning group more likely to become entrained in the Keno Impoundment will experience greater losses at early life stages, decreasing the number of individuals available for eventual recruitment. As 'effective' mortality (rate of individuals removed from the source area thru death plus loss thru emigration) rises, year class success could be dramatically reduced (Hjort 1914).

Materials and Methods

Study area

Upper Klamath Lake (UKL) is connected to both Agency Lake and the Williamson River, its major tributary, along on its northern border. Shoreline springs dot the northeastern shore. At the southern end of UKL, is the Link River Diversion Dam. A short stretch of water, the Link River, connects UKL with Lake Ewauna and the Klamath River. This section, including Lake Ewauna, is known as the Keno Impoundment due to the presence of a dam at Keno, Oregon. (Figure 1).

Upper Klamath Lake is a remnant of pluvial, Pleistocene Lake Modoc, once 75 miles in length. Eleven thousand years ago, the climate became drier and Lake Modoc was reduced to eight separate and smaller lakes, including Upper Klamath, Lower Klamath and Agency lakes (Orr and Orr 1999). Upper Klamath Lake covers approximately 85,000 acres at water surface elevation 1262.9 m (4143.3 ft). The Upper Klamath Basin experiences a high desert climate with hot, dry summers and cold winters (Taylor 2005). The Link River Dam at the lake's terminus is used to store water for the Klamath Irrigation Project and regulate water flow for downstream needs (Buettner and Scopettone 1990).

The Link River Dam replaced a wide, sloping, natural reef that regulated the lake's outflow. Dam construction allowed for greater water withdrawal because a notch was cut in the reef (USFWS 2002). Historical (pre dam) elevations fluctuated between 1261.8 and 1262.8 m (4139.9 and 4143 ft). Late summer elevation was approximately 1262.0 m (4140.5 ft). Current water levels can vary up to 1.8 m (six ft) in one year with elevations ranging between 1261.1 to 1262.3 m (4137.5 and 4143.7 ft) or about a half

meter higher and lower than historic values (Boyle 1987; USFWS 2002; USBR 2001; USBR datum).

Under prevailing northwest winds, flow within UKL consists of a predominant clockwise gyre flowing from the north that turns west at Buck Island then north thru a western shore trench along Eagle Ridge. There is also an eastern boundary current flowing south past Buck Island to the terminus of UKL (Figure 2; Wood et al. 2006; T. Wood personal communication).

The Keno Impoundment is a 32.2 km (20 mile) long body of water that includes Lake Ewauna and the upper section of the Klamath River. The Impoundment ranges in width from 90 to 795 m (300 to 2600 ft) and in depth 3 to 6 m deep (9 to 20 feet) (CH2M Hill 1995). The Keno Impoundment is regulated by the Keno Dam at Keno, Oregon and is typically within 1244 and 1245 m elevation (4083 and 4086 ft) to provide sufficient head for irrigation diversions (USBR datum; USFWS 2002).

Historically, fish passage between UKL, the Lost River System and Lower Klamath Lake was possible through corridors along the upper Klamath River. The Lost River Slough (the Lost River Diversion Canal), about five miles downstream of UKL, was a channel that connected the Lost River system with the Klamath River. Klamath Straits, roughly 15 miles downstream of UKL, connected Lower Klamath Lake with the Klamath River. Both of these channels are now controlled waterways (USFWS 2002; Figure 1).

Historically, the Keno Impoundment, could have allowed larval and juvenile suckers leaving UKL to access rearing habitat in the Lost River System or Lower Klamath Lake. Potentially these suckers could have returned to UKL to spawn since the

natural falls were easily passed (Gilbert 1898; Coots 1965; Andreasen 1975; Miller and Smith 1976; Moyle 2002; Stine 1982; Scopettone and Vinyard 1991; USFWS 2002). Historically, runs were observed migrating up Link River (Golden 1969). Whether these suckers spawned within Link River or returned to UKL is unknown.

The 1996 USFWS Biological Opinion (BO) required the Bureau of Reclamation to provide a new fish ladder to pass adult suckers through Link River Dam. Since August 2001, Oregon State law also requires the owner or operator of an artificial obstruction in waters occupied by native fish to address the fish passage requirements of these fish (ORS 509.580 through 910 and in OAR 635, Division 412). To comply with these requirements the Bureau constructed a ladder navigable by suckers, which became operational for the 2005 migration season. Preliminary data show both species used the ladder and tagged suckers rejoined both river and springs spawning groups (Bennetts 2006).

The 1996 USFWS BO also required the Bureau of Reclamation to screen the A-canal, a large diversion canal leaving UKL, to prevent entrainment of larval, juvenile, and adult suckers. The A-Canal fish screen became operational in April, 2003. The screen is effective at deterring almost 100% of fish > 30mm FL (fork length) and over 30% of larval fish (10 – 30mm) (Bennetts et al. 2004). However, the primary bypass diverts screened fish directly above Link River Dam and the secondary bypass diverts them below the dam into Link River (Marine and Gorman 2005). Although this arrangement reduces A-Canal entrainment, it may increase entrainment into the Link River and the Keno Impoundment. Although this area might have provided rearing areas historically,

the current water quality in the Keno Impoundment does not favor survival (USFWS 2002; Jason Cameron, USBR, personal communication).

Sites

Sites were located along the shoreline of UKL, Agency Lake and the Keno Impoundment (Figures 3, 4). For ease of discussion, this paper will refer to Lake Ewauna as upper Keno and to the area below it, lower Keno. To compare densities within and between UKL and the Keno Impoundment the water bodies were split into five areas from north to south. Area 1, represents the northern and western shores of UKL and Agency Lake, 2, the eastern shore of UKL, including the springs and the mouth of the Williamson River, 3, the southern shore of UKL, 4, upper Keno, and 5, lower Keno (Figure 3).

In 2004, all sites were sampled by larval trawl and beach seine. Sampling began during the initial larval production period (late March – early April) and extended into the summer (July for the larval trawl and August for the beach seine). Physical and biological measurements were taken at each site visit.

Lake wide sites in UKL and in Agency are part of a long-term monitoring effort by Oregon State University and will be referred to as standard sampling. Sites were selected in 1991 for logistical and accessibility reasons with an attempt at equidistant coverage. Sites throughout the Keno Impoundment were added to the long-term project in 2002 and selected in an equidistant fashion. When an equidistant sampling point was inaccessible the nearest accessible site was selected. Standard sampling was conducted

every third and included ten sites in UKL, five in Agency Lake and 30 in the Keno Impoundment (Figure 3; Simon and Markle 2006).

In 2004, additional sites, above and below the Link River Dam, and at the eastern shore springs, were added for the purpose of this study. These sites were located in southern UKL (12 sites), upper Keno (12 sites), and at eastern shore springs with extant spawning groups (10 sites). Sites in southern UKL and upper Keno sites were selected in the same manner as standard sampling sites. Sites at or near springs were taken on spawning substrate and at nearby areas in an attempt to include preferred larval habitat such as vegetated areas (Figure 4).

Field data collection

Gear

The larval trawl has a 0.8 x 1.5 m opening with a 2.5 m long Nitex net of 1000-micron bar mesh and is mounted on an aluminum frame with runners, similar to that described by LaBolle et al. (1985). The larval trawl was set 1-14 m offshore in water about one meter deep and pulled to shore with ropes. Because of disturbance to the area while setting the larval trawl, the net was allowed to soak for ten minutes before being pulled to shore at a swift rate. Larvae were preserved in formalin for 24-36 hours, then transferred to 70% ethanol for long-term storage.

The seine was 6.1 m long with a 2x2x2 m bag, and 4.8 mm bar mesh. Most seining was conducted as a standard swing arc (1/4 circle) beginning with the net in a perpendicular position from shore. Fishes were identified, enumerated, and measure to

the nearest mm. Age-0 suckers were preserved in 95% ethanol. In cases where sample sizes were very large, age-0 suckers were removed from the catch prior to sub sampling.

Sampling methods

Standard larval trawl sampling in Upper Klamath Lake, Agency lake and the Keno Impoundment began the first full week of April and continued through late July, with samples collected every third week for a total of six sampling surveys. During each survey, two samples were taken at each site in UKL and Agency Lake. In UKL, an annual total of 120 samples (Table 1) were taken with an average sampling area of 6.25 meters in length and 0.70 meters in depth. In Agency Lake, a total of 60 annual samples (Table 1) were taken with an average sampling area of 6.28 meters in length and 0.65 meters in depth. One sample per site was collected at Keno Impoundment sites for an annual total of 180 samples (Table 1) with an average sampling area of 6.78 meters in length and 0.66 meters in depth.

Standard beach seine surveys began in late June and continued into August at the same sites used in larval trawl sampling. Samples were collected every three weeks for a total of four surveys. Two seine samples per survey were collected at each UKL and Agency Lake site. A total of 120 samples were collected in Upper Klamath Lake and 40 in Agency Lake (Table 1). One beach seine sample was taken per site, per survey in the Keno Impoundment for a total of 120 samples (Table 1).

Additional larval trawl and beach seine sampling, including sites located at the southern end of UKL (12 sites), in Upper Keno (12 sites), and at eastern shore springs (10 sites), was conducted during the two week interval between lake and river wide sampling.

A single sample was taken at each site on subsequent days, for a total of two samples per site, per survey. One survey was conducted per week. Nine larval trawl sampling surveys were conducted late March thru June, for an annual total of 432 samples in UKL and Keno (Table 1). Average sampling area in UKL was 5.64 meters in length and 0.75 meters in depth. Average sampling area in Keno was 5.56 meters in length and 0.69 meters in depth. Two beach seine surveys were conducted during intervals in standard sampling at the same sites as used in larval trawl sampling in southern UKL and upper Keno. Sampling was conducted during the month of June for a combined total of 96 samples (Table 1).

Additional larval trawl and beach seine sampling at the springs along the eastern shore of UKL coincided with the additional sampling in southern UKL and upper Keno. Larval trawl sampling occurred once a week with 10-12 samples taken per week, for an annual total of 82 samples during eight sampling events (Table 1). Average sampling area was 5.01 meters in length and 0.74 meters in depth. One beach seine survey was conducted at the shoreline springs in June for a total of 10 samples (Table 1).

Environmental measurements

Water quality measurements were taken with each sample using a Hydrolab Reporter Multiprobe and Surveyor 3 Display Logger ®. This unit was replaced in 2004 with an YSI 600 Quick Sample (QS) multiparameter monitoring system ®. The instruments were calibrated before each survey by technicians at the USBR office in Klamath Falls, OR. Water quality parameters measured were: dissolved oxygen (mg/L), temperature (°C), pH, and conductivity (µS/cm). Substrate, vegetation presence or

absence, vegetation type, and *Aphanizomenon* (blue-green algae) density were recorded (Table 2). Flow over the Link River Dam was provided by the U.S. Department of the Interior, Bureau of Reclamation, Mid-Pacific Region. We characterized flow by using a three-day average prior to collection. This approximated flow levels over the weekend in between trips.

Laboratory data collection

Fish identification

Pigmentation patterns corroborated by myomere counts were used to identify larvae < 15 mm (Remple and Markle unpublished). Intermediate specimens and specimens > 15 mm were cleared and stained (Pottholf 1984; Taylor 1967) and post-Weberian apparatus vertebral counts used for final identification. Vertebral counts > 44 were classified as Lost River suckers (LRS), counts of 44 were considered unidentified suckers (UIS), and counts of < 44 were classified as shortnose suckers (SNS) (Markle et al. 2005). After identification, 146 larvae were still classified as unidentified; 113 of these had vertebral counts equal to 44, and 33 could not be determined.

Further attempts were made to differentiate the UIS by plotting their hatch dates and comparing with hatch dates of LRS and SNS. This attempt was abandoned because a group with late hatch dates appeared to represent both LRS and SNS born later in the spawning season. UIS were excluded from the density analysis.

Aging

Larval sucker otoliths were aged following the methods of Terwilliger et al. (2003a), except that a bleach rinse was omitted and both lapilli and sagittae were used. Readings from both types of otoliths were consistent. Fish were much smaller than those aged by Terwilliger et al. (2003a) and few had developed the rostrum and post rostrum projections, which make aging sagittae difficult (Hoff et al. 1997). When projections had developed, sagittae were not used. A second reader (M. Terwilliger) assisted and aged 11% of the otoliths (Figure 5). Otoliths from each fish were read 2 – 5 times, average = 3.2. The median value was the age assigned.

Statistical analyses

Larval trawl and beach seine

Median CPUE (catch per unit effort) values of sucker larvae between regions (UKL and Keno) and between areas were compared with a Kruskal-Wallis one-way analysis of variance for ranks. As is common with rare species data, the larval trawl and beach seine CPUE values are non-normal due to a large number of zeroes and infrequent high values. Data failed to meet normality requirements as tested by measures of skewness and kurtosis even after natural log transformation as described by McCune and Grace (2002). Therefore, the Kruskal-Wallis test was selected to detect differences in median CPUE values, *P*-values of 0.05 were selected as the significance threshold for this and subsequent tests. The tests were performed on all larvae, larvae ≤ 13 mm (small larvae), larvae > 13 mm (large larvae) and age-0 juvenile suckers. Relative frequency values for all larvae captured in areas 2-3 are displayed in Figure 7.

Due to the skewed nature of the data, log transformed mean plots were selected as the most illustrative method of display (Figures 8 - 11), *P*-values were obtained from Kruskal-Wallis tests. Multiple range tests on mean values were used for result descriptions. Statgraphics Plus (version 5.0, Statistical Graphics Corp.) was used for these and subsequent analysis. Results for these tests are presented first as comparisons between UKL and Keno and secondly between areas.

Very few larval suckers were captured in Agency Lake (5). In addition to these, only two SNS and two LRS juveniles were captured. Therefore, most of the analysis and discussion in this study are orientated towards UKL and the Keno Impoundment.

Larval age data

About 9% of the 2004 sucker larvae (116) were used to estimate age at length. Otoliths from an initial 208 were examined, 40% (84) of these were unreadable, eight otoliths were marginally readable and > two standard deviations from the model and removed.

The influences of otolith type, standard length and species on age were investigated with a multifactor one-way ANOVA. Standard length and age data were log transformed in an attempt to satisfy normality and equal variance assumptions. After transformation, standard length data still had slightly high levels of skewness and kurtosis (4.7 and 6.1 respectively) due to several larger measurements. These were retained in the analysis.

A simple linear regression model was used to estimate length at age for all larvae captured in 2004. Differences in hatch weeks between species and between UKL and

Keno were compared with Kruskal-Wallis one-way analysis of variance for ranks tests. The test was selected due to high levels of skewness and kurtosis even after log transformation as described by McCune and Grace (2002). Lost River sucker data met normality requirements and a one-way analysis of variance was used to compare the hatch weeks of Lost River suckers between UKL and Keno. To perform the analysis on hatch weeks, SNS and LRS larvae were assigned a calendar week (the first week of January is week 1) that included their hatch date. Data are displayed with means plots.

Adult spawning and larval hatch

Adult CPUE data was collected with daytime trammel net sampling at the mouth of the Williamson River and at lakeshore springs spawning areas from mid February thru May. Trammel nets were fished 20-60 hours per week (average 36 hours) at the springs and 26-74 (average 54 hours) hours per week in the mouth of the Williamson River (U.S. Geological Survey, Western Fisheries Research Center, Klamath Duty Station, Klamath Falls, OR). These CPUE values are not population estimates and effort between spawning localities was not equal. Suckers do not spawn at the mouth of the Williamson River but are primarily moving thru the area on their way to or returning from spawning areas upstream. Whereas sampling at the springs was conducted directly above spawning gravels. Therefore, the CPUE values are used to describe relative abundance of spawners in each area and as an indication of spawning activity.

Data from shortnose and Lost River larvae hatched at the Klamath Tribe's Braymill Hatchery in 1991 provide an estimate of incubation time. Incubation time was added to a division week, or the week between in which 85% of LRS spawned before and

over 85% of SNS spawned after. The percentages of larvae with hatch dates before and after the midpoint of this division week plus the incubation period was calculated for each area.

Flow and transport

Simple linear regressions were used to investigate the potential influence of flow thru the Link River Dam on the CPUE of both larval species in areas 3 and 4 for each survey. CPUE were calculated for the total number of small and large larvae. The relative increase or decrease in larval CPUE was estimated by subtracting the previous weeks CPUE values. The week-to-week relative changes in CPUE were compared between areas 3 and 4 and patterns analyzed relative to Link River Dam flows (Figure 6). Link River Dam flows were the average of the average flows from three days before a survey. After week 21, there is a greater variation in flow and CPUE between southern Upper Klamath and Upper Keno for LRS. The LRS data, before and after week 21, were analyzed separately. Shortnose suckers were not present before week 21 and analysis are based on CPUE values after this week.

Water quality

Water quality parameters were assessed to quantify and describe differences between UKL and the Keno Impoundment as well as identify possible drivers of water quality. Multifactor ANOVA's were used to quantify and describe seasonal, diurnal, and spatial patterns in levels of dissolved oxygen (mg/L) and water temperature (°C). Differences in median levels of conductivity ($\mu\text{S}/\text{cm}$) were tested using the Kruskal-

Wallis one-way analysis of variance for ranks due to the data's high degree of non-normality. Because of the nature of pH data, the Kruskal-Wallis one-way analysis of variance was used to assess median values. These analyses included water quality data from both larval trawl and beach seine sampling.

Results

Larval and juvenile density

Larval Trawl

Size frequencies, of both Lost River (LRS) and shortnose (SNS) sucker larvae, show a progressive decrease in relative abundance of smaller larvae, and a progressive increase of larger larvae, from area 2 to area 4 (Figure 7).

Larval LRS were captured in higher densities in Keno than UKL ($P = 0.02$) (Figure 8a). There were also differences in median CPUE between areas ($P = 0.003$). Median CPUE of larval LRS was high in areas 2, 4, and 5 and differed from areas 1 and 3 (Figure 8b). Larval SNS were captured in higher densities in UKL than Keno ($P = 0.001$) (Figure 8c). Larval SNS median CPUE was high in areas 2, 3, and 4 and differed from areas 1 and 5 ($P < 0.0001$) (Figure 8d).

Median CPUE of small (<13 mm) LRS larvae did not differ between UKL and Keno ($P = 0.3$) but did differ between areas ($P = 0.02$) (Figures 9a and 9b). Median CPUE was high in area 4 but not different from areas 2 and 5. Small SNS larvae were captured at higher densities in UKL ($P < 0.0001$) (Figure 9c) in areas 2 and 3 and lower densities in 1, 4, and 5 (Figure 9d).

Median CPUE of large (>13 mm) LRS larvae differed slightly between UKL and Keno ($P = 0.07$), and significantly between areas ($P = 0.008$) (Figures 10a and 10b). Large LRS larval CPUE was high in area 4 and differed from areas 1, 2, 3 and 5. Median CPUE of large SNS larvae did not differ between UKL and Keno ($P = 0.1$), but did differ between areas ($P < 0.0001$) (Figures 10c and 10d). Large SNS larval median CPUE was high in areas 2, 3, and 4 and differed from areas 1 and 5.

Beach seine

Age-0 LRS were captured in higher densities in Keno than UKL ($P = 0.0004$) (Figure 11a). There were also differences in median CPUE between areas ($P = 0.0002$) (Figure 11b). Age-0 LRS CPUE was high in areas 4 and 5, CPUE in area 4 differed from all other areas except 5. Area 5 differed from areas 1 and 3 but not 2. Median CPUE of age-0 SNS did not differ between UKL and Keno ($P = 0.6$) but did differ between areas ($P = 0.0008$) (Figure 11c and 11d). Median CPUE in area 4 was higher than areas 1 and 5 but not 2 and 3, CPUE in these areas was different from area 1 but not 5.

Larval age data

Otolith ages from lapilli and sagittae were not statistically different ($P = 0.2$) and median readings from both were included in the analysis. As expected, standard length was highly correlated with age ($P < 0.0000$). Species was not correlated with age ($P = 0.72$) and data from both species were used to obtain length at age estimates.

Hatch dates were calculated for all larval suckers using Eq. 1.1

Eq. 1.1. $\text{Age} = -39.0571 + 4.9612 * \text{standard length}$

This model explained 66% of the variation in age ($F = 225.12$; $df = 1, 114$; $P < 0.0001$).

LRS median hatch occurred about April 21 (week 17) and SNS median hatch fell around May 12 (week 20) ($P < 0.0001$) (Figure 12). Median larval hatch date for all larvae combined was significantly lower in Keno than UKL ($P < 0.0001$), by about one

week. Median LRS hatch date was 7 days less in Keno ($P = 0.02$) and SNS median hatch date was 4 days lower in Keno ($P < 0.0001$).

Adult spawning and larval hatch

In 2004, over 85% of adult LRS were captured before week 17 and over 85% of adult SNS were captured after this week (Figure 13; Table 3) (USGS Klamath Falls office, unpublished data). Of eleven batches of sucker eggs from known parents of both species incubated at 13.2 to 18.0 °C, most (approximately 90%) hatched in 5 - 11 days (Klamath Tribe's Braymill Hatchery Data 1991). The mode, 7 days, was used as an approximate incubation time. This number was added to the 'division' week (week 17) between the LRS (early) and SNS (late) spawning groups. The youngest aged suckers captured were 12, 13, and 14 days old, indicating approximately 2 weeks spent in the gravels after hatch before entering the water column and engaging in drift behavior.

Hatch dates for each species in each area were examined for early or late birthdates, those with hatch dates before the midpoint of week 18 were considered early and those after were considered late (Table 4). There were 14% more early LRS in Keno than UKL but equal percentages of early and late SNS in Keno and UKL.

Flow and transport

LRS larval weekly change in CPUE were not correlated with flow ($P > 0.21$) in area 4, in total, the small (≤ 13 mm) size class, and the larger (> 13 mm size class) before week twenty-one. Change in small (≤ 13 mm) larval LRS CPUE in area 4 after week 21 was positively associated with flow thru the Link River Dam (Eq. 1.2).

Eq. 1.2.

$$Y = -0.242967 + 0.000291624 * \text{FLOW}, R^2 = 64\%, P = 0.03$$

SNS larval weekly change in CPUE was not correlated with flow either before or after week 21 ($P > 0.55$) in area 4, in total, and the small (≤ 13 mm) and large (> 13 mm) size classes.

Water Quality

Mean monthly dissolved oxygen rose from March to June and declined in July (Figure 14). Mean hourly DO was relatively stable during the day but dropped in early evening ($P < 0.0001$) after 1800 hours (Figure 15). Mean DO did not differ between areas ($P = 0.05$).

Mean water temperatures rose in the afternoon (Figure 16). Mean water temperature was slightly lower in areas 2 and 3 (Figure 17).

Median pH varied seasonally ($P < 0.0001$) and was highest in summer (Figure 18). Median pH was highest in early morning and evening, although sample sizes for these hours are small. Median pH was highest in areas 1 and 5 (Figure 19).

Median conductivity ($\mu\text{S}/\text{cm}$) appeared to be influenced by site and season. High readings ($> 150 \mu\text{S}/\text{cm}$) were taken in June and August at sites near the Klamath Falls wastewater treatment plant in Lake Ewauna. Other high readings were recorded in August, downstream of Klamath Straits Drain in the Keno Impoundment. Most readings $> 175 \mu\text{S}/\text{cm}$ occurred during a single survey. No high readings ($> 150 \mu\text{S}/\text{cm}$) were

measured in Upper Klamath Lake, but there was spatial variation, with low readings ($< 100 \mu\text{S}/\text{cm}$) recorded at the mouth of the Williamson River and at eastern shore springs.

Dissolved oxygen levels less than the upper median lethal concentrations ($\text{LC}_{50\text{S}}$) for LRS and SNS larval suckers ($< 2.0 \text{ mg}/\text{L}$; Saiki et al. 1999) were encountered on three occasions: once each in areas 1, 2, and 4 on dates in July and August. Temperatures above the $\text{LC}_{50\text{S}}$ levels for LRS and SNS larval suckers (approximately $> 31.5^\circ\text{C}$; Saiki et al. 1999) were not encountered. The highest temperature encountered in 2004 was 31°C recorded on the western shore of UKL in Ball Bay in August. Ph levels above $\text{LC}_{50\text{S}}$ levels for larvae of both species (approximately 10.4; Saiki et al. 1999) were encountered twice, once in Agency Lake and once in the Keno Impoundment in June. In upper Keno pH levels above 10 were encountered 12 times over a two week period in June.

An analysis of substrate variables is not presented in this thesis due to possible the possibility of confounding factors in the data. Wood substrate is often encountered in upper Keno due to historical and present log storage on the river (USBR 2002). Substrate present in areas of UKL and in lower Keno, such as gravel and sand are not widely available in upper Keno. However, upper Keno is the point of entry for larval and juvenile suckers and therefore suckers are captured in the highest densities in this section of the impoundment, however little choice of substrate is available. Therefore the analysis of substrate selection by suckers in these areas is potentially inappropriate. *Aphanizomenon* was present at medium to high levels (water column difficult to see thru to several inches) in 30 % or more samples in each area.

Discussion

Three factors control larval density patterns in Upper Klamath Lake and the Keno Impoundment: immigration, emigration and mortality. Figure 7 is a first order estimate of larval mortality. The relative increase in frequencies of large larvae of both species from area 2 to 3 to 4 means “apparent mortality” is highest in area 2 and lowest in area 4. The “apparent mortality” in these areas includes emigration, immigration and natural mortality. Assuming constant natural mortality across areas, the decrease in the relative abundance of small larvae from area 2 to 3 to 4 is showing emigration. The increase in the relative abundance of larger larvae from 2 to 3 to 4 is showing immigration. As more larvae emigrate from area 2 and immigrate into area 4 the “apparent” mortality in area 2 is increased and the “apparent mortality” in area 4 is decreased (Smith 1972).

Areas 3 and 4 achieve a balance in relative abundance of larvae at 13 mm (Figure 7). Sucker larvae are 9-10 mm at hatch (Cooperman and Markle 2003), to grow to 13 mm at 0.13 mm per day would take about 25 days (S. Reithel unpublished data). After hatching, larvae spend the first week to two weeks in the gravels (Klamath Tribe’s Braymill Hatchery, unpublished data, 1991). After swim-up, an average of 4-5% of larvae must emigrate into Keno Impoundment per day to achieve equal relative abundances by 13 mm.

Figure 7 also indicates that LRS larval emigration occurs at a fairly steady rate throughout the smaller size classes (11-14 mm). SNS emigration appears to increase when larvae are 13-15 mm. This implies that either SNS emigration rates increase at this size or that SNS are already slightly larger when they emigrate into the Keno Impoundment. The later scenario seems more probable because SNS occur in the highest

relative densities in area 2 at 12 mm and LRS at 11 mm indicating that area 2 is further from the SNS source area and closer to the LRS source area. The implication is further strengthened by previous research that indicates SNS are slightly shorter than LRS at swim-up (Hoff et al. 1997).

Most SNS larvae will be coming from the Williamson and Sprague Rivers shortly after swim up. Even though the travel time is brief, they would experience some growth before arrival in UKL (Cooperman and Markle 2003). LRS larvae hatched at the shoreline springs may “pull” the relative abundances of this species towards a smaller size in UKL and Keno Impoundment.

The difference in emigration patterns between species is apparent at small sizes (Figures 8 – 11). These early differences are potentially responsible for distribution patterns into the juvenile stage. Figure 9 shows that small LRS larvae are captured in equal abundances in UKL and Keno. SNS of this size are captured in greater densities in UKL. As small larvae are captured in the highest densities near source areas it follows that LRS are more susceptible to transport at a small size or that Keno is closer to their source area (Schmidt 1922; Smith 1972). Both species continue to be transported into the Keno Impoundment at larger larval stages and as juveniles, but LRS maintain a higher density relative to SNS (Figures 10 and 11).

Gyres and other currents, upwelling, and frontal regions are some of the transport and retention mechanisms recognized in the marine environment (Smith 1972; Iles and Sinclair 1982; Anderson 1988; Hare et al. 1999; Hinrichsen et al. 2003). The clockwise gyre in UKL potentially aids larval retention, especially of larvae from the Williamson and Sprague Rivers. However, we have no evidence that this is an important mechanism.

Initial results from placing numerical ‘particles’ into a model of the lake’s currents indicate that the particles must be placed far from the eastern shore to be retained within the clockwise gyre above Buck Island. Particles that more closely mimicked larvae and were placed in the lake near the mouth of the Williamson River traveled along the eastern shore and often stalled near Goose Bay (T. Wood unpublished data). Particles placed closer to shore along the springs area were also more likely to enter the eastern shore current and be transported to the terminus of the lake. However, entrainment into the eastern shore current did not necessarily mean 100% direct transport out of the lake.

Any lag time the larvae experience traveling the eastern shore current may enable them to grow to a larger size with increased swimming ability and decreased drifting behavior thereby decreasing the effect of the current on their movement (Manteifel et al. 1978; Pavlov 1978, 1994; Kauffman 1990). Long term monitoring in UKL indicates that larval sucker CPUE in Goose Bay is consistently high, second only to a site at the mouth of the Williamson River (Simon and Markle 2004). Cross-shelf larval transport in the marine environment is known to be highly influenced by shoreline features (Hare et al. 1999). Very few larvae (5) were captured in Agency Lake, probably because they are unlikely to complete the 10-day rotation of the gyre and then swim against the direction of flow in Agency Straits (T. Wood personal communication).

Preliminary results from the UKL current model indicate that more particles leave the lake under high flow conditions. Using Link River Dam flows from 2004, about 85% of particles left the lake under June high flow conditions versus 30% at August flow conditions. Higher flow conditions also resulted in faster transport from the eastern shore to the terminus of the lake. On average this journey takes 6-8 days at the lower discharge

and 3-5 at the higher discharge (T. Wood personal communication). Fish aged for this study indicate that five days separates the age of the youngest larvae in UKL and the youngest larvae in Keno (S. Reithel unpublished data), substantiating travel times estimated by the model (Hare et al. 2002; Jones 2002). Higher lake elevation also resulted in a greater loss of larvae over Link River Dam but this effect was most influential at low flow conditions (T. Wood personal communication).

Lake elevation also affects other components of the system that influence sucker survival. High lake levels provide vegetated areas along the shoreline for larval suckers to avoid predators, these areas also provide spawning habitat for non-native fathead minnows. Field studies have confirmed a negative relationship between fathead abundance and larval sucker survival in the 10-15 mm size class. Therefore, management decisions such as lake elevation that provide habitat for both suckers and fathead minnows, may have both positive and negative impacts on sucker survivorship. These decisions and the corresponding results need to be examined with these ‘trade-off’ functions in mind (Markle and Dunsmoor in press).

Several factors expose LRS to higher rates of entrainment. More LRS spawn adjacent to the eastern shore current (Andreasen 1976; Fortune 1979; Klamath Tribe 1993; Hayes and Shively 2001). Adults spawn earlier (Table 3) and larvae hatch earlier (Figure 12). These early larvae will be exposed to longer periods of drift. Day length in the Upper Klamath Basin increases about 1 hour from mid April to mid May, decreasing the night drift period (Manteifel et al. 1978; U.S. Naval Observatory, Astronomical Applications Dept. 2006). Cooler temperatures in the early spring will most likely cause early hatched larvae to grow more slowly (Houde and Schekter 1989; Clarkson and

Childs 2000). Mean April air temperatures in this area are 4 °C (7.5 F) cooler than mean May temperatures (USBR, Western Regional Climate Center, 2006). In the marine and freshwater setting, temperature is considered to be a major factor controlling larval growth, survival, and year-class success (Benko and Seliverstov 1971; Houde and Schekter 1989; Clarkson and Childs 2000). In the marine environment, larval instantaneous growth and mortality rates have been found to increase by approximately 0.01 per degree temperature (Houde and Schekter 1989). Experiments with a freshwater cyprinid, the Danube bleak, have shown that the metabolic costs of swimming at the larval stage are higher at cooler temperatures (Wieser and Kaufmann 1998). During early spring the higher metabolic costs of transport could translate into higher metabolic costs of seeking out habitat and searching for food and result in lower growth rates for early hatched fish.

Experiments with another freshwater cyprinid, the roach, show that as larvae grow they tend to drift fewer hours each night. Drifting typically ceases with the attainment of the juvenile stage and as stage duration is inversely related to temperature, cooler temperatures and slower growth will cause larvae to drift longer each night and for more nights (Manteifel et al. 1978; Houde and Schekter 1989). In addition, Lost River suckers appear to be thinner-bodied and less developed than SNS at small sizes (unpublished data).

Variability in sucker spawning strategy is likely a result of the variability in the environment (Den Boer 1968). Cooperman (2004) found that low wind and warm temperatures favored larval sucker survival. Cohort survival was dependant on larvae coinciding with a “window” of favorable conditions in UKL. Over the seven years of his

study, conditions varied but appeared to be controlled by large-scale climate patterns that may persist for many years.

The longevity and iteroparous nature of suckers in the Upper Klamath Basin may have enabled them to sustain population size in between favorable “windows” for progeny and allowed them to establish prolific populations and many spawning stocks in the basin (Den Boer 1968; Lambert and Ware 1984). However, even long-lived suckers are affected by chronic stresses and prolonged lack of recruitment as shown by population declines and loss of spawning groups in these and other lake suckers (Scoppettone and Vinyard 1991).

Presently, in the Upper Klamath Basin, retention in UKL is undoubtedly the most favorable outcome for larvae. Prey abundance in Upper Klamath Lake is not considered a limiting resource (Markle and Clausen in press). Therefore, larvae retained in the lake would be “matched” with their food resource and given an overlap with favorable temperatures and wind conditions, these larvae have the best chance of survival (Cooperman 2004). In the Keno Impoundment, seasonally degraded water-quality and lack of connectivity with Lower Klamath Lake and the Lost River system lessen or negate larval survival and return to Upper Klamath Lake (Martin and Saiki 1999; Saiki et al. 1999; USFWS 2002; Jason Cameron, USBR, personal communication). Any species, such as Lost River sucker, or a particular spawning group such as the early spawning shoreline springs group, that is more likely to become entrained into Keno would potentially experience greater initial loss of larvae and have fewer individuals available for eventual recruitment.

Conclusion

In 2004, Lost River sucker larvae appeared more likely than shortnose sucker larvae to be transported into the Keno Impoundment. The capture of Lost River suckers in greater densities in Keno at both larval and juvenile stages suggests that the degree of loss may be substantial. The capture of equal densities of juvenile shortnose suckers in Upper Klamath Lake and Keno suggests they are not immune to entrainment. Poor water quality in the Keno Impoundment in late summer suggests that all or nearly all entrained larvae and juveniles are lost to eventual recruitment (Jason Cameron, USBR, personal communication).

Further refinement of T. Wood's UKL circulation model would help test the influence of environmental factors on entrainment. Further data analysis and identification of larval specimens collected by OSU in years preceding and following this study, would further indicate how entrainment rates differ between species and hatch dates. Currently, identification by pigmentation patterns leaves about 50% of the larvae unidentified. Clearing and staining larger larvae, damaged fish, etc should bring the total number of unidentified fish closer to 10-15%. Due to the low number of larval suckers captured in many years (less than 1000 in 2002 and 2003) high proportions of species identification are necessary for species based analysis of these data.

Further work to distinguish larvae from river and shoreline spawning groups would help determine if there are differences between the progeny of these groups in their susceptibility to entrainment. This data should help indicate to what extent entrainment rates for each species (and potentially between spawning groups within a

species) differ due to differences in larval production and environmental conditions from year to year.

The relationship between sucker year-class survival and lake elevation is not linear. Lake elevation also alters other components of the system. The nonnative fathead minnow, *Pimephales promelas*, is the numerically predominant fish in UKL. Field studies confirm fathead minnow abundance is negatively correlated to larval sucker survival. Lab experiments have shown that sucker survival, in the presence of fathead minnow, is higher when more habitat is available. Higher lake elevation provides more habitat for age-0 suckers but may also benefit fathead minnow. Higher lake elevation may also aid in adult survival in several ways (Markle and Cooperman 2002). Thus, the management decisions focused on lake elevation are not simple.

Increased effort in hatchery operations in the Klamath Basin are likely to commence within the next few years (Barnard 2006). These programs have been used to address declining populations of lake suckers in other systems (Scoppettone and Vinyard 1991). For the species to recover healthy populations, it is important to understand the pressures experienced by early life stages in the natural environment.

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Appendices

Figures

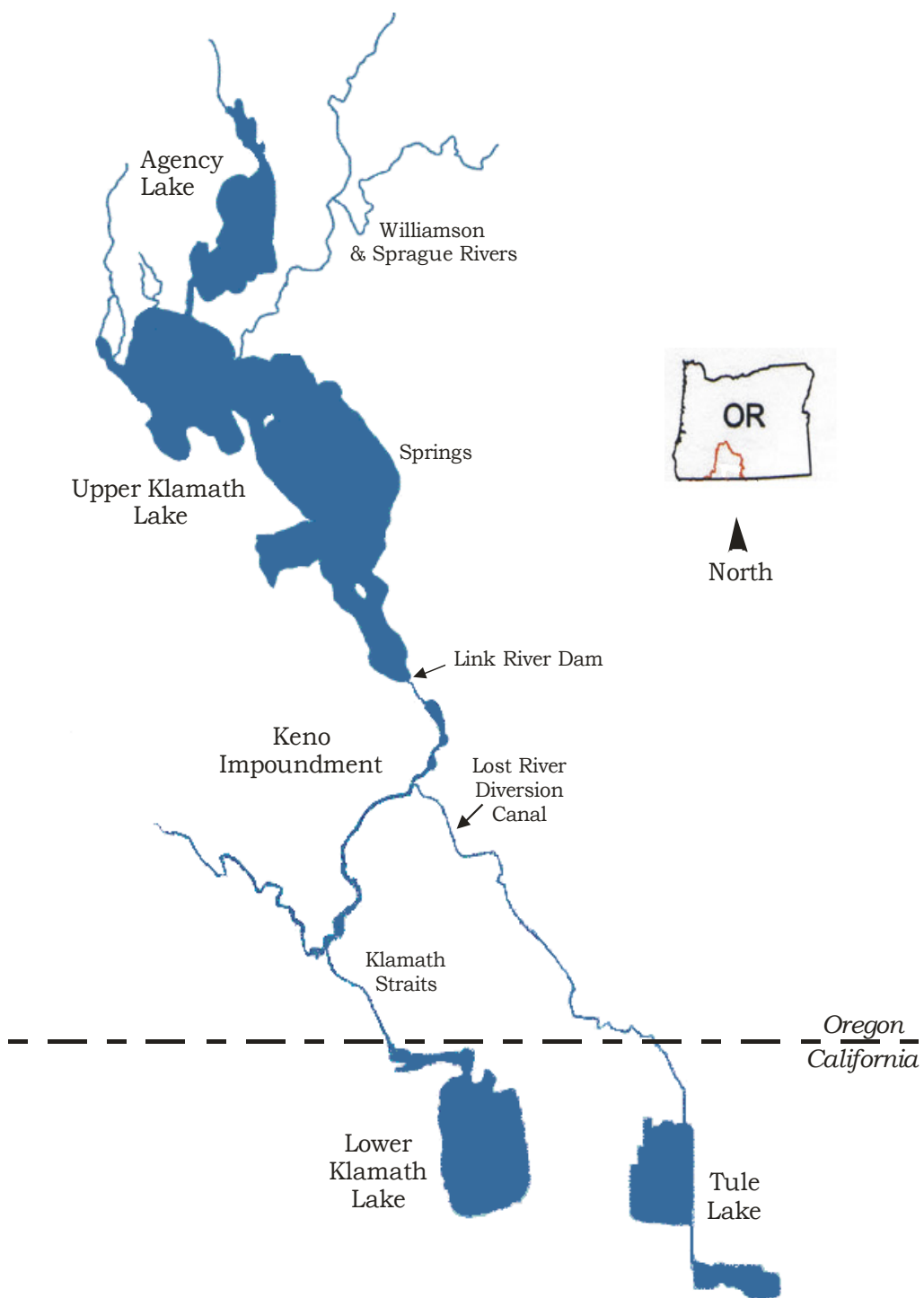


Figure 1.—Map of Upper Klamath Basin.

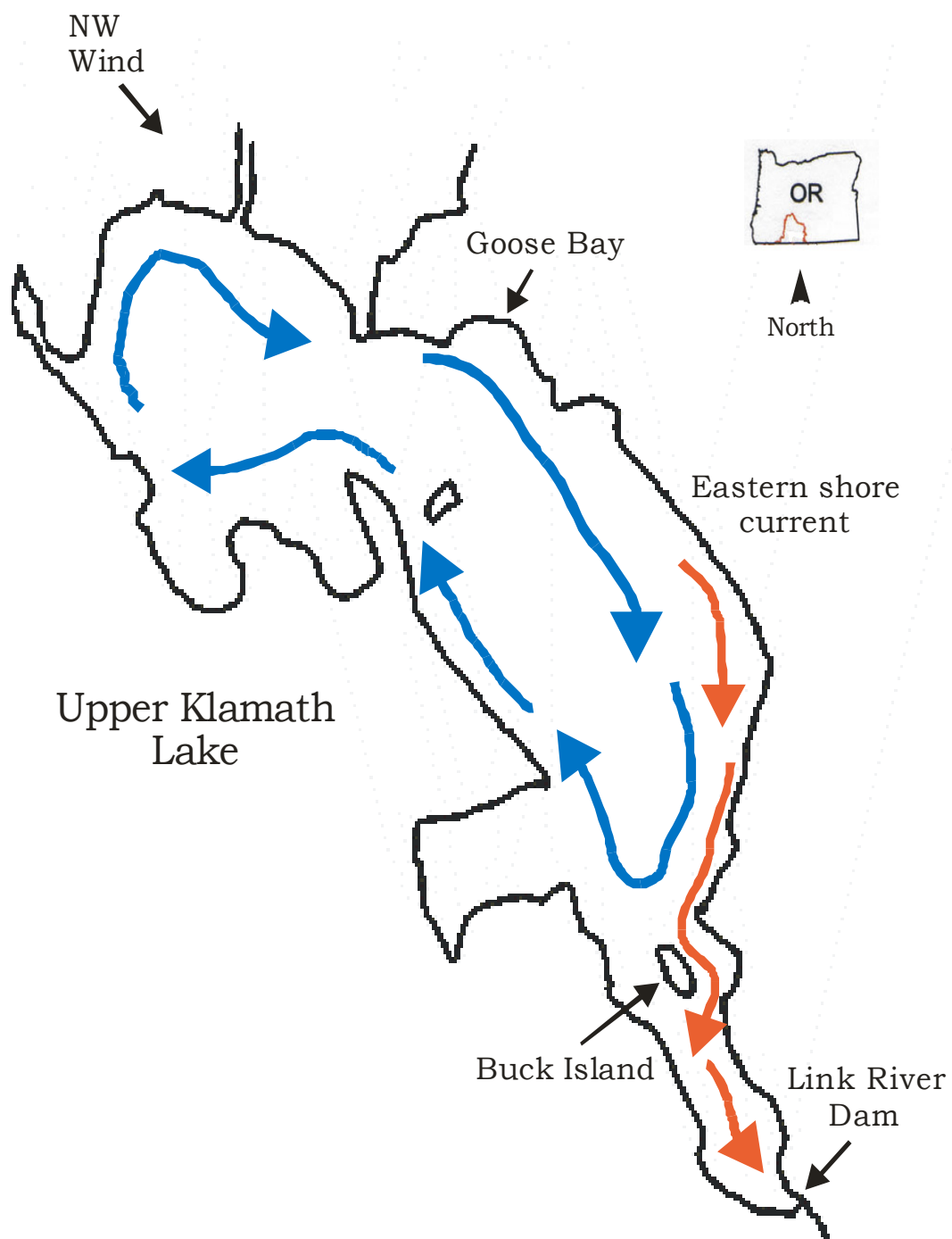


Figure 2.—Upper Klamath Lake circulation (modified from Wood et al. 2006).

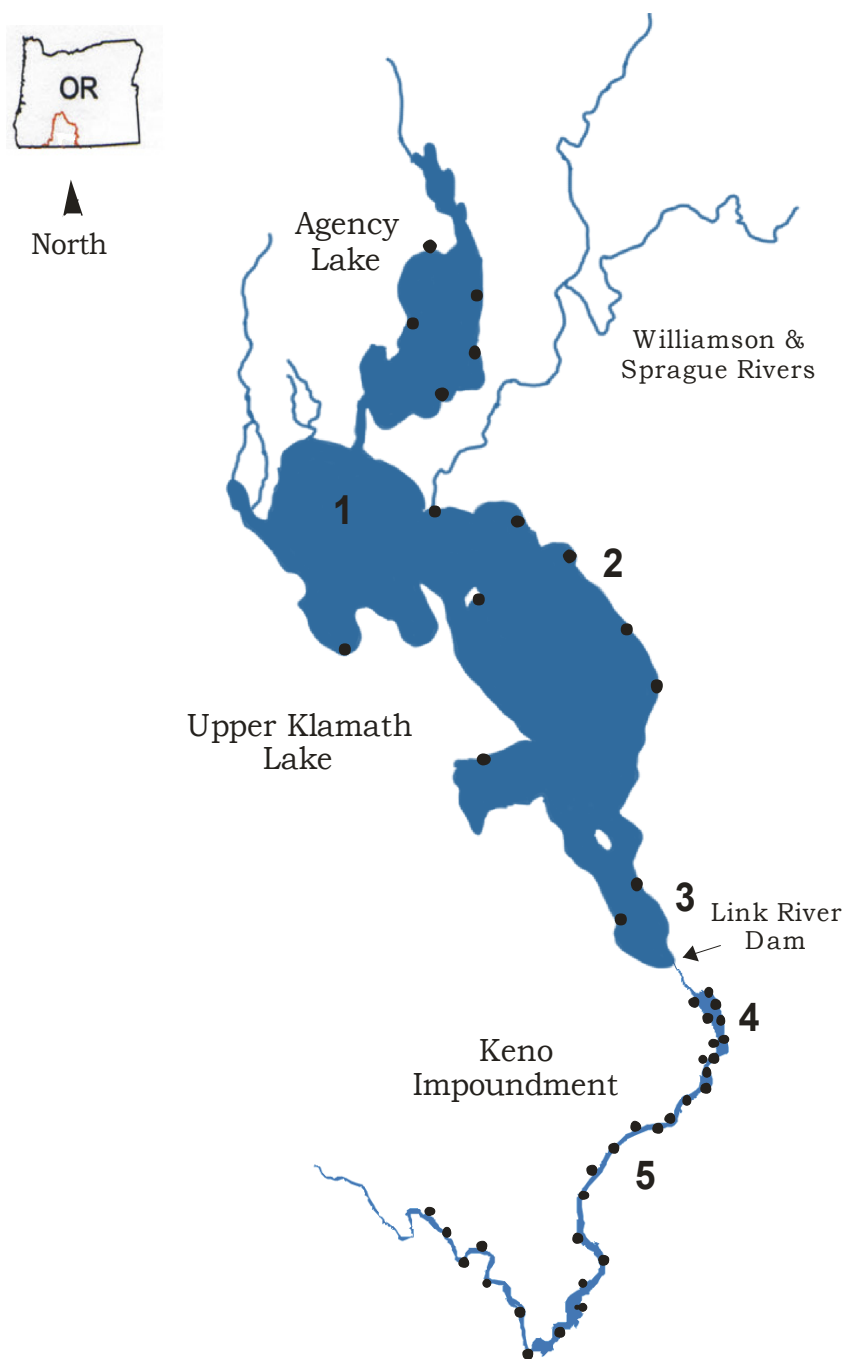


Figure 3.—Lake wide and river wide standard sampling sites in Upper Klamath Lake, Agency Lake, and the Keno Impoundment.

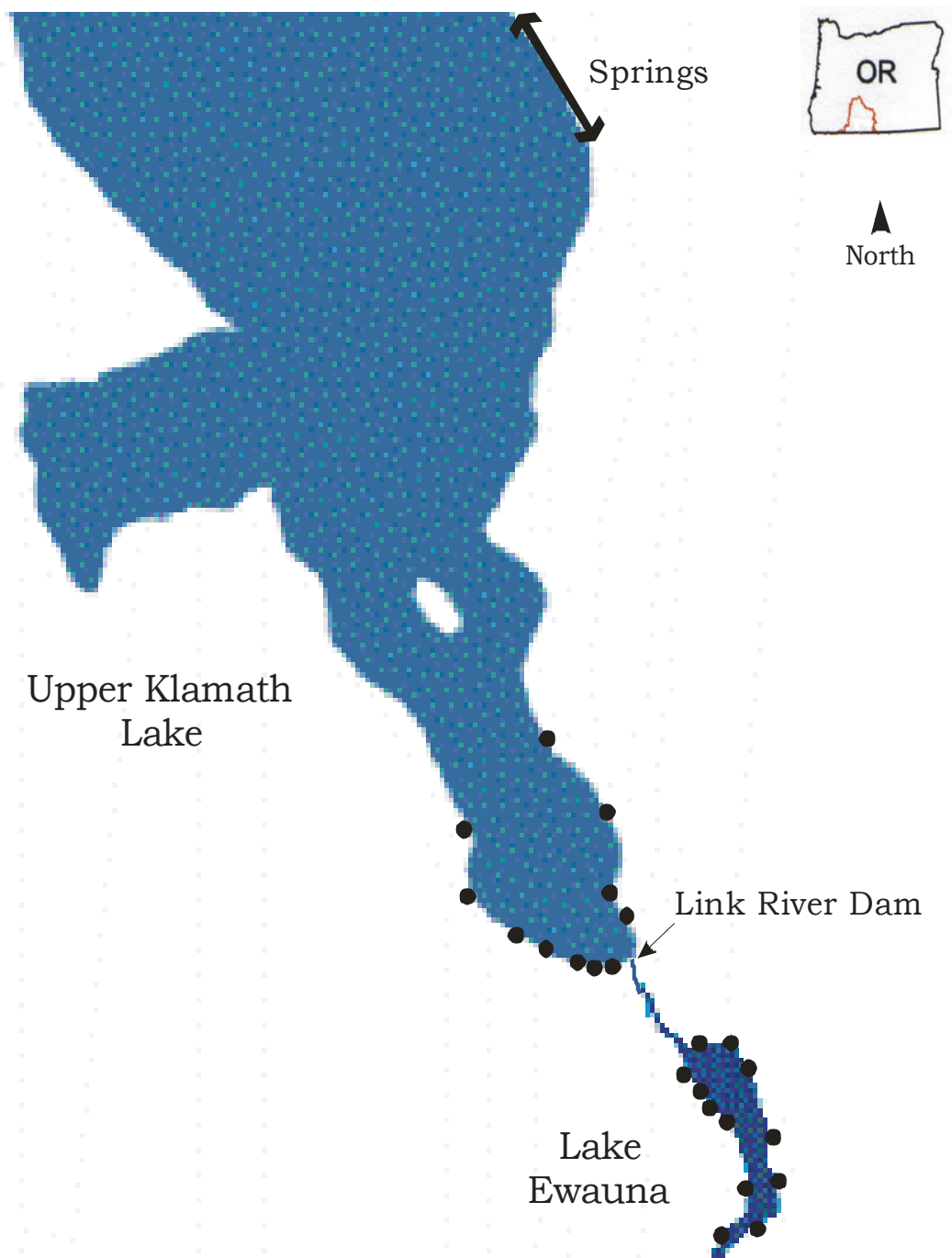


Figure 4.—Sites above and below the Link River Dam and the lakeshore springs.

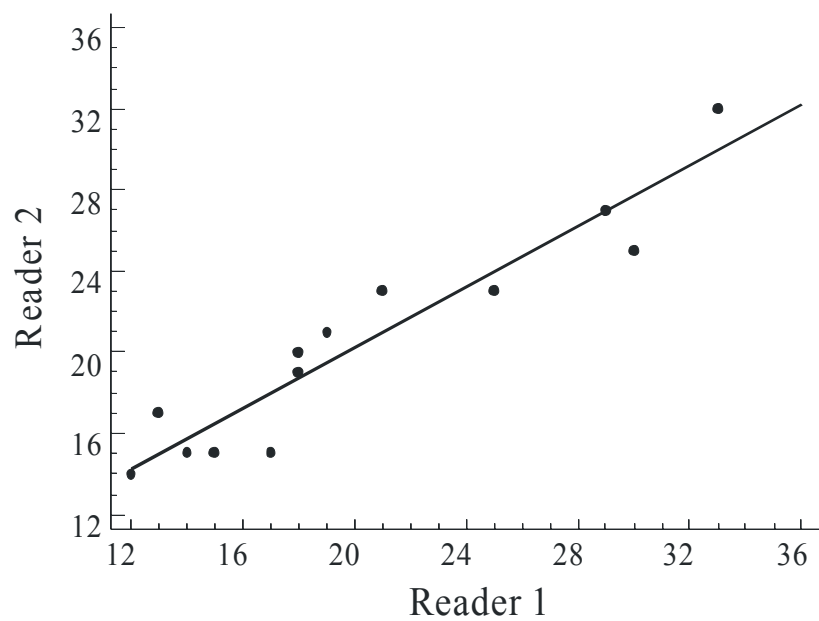


Figure 5.—A comparison of median reads of age in days, made by readers one and two, showing relatively good consistency.

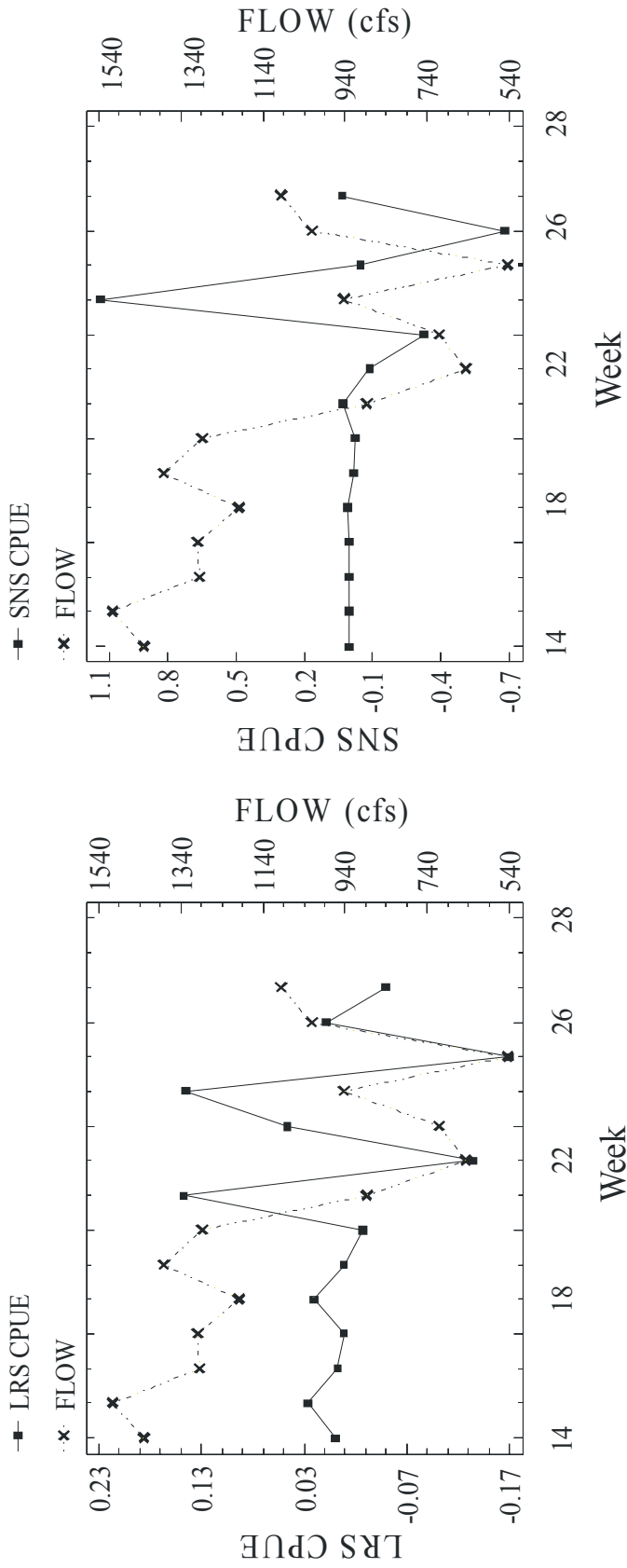


Figure 6.—Lost River and shortnose sucker CPUE (area 4 – area 3) and flow thru the Link River Dam by calendar week.

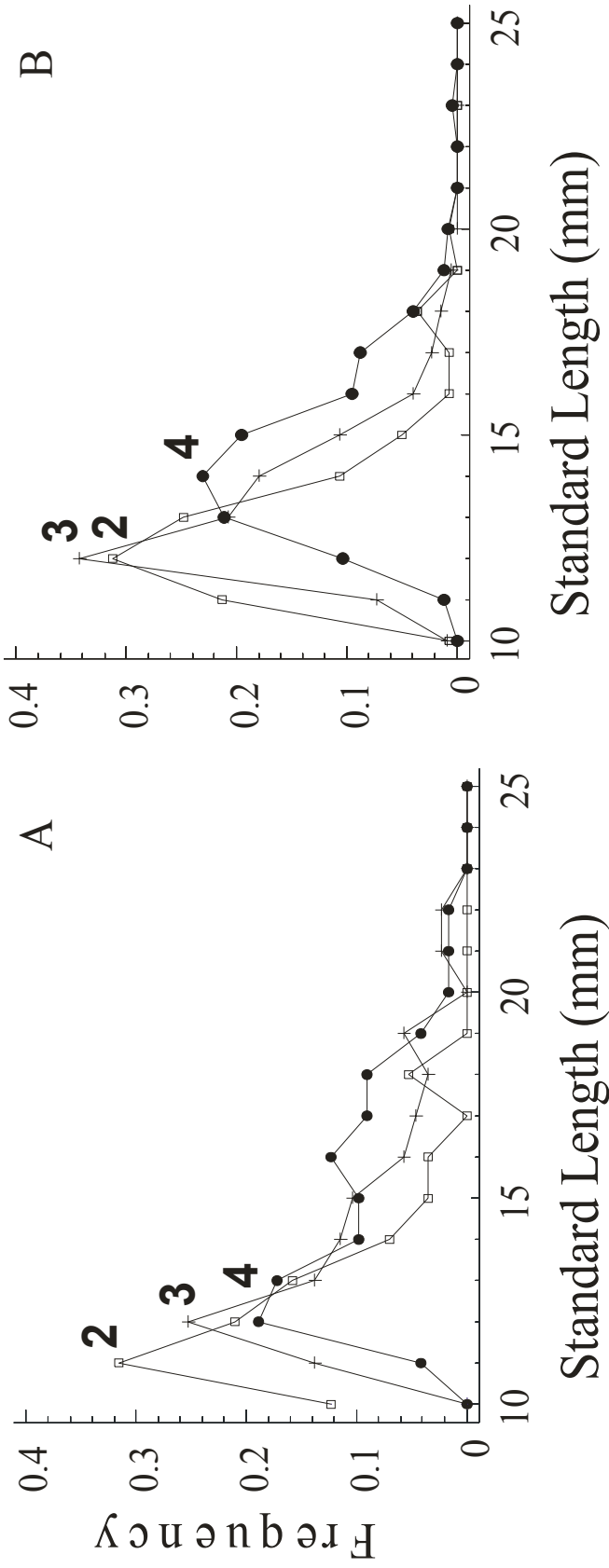


Figure 7.—The size frequency of sucker larvae captured in 2004 showing transport away from Upper Klamath Lake's east shore (2—square), south shore (3—cross), and upper Keno Impoundment (4—dot). (A) Lost River larvae. (B) Shortnose larvae.

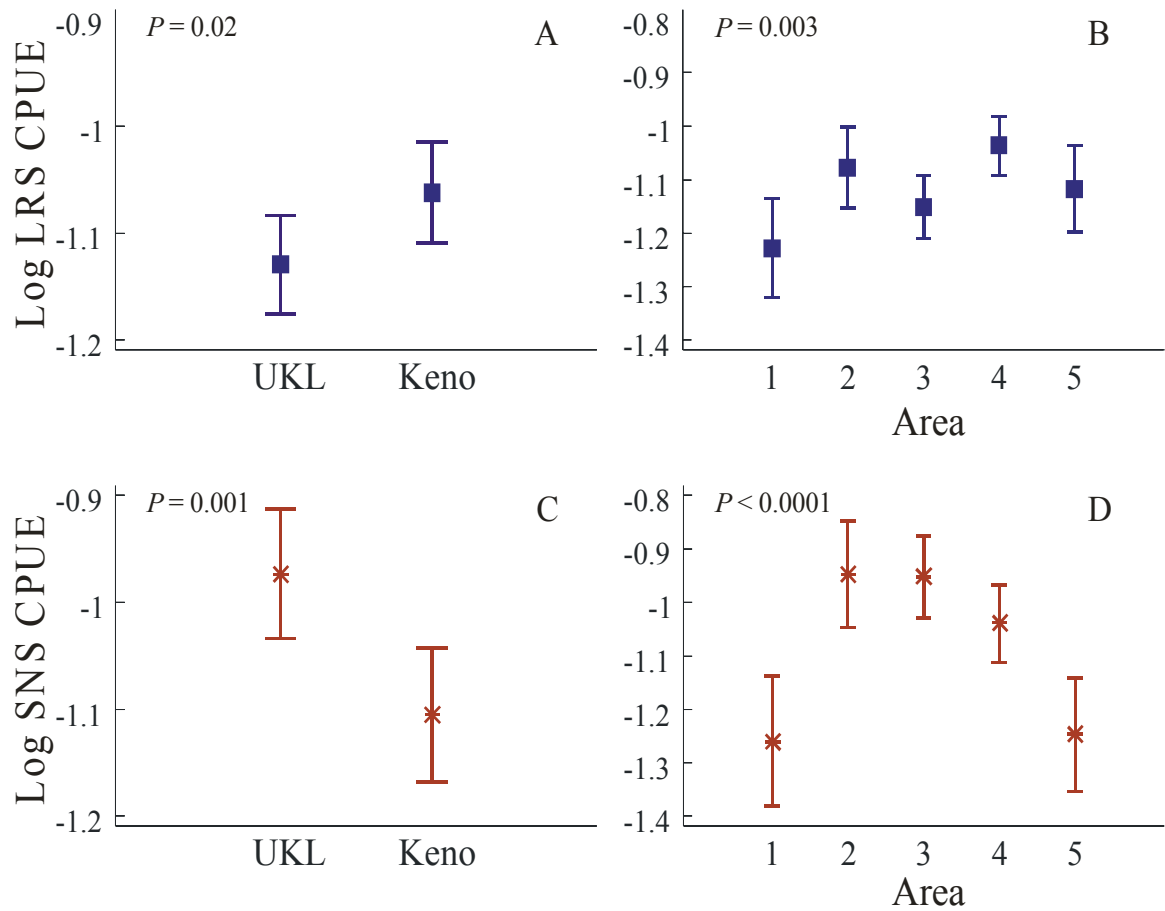


Figure 8.—Comparison of log transformed CPUE of sucker larvae showing means and 95% confidence intervals between Upper Klamath Lake and the Keno Impoundment and among areas.

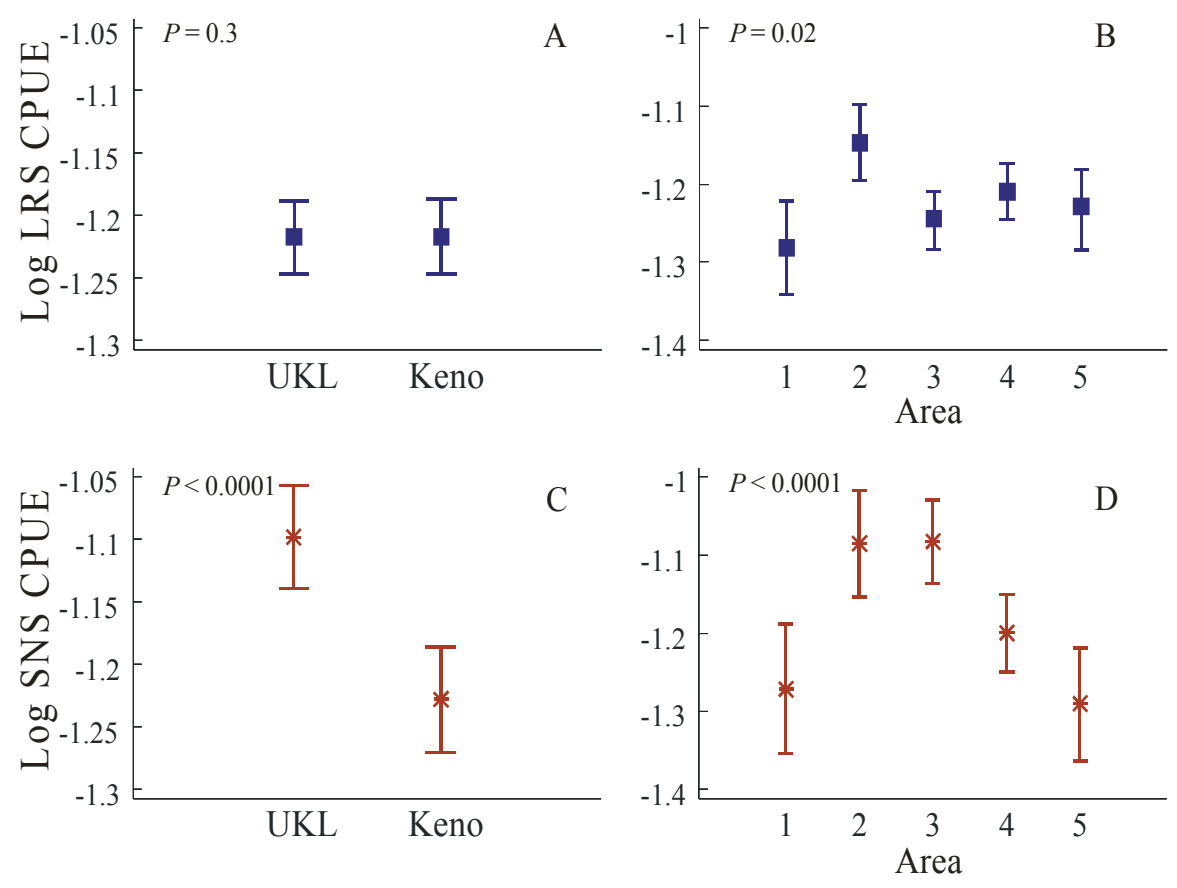


Figure 9.—Comparison of log transformed CPUE of small sucker larvae (≤ 13 mm) showing means and 95% confidence intervals between Upper Klamath Lake and the Keno Impoundment and among areas.

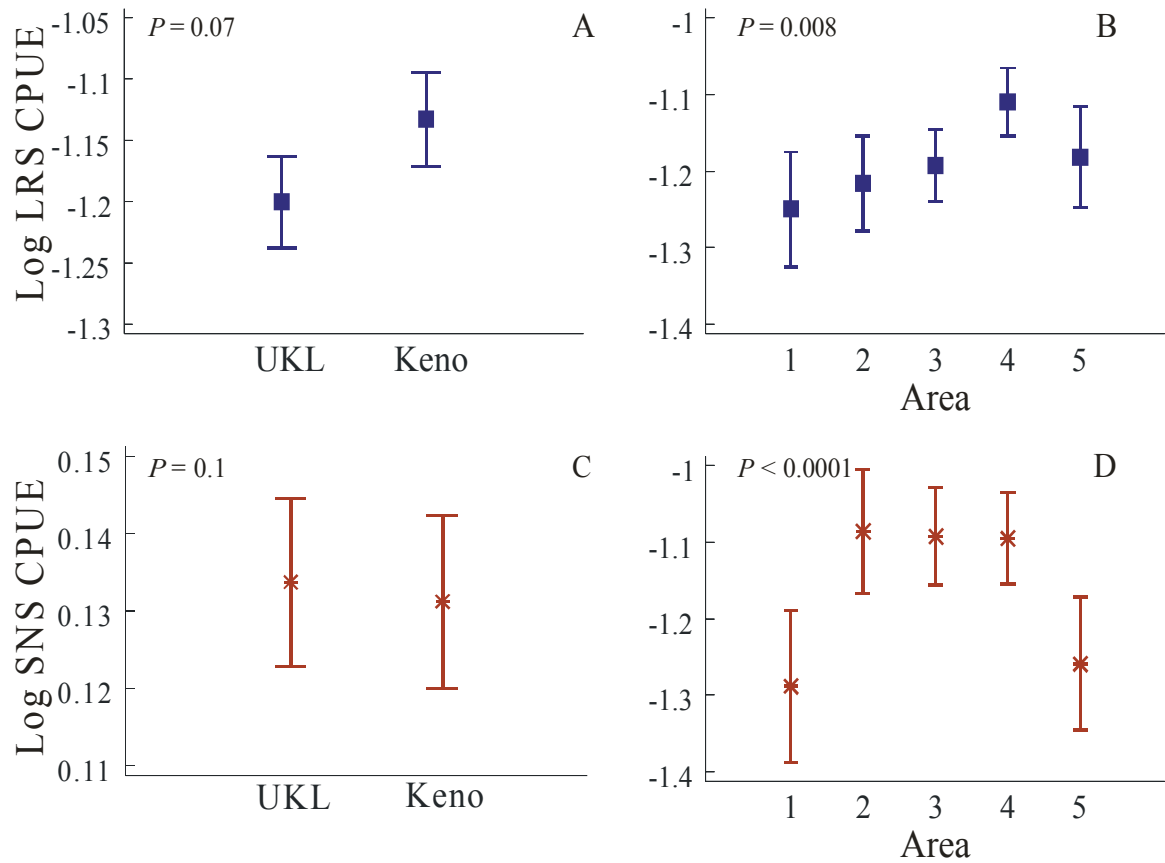


Figure 10.—Comparison of log transformed CPUE of large sucker larvae (> 13 mm) showing means and 95% confidence intervals between Upper Klamath Lake and the Keno Impoundment and among areas.

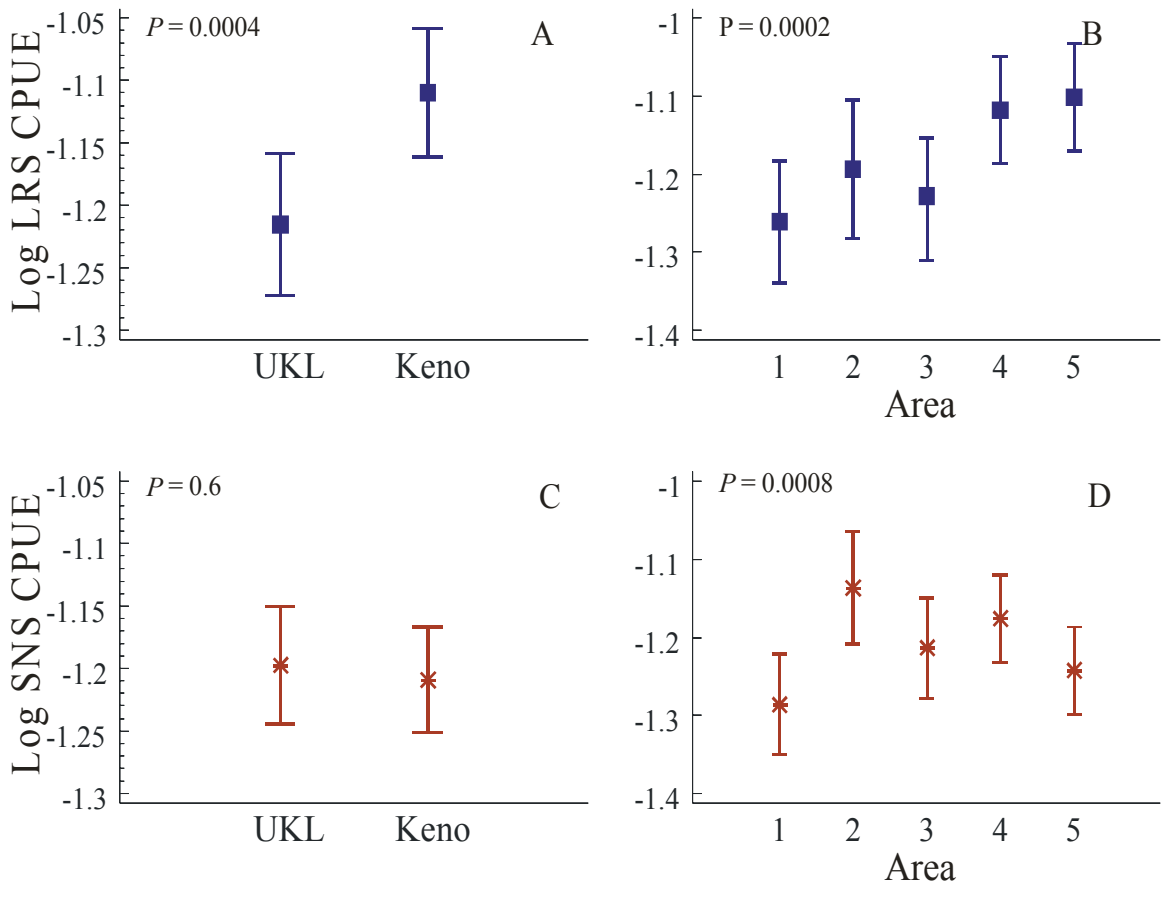


Figure 11.—Comparison of log transformed CPUE of age-0 suckers showing means and 95% confidence intervals between Upper Klamath Lake and the Keno Impoundment and among areas.

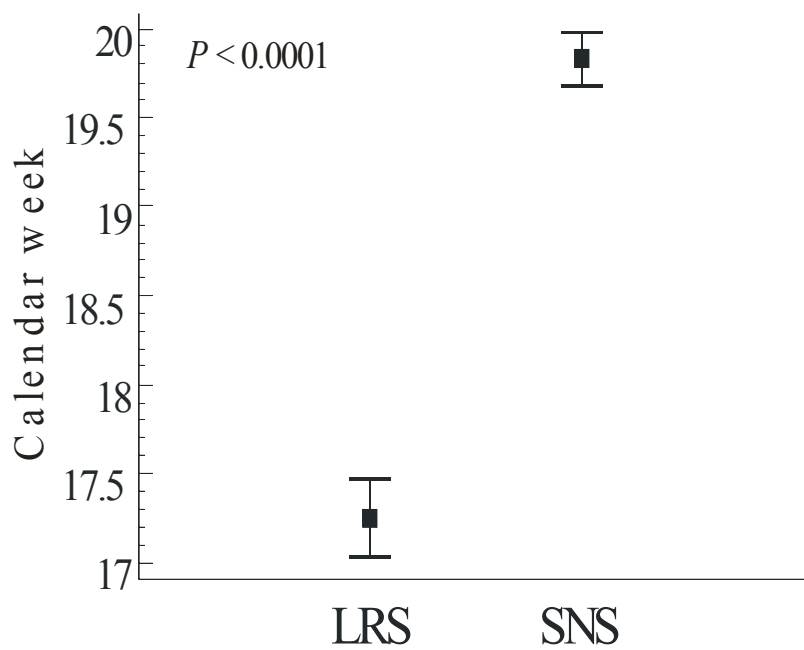


Figure 12.—Comparison of mean hatch weeks between Lost River and shortnose suckers ($P < 0.0001$). Weeks are calendar weeks starting with the first week of January.

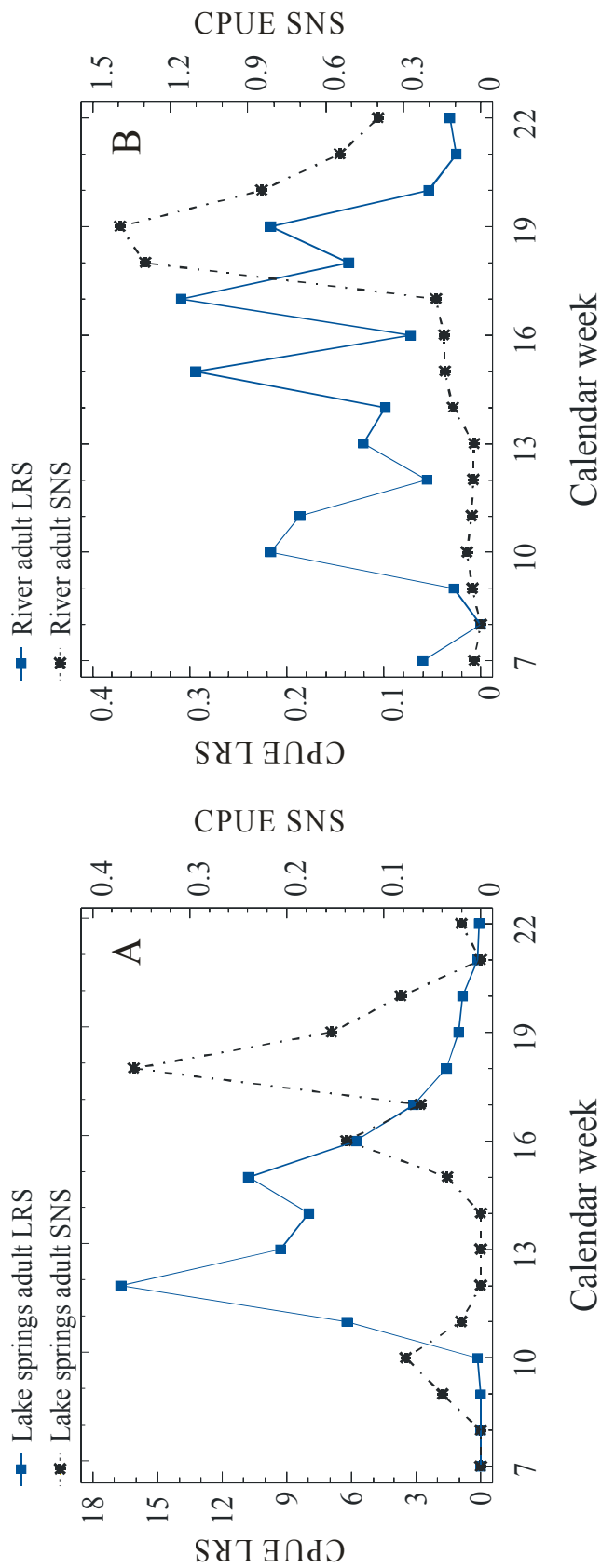


Figure 13.—A temporal comparison of springs (A) and river (B) spawning groups by CPUE per calendar week.

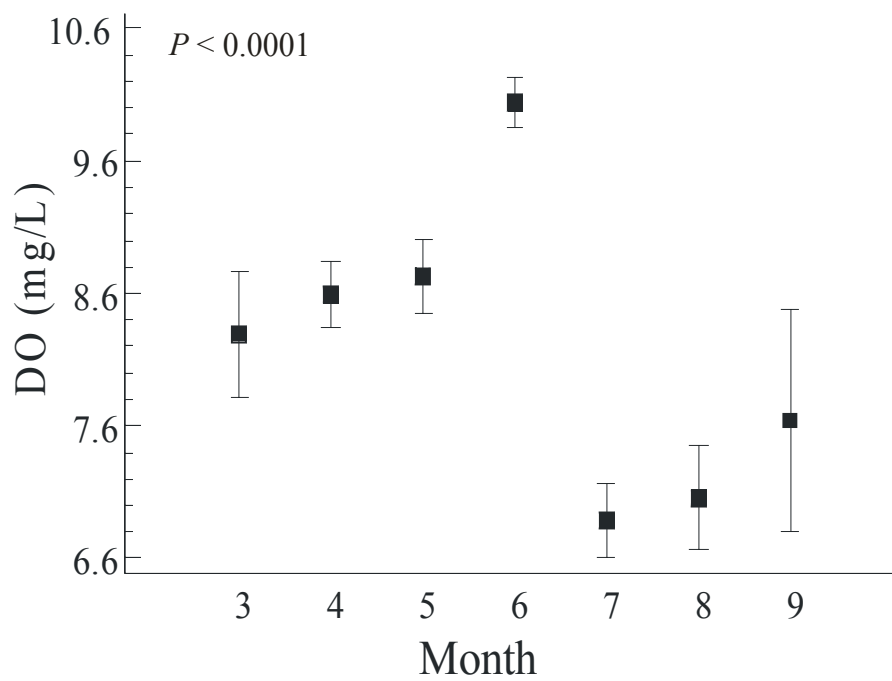


Figure 14.—Monthly mean dissolved oxygen levels (with confidence intervals) for all samples.

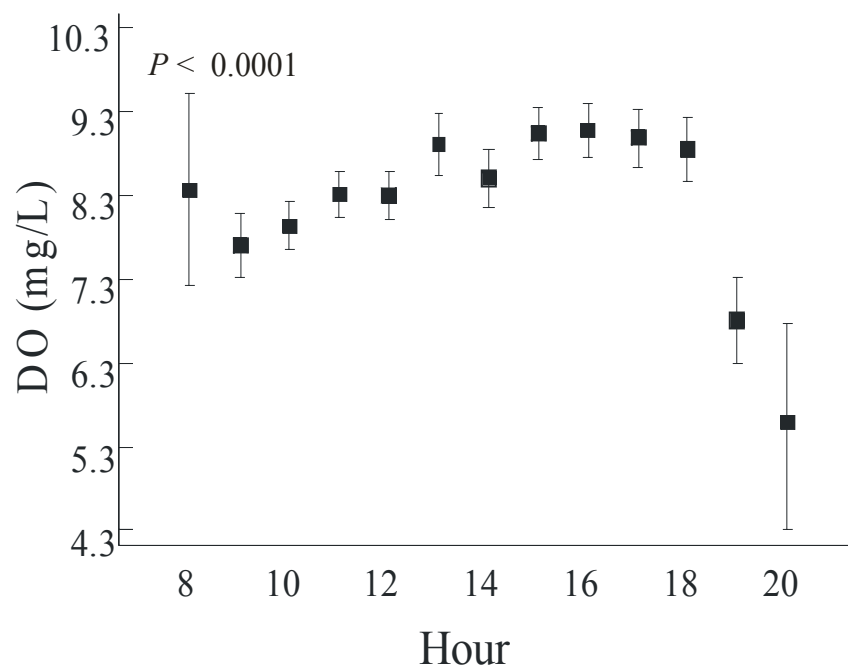


Figure 15.—Hourly mean dissolved oxygen levels (with confidence intervals) for all samples.

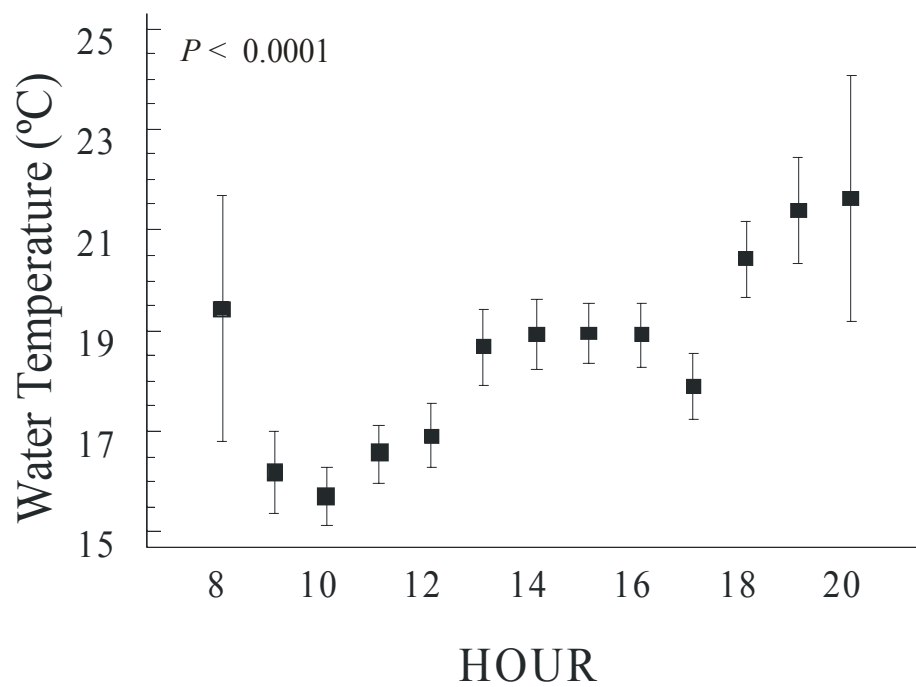


Figure 16.—Hourly mean water temperature (°C) (with confidence intervals) for all samples.

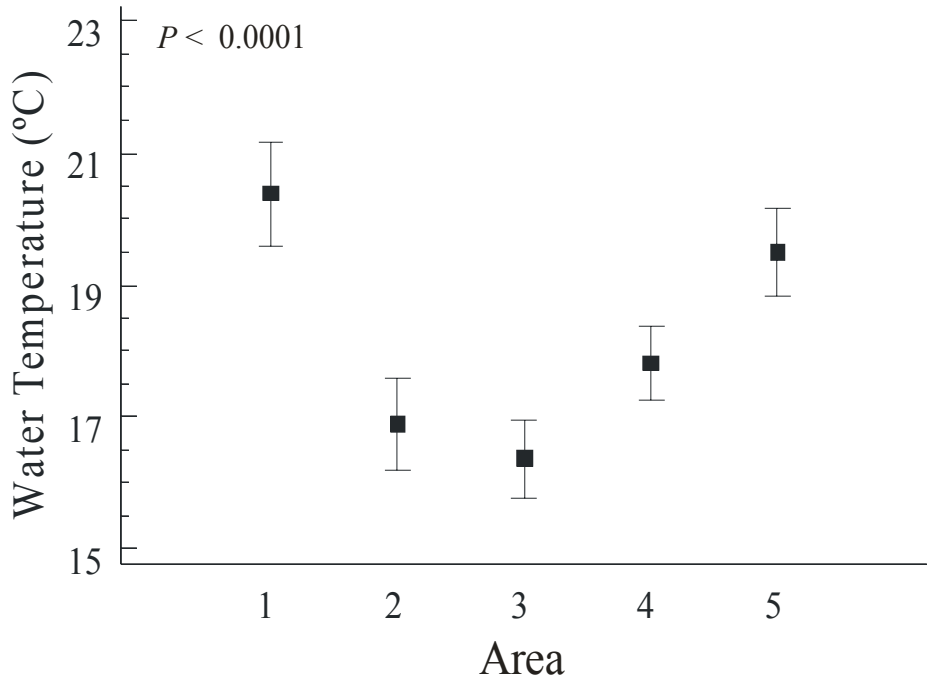


Figure 17.—Mean water temperature (°C) (with confidence intervals) among areas for all samples.

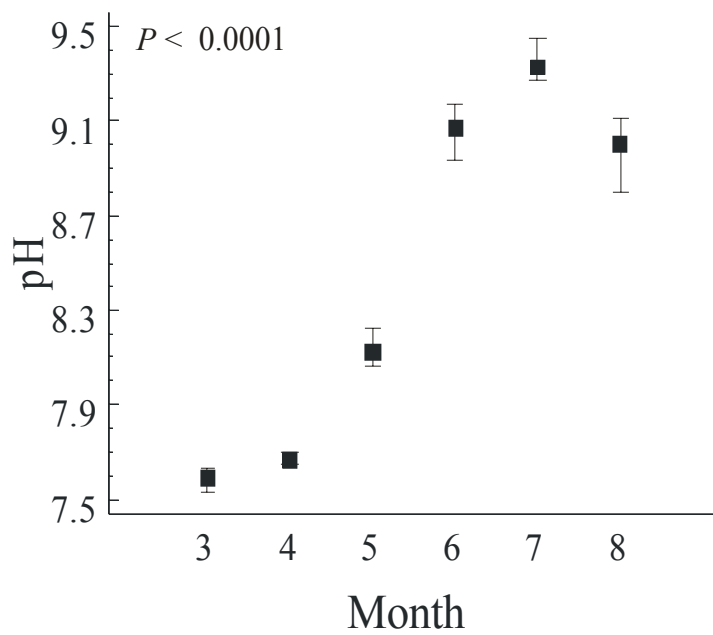


Figure 18.—Median pH (with confidence intervals) among months for all samples.

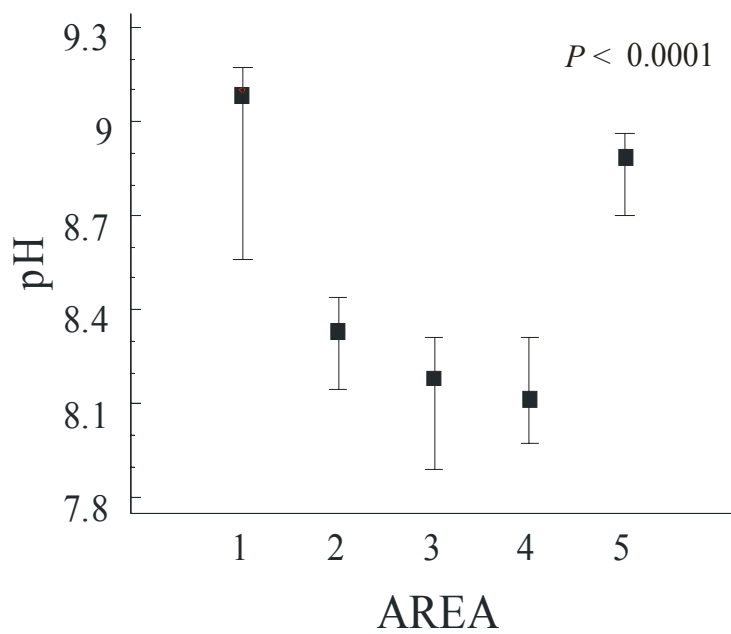


Figure 19.—Median pH (with confidence intervals) among areas for all samples.

Tables

Table 1.—Frequency of larval trawl and beach seine sampling.

Lake/location	# sites	Sampling type	Samples per visit	Samples per survey	Total samples		Fish Captured	
					Larval Trawl	Beach Seine	Larval Trawl	Beach Seine
UKL	10	standard	2	20	120	80	190	96
UKL (southern end)	12	additional	1	24	216	48	469	40
UKL (springs)	10-12	additional	1-2	10-12	82	10	55	79
Keno	30	standard	1	30	180	120	218	201
Keno (upper)	12	additional	1	24	216	48	314	91
Agency	5	standard	2	10	60	40	5	4
TOTAL	81	-	-	-	874	346	1251	511

Table 2.—Environmental variables measured in Upper Klamath Lake, Agency Lake and the Keno Impoundment.

Abiotic variable	Source
Sampling site	
Depth (of water quality sample)	Hydrolab ® / YSI ®
Depth (of larval trawl)	Field Measurement
Temperature	Hydrolab ® / YSI ®
Conductivity	Hydrolab ® / YSI ®
Dissolved oxygen	Hydrolab ® / YSI ®
pH	Hydrolab ® / YSI ®
Substrate	Field Classification
Study area	
Flow over the Link River Dam	Bureau of Reclamation
Biotic variable	Source
Sampling site	
Aphanizomenon density	Field classification
Vegetation	Field classification

Table 3.—Seasonal abundance of spawning Lost River sucker (LRS) and shortnose sucker (SNS) captured before the midpoint of week 17, 2004.

Species	Spawning group	<i>N</i>	Before Week 17
LRS	Williamson River	129	71.3%
	Lake springs	1481	87.5%
	All	1610	86.2%
SNS	Williamson River	403	10.4%
	Lake springs	35	33.3%
	All	438	12.3%

Table 4.—Percentage of larval suckers with hatch dates on/or before the midpoint of week 18, 2004.

Area	<i>N</i>	LRS		SNS	
		On/before week 18	<i>N</i>	On/before week 18	
1	12	92%	7	0%	
2	57	72%	141	11%	
3	87	46%	356	13%	
4	122	69%	251	12%	
5	56	79%	11	27%	
Agency	4	100%	1	0%	
UKL	152	58%	503	13%	
Keno	178	72%	262	13%	
Total	334	66%	766	13%	