AN ABSTRACT OF THE DISSERTATION OF

Michael S. Cooperman for the degree of Doctor of Philosophy in Fisheries Science presented on January 28, 2004.

Title: Natural History and Ecology of Larval Lost River Suckers and Larval Shortnose Suckers in the Williamson River – Upper Klamath Lake System.

Abstract approved:

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Douglas F. Markle

We monitored larval Lost River and shortnose suckers from natal beds in the Williamson and Sprague rivers to nursery grounds in Upper Klamath Lake. Downstream movements occurred at night, in the middle of the channel, and on the falling limb of the hydrograph. Ages, sizes, and developmental stages of larvae from spawning beds and the river mouth were similar, while larvae collected contemporaneously from the lake tended to be larger and better fed. Our results indicate in-river rearing was rare, that a rapid outmigration to the lake was favorable for larval survival, and that modification of the lower Williamson River does not appear to have prohibited rapid entry or preclude access to Upper Klamath Lake. Within the Williamson River and Upper Klamath Lake, emergent macrophytes supported significantly higher abundance, larger mean sizes, and better fed larvae than submerged macrophytes, woody vegetation, or open water areas. Analysis of seven years of larval sucker production and survival corroborated the habitat analysis by identifying a positive relationship with emergent macrophyte availability as well as a positive relationship with air temperature and a negative relationship with high wind. These findings illustrate the importance of fast growth, appropriate habitat and calm hydrological conditions for larvae, and are highly consistent with other larval fish studies.

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Natural History and Ecology of Larval Lost River Suckers and Larval Shortnose Suckers in the Williamson River – Upper Klamath Lake System

by

Michael S. Cooperman

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

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Michael S. Cooperman, Author

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I don't think a graduate student could ask for a more rewarding experience. At the start, the research was enough – to study a critical life history stage of an imperiled fish with the hope of contributing to its persistence and recovery. Then, the drought of 2001 hit and, empowered by the Klamath Basin Crisis, I interacted with myriad academics, government personnel, private sector consultants, Native American Tribes, 'Blue Ribbon' panels and the people of the Klamath Basin. Through it all, I've been able to contribute to the best of my abilities and dissent as I see fit. The extra opportunities and obligations lengthened my program, but the satisfaction far out-weights the price.

I thank Doug Markle for the opportunity to join his lab group, for the supportive atmosphere and countless hours of discussion he provided, and for realizing sometimes thought and production are best when they are not rushed. I have deep appreciation for my committee members, Hiram Li, Gordon Grant, Cliff Pereira, Larry Dunsmoor, Carmo Vasconcelo, and Darius Adams, as each has been highly available and helpful through out this process.

I'm grateful to my parents for many things, including the endless stream of newspaper clippings on Klamath events. I know it wasn't the Klamath they were interested in.

Finally, there's Anne and Paco. They came along right when things were getting difficult and made it fun. Both listened well as I rambled on, but only Anne ever asked any questions.

"... We fish keep company it is true, but our thoughts are our own & utterly incommunicable. Our thoughts deepen & we understand each other with a complete profundity only those unburdened by speech & its complications could understand. It is then untrue that we neither think nor feel...

I like my fellow fish. They do not whinge about small matters of no import, do not express guilt for their actions, nor do they seek to convey the disease of kneeling to others, or of getting ahead, or of owning things.... Their violence to one another – murder, cannibalism – are honest & without evil.

..... And you are just going to have to begin as I did: by looking long enough into the fish's eye to see what I must now describe."

---- Richard Flanagan, Gould's Book of Fish

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Natural History and Ecology of Larval Lost Lost River Suckers and Larval Shortnose Suckers in the Williamson River – Upper Klamath Lake System

CHAPTER 1

INTRODUCTION

Michael S. Cooperman

It's not easy being small, and larval fish are tiny relative to their environment (Miller et al. 1988). Small sizes, combined with incomplete fin and sensory organ development (Snyder 1983, Blaxter 1986), mean larvae have limited locomotive abilities (Dabrowski et al. 1986, Diana 1995, von Herbing 2002), energy reserves (Diana 1995, Horn 1995), prey-capture abilities (Miller et al. 1988, MacKenzie et al. 1990), and predator escape abilities (Oiestad 1983, Blaxter 1986, Johnson et al. 1993, Belk et al. 2001). Consequently, larval fish experience extremely high natural mortality rates, often between 10% to 80% day^{-1} (Houde and Zastrow 1993, Houde 2002). Several mechanisms contribute to the high attrition rate, including transport away from preferred habitats or to inhospitable conditions (Harvey 1987, Sinclair 1988), starvation (Cushing 1975, Lasker 1981), predation (Oiestad 1983, Houde 2002) and disease (Houde 2002). Competitive exclusion from preferred habitats often intensifies these conditions (Harvey 1991, Sogard 1994). The limitations of small size are exacerbated when post-hatching parental care is limited or absent, as is often the case for fishes that produce many small eggs and altricial larvae (Duarte and Alcaraz 1989, Diana 1995). But, producing many small larvae is one way to counter low survival caused by small size because as the number of larvae produced increases, so do the odds that at least a few will encounter favorable conditions (Winemiller and Rose 1993).

In general, all larvae have the same basic requirements; an abiotic environment where conditions are within their physiological tolerances, accessible food, protection from predators, and the ability to avoid entrainment and transport away from desirable locations. Areas that provide all these serve as nursery 'rearing grounds.' However, rearing grounds often do not provide suitable conditions for adult spawning or egg incubation making it necessary, in may cases, for newly hatched larvae to move from spawning grounds to rearing grounds (McDowall 1987, Sinclair 1988, Pavlov 1994).

Given the wide array of things that can go wrong for a larva, it is true that, "The average larva is dead. Why study the average larva?" (Gary Sharp, fisheries biologist, personal communication). Consequently, research on larval fish natural history and ecology should emphasize understanding conditions that produce good survival, with caution applied to inference based on description of what the mean

larvae does or did. For the endangered Lost River sucker (*Deltistes luxatus*) and shortnose sucker (*Chasmistes brevirostris*) of Upper Klamath Lake (UKL) in south-central Oregon, neither the dynamics of larval movement from spawning to nursery grounds nor the specific habitats used as nursery grounds are well described. Indeed, following a century of extensive habitat and fish community modifications, plus on-going water management protocols, it is unclear if acceptable larval sucker nurseries remain in the UKL system.

Lost River and shortnose suckers are endemic to the shallow lakes of the upper Klamath River watershed. Both species are long-lived, iteroparous, and highly fecund. They are obligate lake dwellers, except during annual spawning when the majority of adults migrate up in-flowing tributary streams to spawn (Markle and Cooperman 2002). The abundances of both species are greatly reduced from pre 1900 levels, and in 1988 both were protected as endangered under the federal Endangered Species Act (USFWS 1988). The largest populations of both species are in UKL (Markle and Cooperman 2002), where age data derived from fish kills in the 1980s and 1990s indicated limited recruitment to adult populations during the 1970's and 1980's (Scoppettone and Vinyard 1991, Markle and Cooperman 2002). Although large year-to-year fluctuations in young-of-year survival and resulting inter-annual variability in recruitment are common in long-lived iteroparous fishes (Hjort 1914, Cowan and Shaw 2002), inability to correct or compensate for persistent sucker year-class failure will hinder recovery.

Population monitoring conducted in Upper Klamath Lake since 1995 demonstrates inter-annual variation in numbers of sucker larvae produced (mean CPUE differences >5x), and the inter-annual variation increases for summer beach seine indices (mean CPUE differences >12x), and September cast net indices (mean abundance differences >544x for shortnose sucker and >68,000x for Lost River sucker) (Simon and Markle 1996, Simon et al. 2000, Simon and Markle 2001; Cooperman 2003 Ch. 1). In most years, small numbers of age-0 juveniles seem to survive through the first winter (Simon et al. 2000, Simon and Markle 2001), suggesting the root of the recruitment bottleneck may lie in survival during the first year. Although many indirect effects may be contributing to poor YOY sucker

survival (e.g., outbreeding depression related to hybridization or poor egg quality caused by poor parental condition), proximal causes hypothesized to account for poor YOY sucker survival include habitat loss and/or modification, stressful water quality, export out of the system, and negative interactions with other fishes (USFWS 1993, USFWS 2001). However, lack of detailed information on the natural history and ecology of larval and age-0 juvenile suckers precludes a detailed assessment of the impact of each potential survival hurdle.

Between April and August, 1998-2000 I conducted intensive larval sucker sampling in the Williamson and Sprague rivers and UKL. My sampling program was designed to track the movement, habitat use, feeding success, and growth of larval suckers from swim-up to conclusion of the larval stage. Additional samples were collected during the drought of 2001 to evaluate the affect of the drought on larval suckers. These data were supplemented with annual larval sucker monitoring data collected between 1995 and 2001 (Simon and Markle 2001), and used to construct environmental predictors of larval sucker production and survival. The research presented herein attempts to address questions surrounding the movement and rearing of larval suckers in the Upper Klamath Lake system, with an emphasis on describing conditions that promote larval sucker survival.

In chapter 2, 'Rapid outmigration of Lost River and shortnose sucker larvae from in-river spawning beds to in-lake rearing grounds,' I describe how larval suckers use the Williamson River as they move downstream from their natal beds to nursery grounds in UKL. Topics addressed include diel habitat selection and foraging success within the Williamson River, the timing and means of downstream movement to UKL, and differences in size distributions between the river and UKL nursery grounds. I discuss potential impacts of past modifications of the lower Williamson River on the outmigration process and the recruitment bottleneck, and the potential value of proposed remedial actions.

In Chapter 3, 'Abundance, size, and feeding success of larval shortnose suckers and Lost River suckers from different habitats of the littoral zone of Upper Klamath Lake', I focus on habitat utilization patterns in the UKL nursery. Specifically, I evaluate larval sucker diel abundance, size distribution, developmental stage

distribution, and foraging success between different habitat types present in lower Williamson River and UKL nursery grounds. I also evaluate differences between the fish communities in different habitat types. The chapter evaluates the principle influences that dictate habitat utilization patterns and the significance of emergent macrophytes, a subject of management concern (USFWS 2001, Markle and Cooperman 2002, Cooperman and Markle 2003).

In Chapter 4, 'Seasonal and inter-annual effects of weather and habitat on survival of larval shortnose suckers and Lost River suckers in Upper Klamath Lake', I describe the construction and use of a larval production estimate (LPE) generated from seven years (1995-2001) of systematic larval sampling. Results of the LPE were used to evaluate factors associated with the production and survival of 10-14 mm and 15-19 mm suckers. The LPE environmental models were used to estimate larval sucker abundance and survival for 1960-2001 and the results compared to estimated adult sucker recruitment. The patterns are used to discuss the relative contribution of larval and juvenile population dynamics to year class formation in these species.

CHAPTER 2

RAPID OUTMIGRATION OF LOST RIVER AND SHORTNOSE SUCKER LARVAE FROM IN-RIVER SPAWNING BEDS TO IN-LAKE REARING GROUNDS

Michael S. Cooperman and Douglas F. Markle

Abstract

We examined the process of larval outmigration of endangered Lost River and shortnose suckers from spawning grounds in the Williamson and Sprague rivers to rearing grounds in Upper Klamath Lake. Most downstream movement occurred at night when larvae drifted in surface currents at the center of the channel. During daylight, larvae were absent in the drift and abundant near the periphery of the wetted channel in areas that lacked current. Ages, sizes and developmental stages of larvae from spawning grounds and river mouth were similar, indicating larval suckers transit from spawning grounds to lake as quickly as one day and that in-river rearing was rare. The percent of larvae with empty guts declined from upriver towards the mouth, suggesting that first feeding is an important driver of the outmigration process. Sucker larvae greater than 13 mm standard length were rare in the rivers but abundant in the lake, suggesting outmigration to Upper Klamath Lake is advantageous. Warmer temperatures and more food may be important attributes of lake nursery grounds that are not found in the river. Most larvae entered the system on the falling river hydrograph, a strategy that does not promote floodplain access. Also, larvae of related species do not use floodplains. Therefore, suggestions that channelization and dredging of the lower Williamson River and severance of river-floodplain connectivity by levee construction have negatively affected larval suckers by slowing the outmigration process or eliminating preferred habitats were not supported.

Introduction

Adfluvial fish spend the majority of their lives in freshwater lakes, but may enter flowing waters as part of their reproductive cycle. Energetically demanding spawning migrations may have evolved as a mechanism whereby adults ensure eggs are released in locations favorable for successful incubation (Welcomme 1979; Dando 1984), to prevent young being exported out of the geographic range of their population (Sinclair 1988), or to increase the probability that progeny will find favorable rearing conditions, such as those associated with seasonally inundated floodplains (Welcomme 1979; Northcote 1984; Lowe-McConnell 1987). When adfluvial fishes spawn upriver of adult habitats, options for newly emerged progeny are to remain near natal grounds, move to intermediate habitats including floodplains, or immediately drift downstream to a lake. Factors that might influence an adfluvial species' early life behavior include the balance between food availability, competition and predation pressures, and physical and chemical constraints such as current patterns, water temperatures and dissolved oxygen levels. Access to floodplains may benefit young fish in a number of ways, by providing greater food resources, more protection from predators than the river's mainstem, and/or more favorable water temperatures (Welcomme 1979; Lowe-McConnell 1987; Bayley 1991; Bayley and Li 1996).

Lost River suckers *Deltistes luxatus* and shortnose suckers *Chasmistes brevirostris* are endemics of the large shallow lakes of the upper Klamath River watershed, including Upper Klamath Lake, Clear Lake, and Tule Lake. The suckers are long lived, iteroparous, highly fecund, and lithophilous spawners. Both are obligate lake dwellers except during spring when the majority of adults move up inflowing tributaries to spawn, while others spawn in springs along the eastern shore of Upper Klamath Lake. Abundances of Lost River and shortnose suckers are greatly reduced from pre-1900 estimates due to over-harvest of spawning adults, degraded water quality, habitat loss and modification, and, potentially, negative interactions between young suckers and exotic species (USFWS 1993, 2001). Symptoms of the decline include loss of spawning populations, simplification of the age/size structure, periodic large fish kills, and limited recruitment (Markle and Cooperman 2002). Both species were listed as endangered under the federal Endangered Species Act in 1988.

A primary goal of the recovery program (USFWS 1993) is to improve young of year survival and recruitment to adult populations. The potential success of recovery efforts is hampered by lack of detailed information on natural history and ecology of early life stages, as detailed studies on catostomids in general and these species in particular have been limited. All three early life history strategies (upriver residence, rapid outmigration, and floodplain usage) have been observed in young-of-year (YOY) suckers in western North America, including multiple patterns within a species (Hauser 1969; Scoppettone et al. 1983; Radant and Hickman 1985; Modde and Muirhead 1994; Kennedy and Vinyard 1997).

The behavioral and ecological strategy of YOY Lost River and shortnose suckers are unclear and confounded by extensive modifications to their ecosystem. Many of the habitat modifications in the Upper Klamath Lake system have occurred to inflowing tributaries and the effect on YOY Lost River and shortnose suckers is unknown. The lowest segment of the Williamson R, the lake's largest tributary, has been widened and deepened by dredging which converted the channel from U-shaped with bank to bank current and near continuous riparian vegetation to a trapezoidal channel with extensive slackwaters along each bank and limited stream-side vegetation. Channel straightening and levee construction isolated the lower river from its floodplain, and combined with diking and in-filling of meander loops and two of three historic distributary channels, shortened this portion of the river 4.4 km (from 8.4 to 4.0 km) and reduced sinuosity from 1.68 to 1.20 (Gearheart et al. 1997). The Sprague R, the largest tributary of the Williamson, has been dammed upstream of its confluence with the Williamson, about 20 km upstream of Upper Klamath Lake. Although equipped with a rudimentary fish ladder, this run of the river dam is suspected to block many suckers from accessing the upper 70+ km of river channel and forces most Upper Klamath Lake river-spawning suckers to spawn in the 10 km of river immediately below the dam. Anecdotal claims that large numbers of suckers moved far up the Sprague during annual spawning activities exist, but the true extent of pre-dam upstream movement by spawning Lost River and shortnose suckers is unknown.

No information exists on young sucker use of artificial slackwaters of the lower river. It has been suggested slackwaters may interfere with movement of young suckers from spawning beds to rearing grounds and may trap outmigrating suckers causing large losses via starvation and/or predation (KBWUPA 1993; USFWS 1993). Alternatively, channelization and channel shortening may have accelerated the outmigration process by eliminating riverine rearing grounds, prohibiting young suckers from attaining a necessary critical size prior to entry to Upper Klamath Lake (USFWS 1993). Similarly, the effect of severance of river-floodplain connectivity is unknown, as no information exists on whether or not young Lost River or shortnose suckers utilized the Williamson R floodplain in its pre-modification condition, or if suckers would use restored floodplain habitats. Additionally, the impacts of Sprague Dam on larval sucker production, outmigration and survival dynamics is unclear.

In this paper we characterize larval Lost River and shortnose sucker use of lotic environments as they move from spawning beds in the Williamson and Sprague rivers to Upper Klamath Lake, and we discuss the effects of modifications to the river system on the outmigration process. We address three questions: 1) Do outmigrating young of year suckers use the present configuration of the Williamson R for rearing habitat or only as a transit corridor to Upper Klamath Lake; 2) Do lower river slackwaters have a measurable effect on outmigrating suckers; and 3) What is the likelihood and potential importance of outmigrating suckers accessing and using floodplains if river-floodplain connectivity was restored. We discuss our results in the context of the evolution of the sucker's life history patterns and management options for the recovery of these endangered species.

Study site

The Upper Klamath Basin is semi-arid, lying in the rain shadow east of the Cascade Range in south-central Oregon (Figure 1). Dominant land use in the study area is irrigated agriculture and cattle grazing. The Williamson River and its tributary the Sprague River are the largest tributaries to the lake, with catchment areas of 3,679 and 4,093 km^2, respectively. Annual discharge pattern of the Williamson R below the

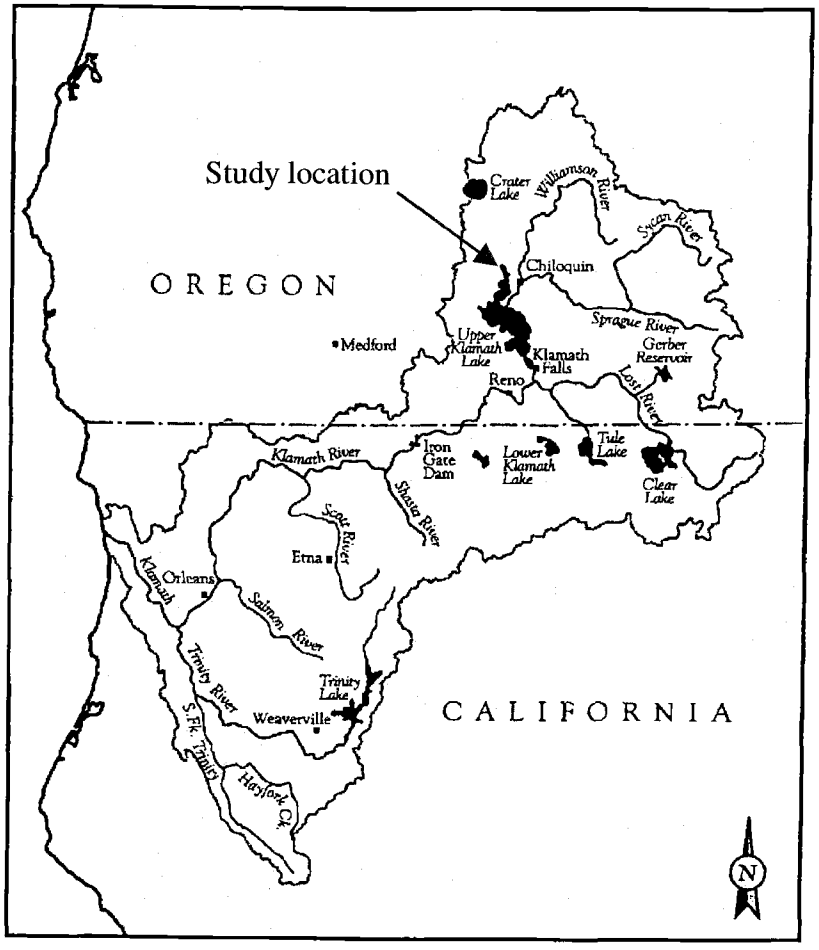


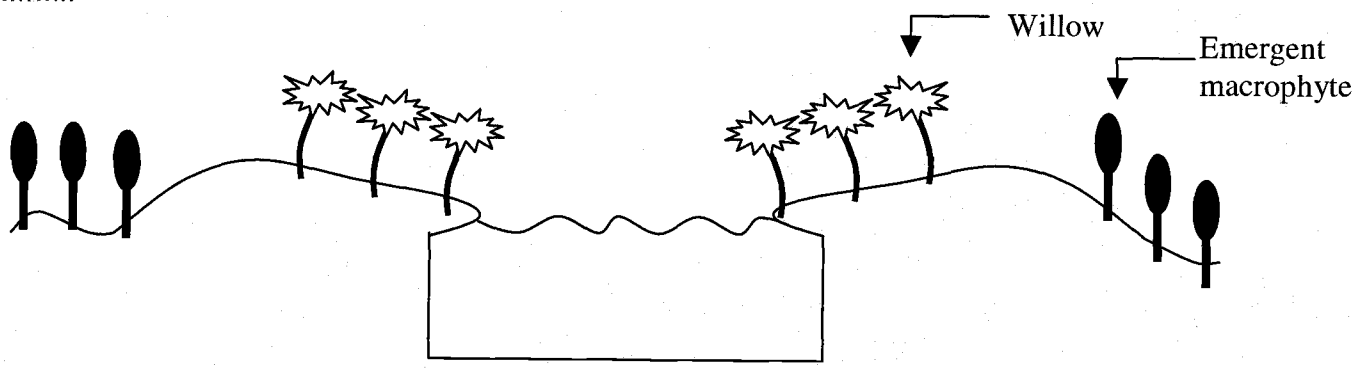
Figure 1. Klamath River watershed, south-central Oregon and Northern California. Map reproduced from National Research Council 2002.

Sprague R confluence includes a predictable increase between March and May of each year corresponding to snow melt run-off. Rain-on-snow events can cause infrequent extreme discharge events between November and March. Mathews and Barnard (1996) calculated the two-year recurrence flow for the Williamson below the Sprague confluence as 82 m^3/s. Based on flow frequency analysis, they conclude bankfull discharge for the premodification lower Williamson R was approximately 80 m^3/s, and that historic records indicate this discharge was exceeded an average of 14 days per year. This is more than would be expected if bankfull discharge was determined solely by the 2 year recurrence flow (Mathews and Barnard 1996). Frequency and/or duration of out-of-channel flows were likely also affected by backwater effects from the lake, although specific data on the magnitude of effect are not available.

Our study focused on portions of the Sprague and Williamson rivers between the Sprague River Dam in Chiloquin, OR and Upper Klamath Lake, a distance of approximately 20 river km. Between U.S. Highway 97 bridge and the Modoc Point Road bridge, approximately 10 km above Upper Klamath Lake, the Williamson R transitions from its upland to its delta configuration. In the study area, the upland river alternates between a basalt channel with moderate amounts of overlying alluvium and a U-shaped channel dominated by fine sediments. Geomorphology of the upland river in the study area is largely unmodified from historic conditions. The deltaic portion of the lower Williamson R grades from sandy loam soils to silt loams and muck. Channel straightening, widening and deepening, and levee construction in the 1920s and 1950s extensively modified this area (Figure 2). In the slackwaters along the bank there are emergent and submergent macrophytes (*Scirpus* sp., *Sparganium* sp., *Polygonum* sp., and *Potamogeton* sp.), and recent efforts have established willow clusters along the inside bank of the river confining levees. Even at lake elevations as low as 1261.7 m (4139.5 ft) above mean sea level (msl) backwater effects extend beyond Modoc Point Rd. bridge and at higher elevations may reach the highway 97 bridge near km 11 (Gearheart et al. 1997). Channel modifications combined with the backwater effect may slow the outflow into Upper Klamath Lake, although detailed studies on river current velocities and sediment dynamics have not been done and the actual effect on flow dynamics are unknown.

Figure 2. Characterization of past and present condition of the lower Williamson River at Site 5 based on descriptions provided by Graham-Mathews and Barnard (1996) and the author's knowledge of the river. Wavy line represents water surface at bankfull discharge. Historically, the river had a U-shaped channel lined by willows and over bank flow occurred an average of 14 days per year. Extensive riverine wetlands dominated by emergent macrophytes existed outside naturally occurring river levees. At present, extensive slackwaters dominated by emergent macrophytes line the periphery of the wetted channel and levees prevent out of channel flow. Some willows occupy higher elevations of the inner bank of the levees. Riverine wetlands have been converted to agricultural lands. The four habitat zones referenced in the text are identified. Figure is not to scale, but representative of the magnitude of change.

Historic condition



Present condition

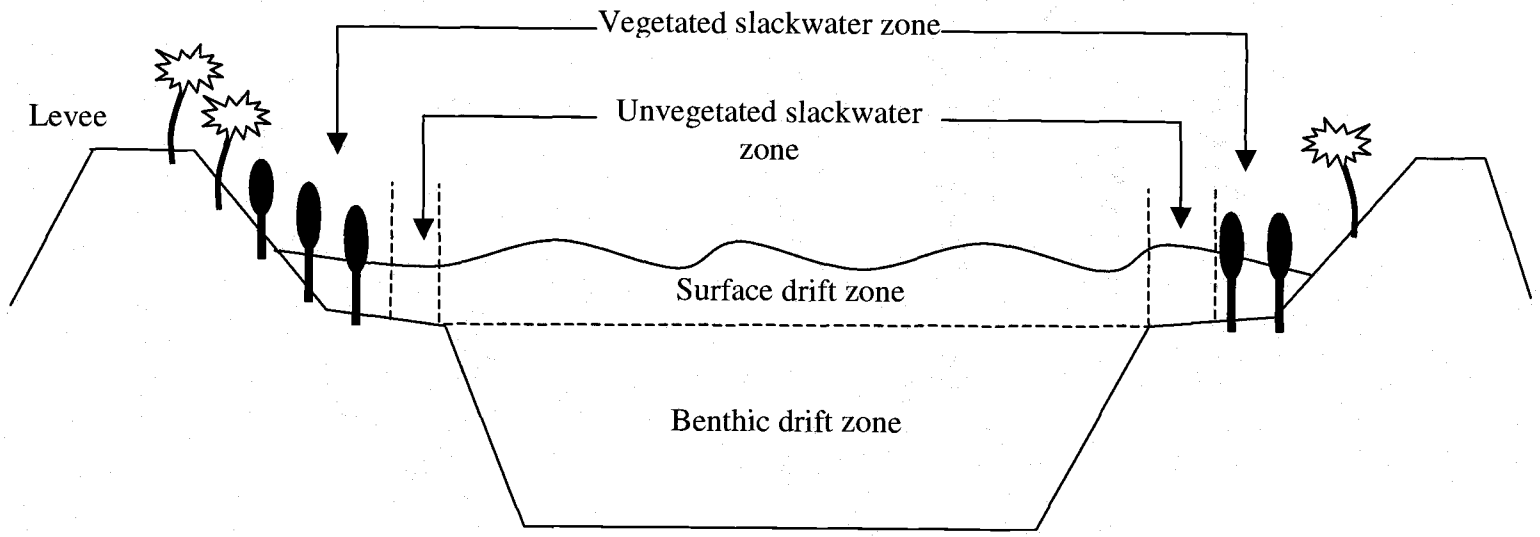


Figure 2.

Materials and Methods

Sample sites

We selected sites to provide spatial coverage from upriver spawning grounds to potential rearing grounds in Upper Klamath Lake and in areas of potential restoration activities (Figure 3).

Five river sites were numbered sequentially from upriver to downriver. Site 1 was in the Sprague R, approximately 2 km below the Sprague dam and 16 km above Upper Klamath Lake. Site 1 was near the upper extent of sucker spawning (excluding spawning that occurred above the dam). The river flows through a constricted channel lined by bedrock. Site 2 was immediately upstream of the highway 97 bridge, approximately 11.5 km above the river mouth and near the lower boundary of sucker spawning. The channel is U-shaped, dominated by fine sediments interspaced with riffles of coarser material. Sporadic willow clusters line the channel and some bank slumping has occurred between willow clusters creating pockets of slackwater. Slackwaters were either unvegetated or contained mixtures of reed canary grass, sedges, *Scirpus* sp., and/or submergent macropytes. Site 3 was just below the Modoc Point Rd. bridge, 7.6 km upstream of Upper Klamath Lake, near the upper extent of channel dredging. Nearshore areas of site 3 were shallow with little or no current due to over-widening of the channel via bank slumping and current eddies created by patches of willows. Reed canary grass, assorted rushes, and filamentous green algae were common in slackwaters. Site 4 was halfway between Site 3 and the mouth of the river and the location of a proposed river-floodplain restoration effort. Site 4 is similar to Site 5, which was immediately upstream of the mouth of the river. Both sites were within the dredge zone (Figure 2). Nearshore areas had a 3-8 m wide band of slackwater typically 20-100 cm deep. The first 2-5 m nearest the banks were densely vegetated by intermixed patches of willows and emergent macrophytes with sporadic patches of shallow sandy unvegetated areas. Offshore portions of the slackzone were unvegetated. By late July each year, submergent macrophytes, mainly *Potamogeton* sp., established along the outer edge of the slackzone. Offshore of the slackzone, the river bottom dropped rapidly into deeper water where the river flows though a trapezoidal channel.

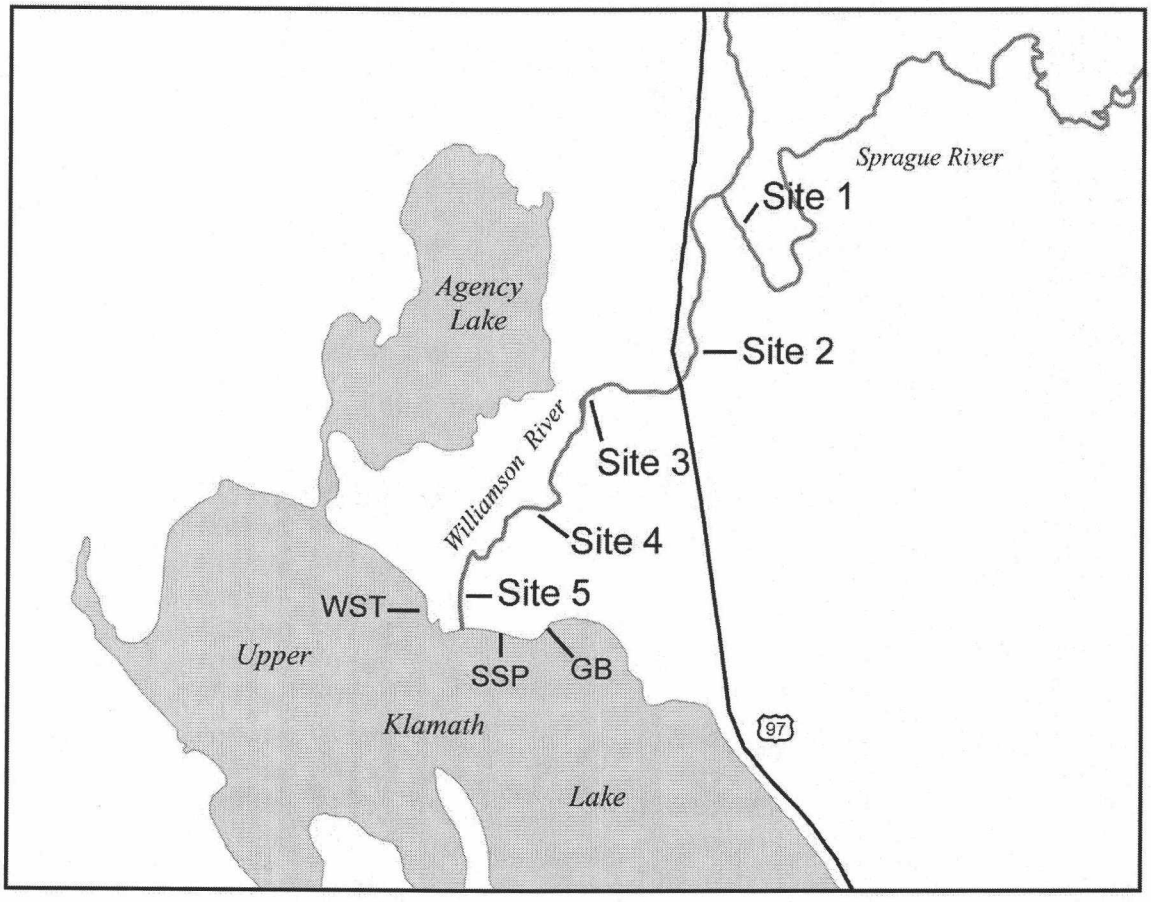


Figure 3. Sample site locations and key features in the Sprague and Williamson Rivers. Site 1 is immediately below Sprague River Dam. Sucker spawning occurs between Sites 1 and 2.

There were three lake sites. West-shore Tulana Farms (WST) had an organic muck bottom and extensive stands of *Sparganium* sp. and *Scirpus* sp. The blue-green alga, *Aphanizomenon flos-aquae*, was abundant by mid-June of each year. South-shore delta preserve (SSP) and Goose Bay (GB) had sandy bottoms and a mixture of willows, emergent macrophytes (e.g. *Scirpus*, *Sparganium*, *Polygonum*) and open water. *Aphanizomenon* was typically present, but not as abundant as at WST. All lake sites had moderate exposure to wave action and samples were not collected when white-capped waves were breaking along the shoreline.

Sampling gears and protocols

From April thru August of 1998-2000, we used popnets (Larson et al. 1986; Dewey et al. 1989) to sample shallow areas of the river and lake that lacked measurable currents ('slackwaters') and drift nets to sample offshore areas of the river and Upper Klamath Lake.

Popnets consisted of two parts; a floating frame constructed from sealed PVC piping with attached net and retention straps (surface area of frame: 1 m^2, net: 100 μm mesh Nitex, dyed grey), and a stainless steel base equipped with attachment points for retention straps and a remote release device. During use, the floating frame was attached to the sinking frame and the unit placed in the desired location, typically water 20–110 cm deep. To compensate for vegetation flattening that occurred when a popnet was set in a vegetated location, bamboo rods, weighted on one end and painted green, were placed into popnets at densities approximating the natural vegetation. Popnets were left undisturbed between 30 and 60 minutes before releasing the floating frame from the base. Samples were collected using a battery operated wash down pump to clean the contents of each net into a cod-end (100 μm mesh) and contents of the cod-end into the sample jar. Pump water was always applied to the outside of the nets.

Each popnet sample at a site was assigned to one of four habitat types based on habitat within a 1 m^2 area of the net. Non-woody samples were dominated by either emergent or submergent macropytes, although submergent macrophytes were rare at our sample sites during the study. Woody samples had willow branches providing most in-water structure. Open water sites lacked vegetation. Combination samples had

a mixture of habitat types, and a composite description (e.g., 'Non-woody + Woody') used. All sample equipment was cleaned with a hose and visually inspected for holes and entangled fishes prior to re-use.

Drift nets were 8 ft long 800 *u*m mesh Nitex with one ft diameter circular mouths mounted in a weighted rectangular frame with a flow meter mounted in the mouth of the net. At Sites 1 and 3, drift nets were deployed from bridges in the thalwag; at all other sites drift nets were mounted on outriggers and towed as pairs, one to each side of a boat. Drift nets were deployed from bridges for 10 minutes and towed drift nets were set between 0.5 and 3 minutes based on anticipated abundance of larval suckers and algae. Drift nets were deployed either as a surface sampler with the upper rim of the net approximately 5 cm below the water surface (surface drift), or as a benthic sampler within 0.5 m of the bottom (benthic drift).

The 1998 field season served as a pilot. In 1998, sampling followed a three-week cycle, with one week of daytime popnetting followed by a week of drift sampling at multiple locations two hours after sunset and a week of hourly drift sampling over a 24 hour period at Site 3. In 1999 and 2000, each site was sampled during daytime about once per week with popnets. Additionally, half of the sites were sampled at night with similar popnetting effort and surface drift sampling. Night sampling began two hours after sunset. Sample effort varied between sites and dates based on habitat availability, equipment failure, and time available for sampling. Typically, six popnet samples were collected at each site for each day or night of sampling (Table 1). Popnet sample effort was distributed among habitat types (non-woody, woody, open water, combination) in proportion to availability. Popnets were selectively located within each habitat type in an attempt to maximize the number of suckers collected.

In each year, sampling began before larval suckers were observed in the river and ended after two weeks of zero catches of larval suckers. Unless otherwise noted, data from each year were analyzed separately. At the present time, we cannot differentiate larvae of the three upper basin sucker species (Lost River, shortnose, and Klamath largescales *Catostomus snyderi,* KLS), but assumed most were Lost River and/or shortnose suckers. Although Lost River sucker larvae are larger than shortnose

Table 1. Date Classes, daytime river popnet sample effort and numbers of suckers caught in day river popnets in 1999 and 2000.

Year	Sample dates	Date Class	Samples – Number of suckers			
			Site 2	Site3	Site 4	Site 5
1999	Apr 28 – May 8	2	6 - 0	3 - 0	3 - 0	10 - 0
	May 11 – May 21	3	9 - 0	7 - 0	6 - 0	9 - 0
	May 25 – Jun 3	4	12 - 0	9 - 0	12 - 6	12 - 16
	Jun 8 – Jun 18	5	11 - 8	12 - 243	12 - 663	12 - 469
	Jun 19 – Jul 1	6	10 - 4	6 - 193	12 - 47	12 - 27
	Jul 6 – Jul 16	7	6 - 0	2 - 0	9 - 1	12 - 17
2000	Apr 19 – Apr 27	1		6 - 0		12 - 1
	May 1 – May 12	2		12 - 0		12 - 1
	May 13 – May 26	3		12 - 39		12 - 112
	May 30 – Jun 9	4		11 - 83		12 - 500
	Jun 13 – Jun 22	5		9 - 477		12 - 49
	Jun 26 – Jul 7	6		8 - 0		12 - 28
	Jul 10 – Jul 20	7		6 - 2		11 - 6

larvae of the same developmental stage (D. Markle, unpublished data), size differences within a developmental stage are small relative to the size range of the entire larval life history period. We assume inter-species size differences are insignificant to the questions addressed and treated all larval suckers as a single population.

We measured water temperature and pH when each sample was collected. Readings were collected 15 cm below the water surface. For drift samples, readings were taken at the location where sample collection began, while popnet readings were taken within the popnet after the floating frame was released from the base but before removing the net from the water. We also noted weather conditions (i.e., wind speed and direction, cloud cover, precipitation, air temperature). Immediately following collection, all samples were preserved in 10% formalin solution and stained with rose bengal. Within 72 hours of collection, samples were sorted and all fishes removed and preserved in 70% ethyl alcohol.

In the months following the end of the field season, all collected fish were placed under a variable power stereo-microscope and assessed for lowest possible taxon, standard length to nearest tenth of a millimeter, developmental stage, and gut fullness. Our developmental stages were a modification of Snyder and Muth (1990). For suckers, the larval stage begins at hatching when larvae are preflexion with a typical standard length 11.0 mm. Transition from larvae to juvenile occurs with absorption of the last remnants of the anal fin fold and presence of full complement of fin rays at a typical standard length of 22.0 mm. Specimens intermediate between two developmental stages were assigned to the more developed stage. Gut fullness was a qualitative categorical variable based on visual inspection of the percentage of gut capacity occupied by material. Categories were empty (no food), low (less than 20% gut capacity occupied), medium (20-50% gut capacity occupied), medium-high (51-75%) or high (>75%). We use YOY to refer to both larvae and juveniles.

Spatial patterns

A sample unit was all suckers collected by a gear type, at a location, during a sample cycle (Date Class). Date Classes were typically 8 - 12 days during which we made a series of collections that comprised two sample events per location (Table 1).

Suckers captured in weekly night drift samples at Site 5 were used to track changes in size of young suckers exiting the Williamson R. During each sample event, a pair of drift samples was collected two hours after sunset. Analysis of variance (ANOVA) was used to determine if standard lengths of outmigrating suckers changed significantly between Date Classes.

Suckers collected in day popnet samples were used to track spatial changes in developmental stages of suckers. In 1998 and 2000, Sites 3 and 5 were sampled once every third week in 1998 and weekly in 2000. In 1999, Sites 2 thru 5 were sampled weekly. Variability in the number of suckers collected per sample was large and therefore limited the utility of traditional statistical analyses (Cliff Pereira, Statistics department, Oregon State University, personal communication). We used 'percentage of preflexion suckers' as our response variable because more developmentally advanced suckers were rare. We limited our assessment to a graphical analysis because the trends were unambiguous and consistent between years.

We restricted analyses of spatial trends in gut-fullness to suckers collected in non-woody daytime popnets in order to eliminate confounding influences of habitat types. Our interest was whether foraging ability or food availability changed with progression downstream, rather than between habitats within a site. Young suckers were most abundant and gut-fullness was typically highest in Williamson R non-woody daytime popnets. We used 'percentage of suckers with empty guts' as our response variable and limited analysis to graphical inspection.

A subset of suckers collected in contemporaneous hourly drift samples at Sites 1 (n = 25) and 5 (n = 25) on 4-5 Jun 1999 were aged using lapilli. Three suckers were taken from each sample collected at 2200, 0000, 0200, 0400 and 4 from the 0100 hour samples. We aged the smallest, largest, and one or two specimens of the median length from each time interval. Ages were determined by counting daily growth increments (Hoff et al. 1997). We used a 1-sided t-test to assess if age at Site 5 > age at Site 1.

Day-night patterns

The daily timing of downstream movements was examined with hourly drift samples collected contemporaneously at Sites 1, 3, and 5 between 2100 and 0500 hours on 4-5 Jun 1999, 28-29 Jun 1999 and 1-2 Jun 2000. The question of interest was

consistency in the pattern of daily movement from spawning grounds to the mouth of the river. Because observed densities of larval suckers ranged over three orders of magnitude between sample dates, traditional analyses via means and standard errors were not appropriate. We standardized results as a percentage of the sum of densities observed at each site over the nine hours of one day's sample event (e.g., the nine hourly densities at each site and date were summed, and each hourly density expressed as a percentage of the sum; we call this value 'relative density'). To provide a measure of variability, we present values from all three sample dates. The data point is the middle value of the three relative densities, low and high whiskers are the low and high values. Trend lines were added to assist in visual comparisons.

We used multi-factor ANOVA to compare catches of YOY suckers in day and night popnet samples at Site 5 to determine if/when suckers utilize the slackwaters of the lower Williamson R and to evaluate how channel modifications may have affected the outmigration process. 'Number of suckers caught' in each popnet sample was the response variable, 'day or night' the main effect. 'Date Class' was incorporated as a covariate to remove the effect of seasonal dynamics of sucker abundance from the analysis. Sampling was done as part of the routine sampling programs of 1999 and 2000. To determine if diel changes in sucker abundance in slackwaters was correlated with changing abundance in the middle of the river channel we sampled the surface drift zone contemporaneous to popnet sampling. Prior work has established that suckers do not drift during day time and are rarely found drifting deeper than 1 m below the surface during the night (L. Dunsmoor, Klamath Tribes, unpublished data; M.S. Cooperman, unpublished data), so only night surface drift samples were collected.

River-lake comparisons

We compared the standard lengths of all suckers collected in day popnets in the Williamson R to those captured in comparable samples from Upper Klamath Lake. Because size distributions were similar in each year, we combined our three years of length data into a single graphical presentation. Because differences were large, we limited analysis to visual inspection.

We used multi-factor ANOVA to examine differences in water temperatures between locations after removing seasonal and diel influences. We used temperature data from all popnets collected in 1999 and 2000. Main effect was 'location' defined as, 'upper river' (Sites 2 and 3; Site 2 sampled 1999 only), 'lower river' (Sites 4 and 5; Site 4 sampled 1999 only) and 'lake' (WST, GB, SSP; SSP sampled in 2000 only). Covariates were 'Date Class' and 'Time Class.' Time Classes were defined as morning (0800 to 1159), afternoon (1200 to 1700) and night (2130 to 0100). Years were analyzed separately. We applied a multiple range test (Fisher's least significant difference procedure) to determine significantly different locations and to measure mean size of observed differences.

Floodplain use

We assessed the potential for larval suckers to access the floodplain of the lower Williamson R prior to channel modifications by relating the timing of larval sucker appearance in the system to river discharge and estimates of historic bankfull river discharge volume (Mathews and Barnard 1996). Larval sucker density in drift samples was monitored between April and July of 1998, 1999, and 2000 at Site 3. In 1998, we sampled two hours after sunset, two nights a week, every third week. Two sequential samples were collected each night and a daily average density calculated. In 1999 and 2000, a single sample was collected at 0400, Monday thru Thursday, every week and a daily density calculated. Williamson R discharge data was obtained from USGS gage #11502500, located in the Williamson R below Sprague R confluence.

Results

During the three years of our study, we collected 347 drift samples and 549 popnet samples from the rivers. River drift samples captured 5,196 suckers; 4,384 (84%) were preflexion and 10 (0.002%) had completed flexion. River popnet samples captured 3,098 suckers; 2,288 (74%) were preflexion and 56 (0.02%) had completed flexion. Of the 66 post-flexion suckers we collected from the rivers, 37 were larvae and 29 were juveniles. Nineteen of the 29 juveniles appear to be Klamath largescale suckers (KLS), a river dwelling species common in the upper basin and difficult to positively separate from Lost River or shortnose suckers at smaller sizes. Four

juveniles are probably either Lost River or shortnose, and five are of uncertain identity.

We also collected 36 drift samples and 579 popnet samples from Upper Klamath Lake. Lake drift samples captured 155 suckers; 65 (42%) were preflexion and 33 (21%) had completed flexion. Lake popnet samples captured 2,451 suckers; 177 (7%) were preflexion and 1,152 (47%) had completed flexion. In other work we have seldom caught juvenile Klamath largescales from Upper Klamath Lake and assumed all lake-captured suckers were either Lost River or shortnose sucker.

Spatial patterns

In 1999, night surface drift samples at Site 5 collected 413 YOY suckers and in 2000 collected 1,658 YOY suckers. The first suckers were collected 24 May 1999 and 4 May 2000 and the last on 28 Jun 1999 and 21 Jun 2000. Mean standard lengths fell into three significantly different groups each year, with smaller lengths occurring earlier each year (Figure 4). However, the range of means was less than 1 mm and represented a small portion of the size range of the larval stage.

In 1999 and 2000, the proportion of preflexion larvae collected in daytime river popnet samples tended to be high (>50%) through mid June (Date Class 1-5; Figure 5). After mid-June at Site 3, the proportion of preflexion larvae remained high (ca. 75%) but near the river mouth (Site 5) an increasing proportion of larvae had initiated flexion.

The proportion of suckers with empty guts tended to be lower near the river mouth (Site 5) than further upstream (Figure 6). Over the entire sampling period, the percent of suckers with empty guts at Site 5 was 30% and 39% in 1999 and 2000, respectively, but 65% and 100% at sites 2 thru 4 combined.

A one-sided t-test of the otolith ages of suckers collected at Sites 1 (n = 24) and 5 (n = 23) on the evening of 4-5 Jun 1999 found no significant difference in ages ($p = 0.110$, power to determine an effect size of 1 day = 0.770, 2 days = 0.997; Figure 7). Mean age (95% CI) at Site 1 was 12.50 (+/- 0.44) and at Site 5 13.48 (+/- 1.23).

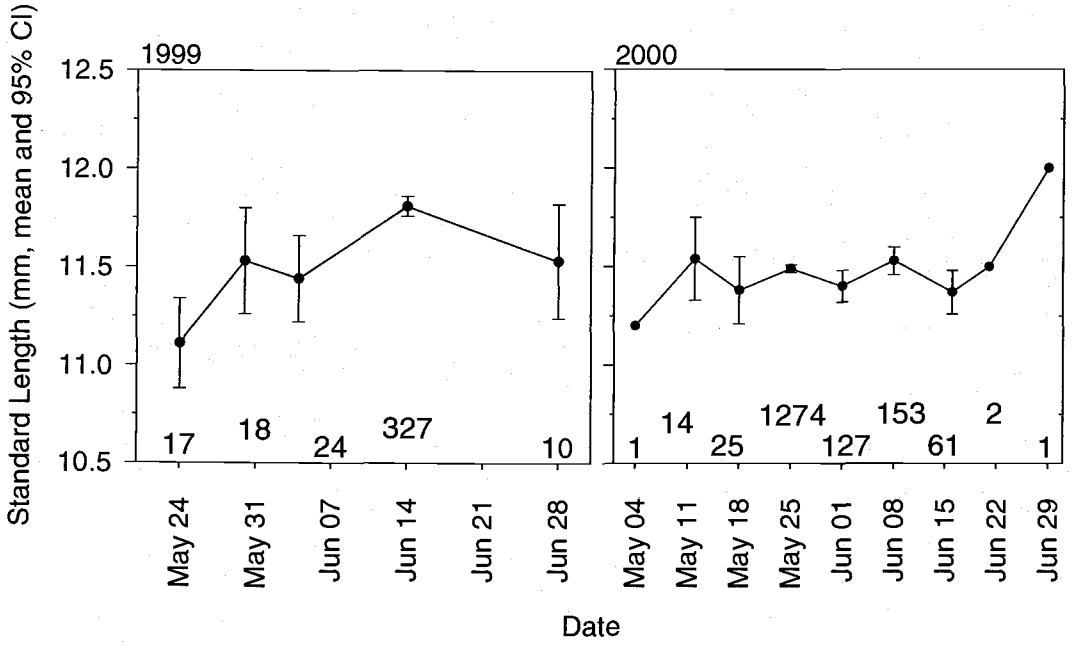


Figure 4. Mean and with-in sample 95% confidence intervals calculated from sample variance for standard lengths of suckers captured in drift samples at Site 5 in 1999 and 2000. Numbers above the x-axes are the number of larvae usedin calculating daily values. Range of weekly means was 11.11 – 11.81 (1999) and 11.20 – 12.0 (2000). On 3 dates in 2000, insufficient numbers of suckers were collected for confidence interval calculation. No sample was collected 21 Jun 99 due to equipment failure.

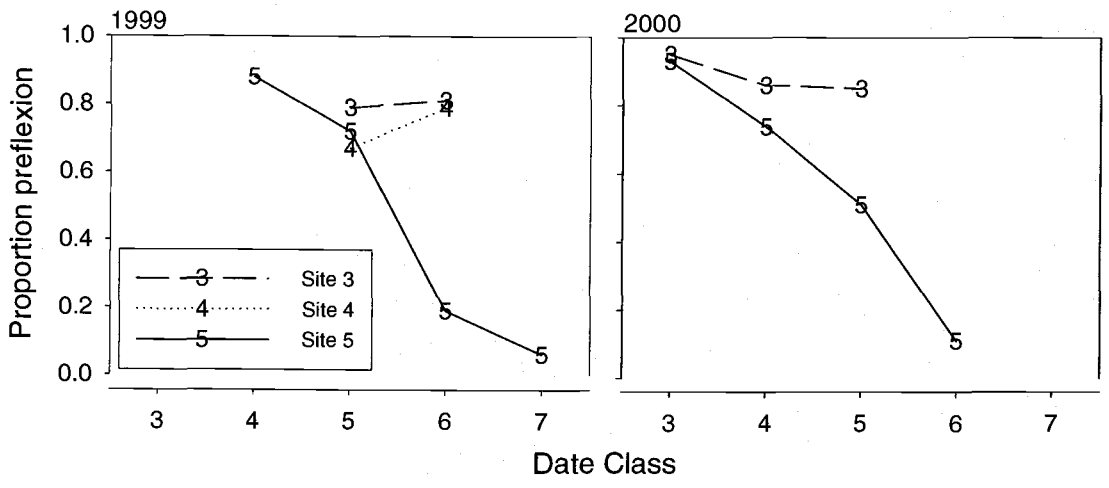


Figure 5. Proportion of suckers collected in day popnet samples that were preflexion. Only data points calculated from >10 suckers are shown.

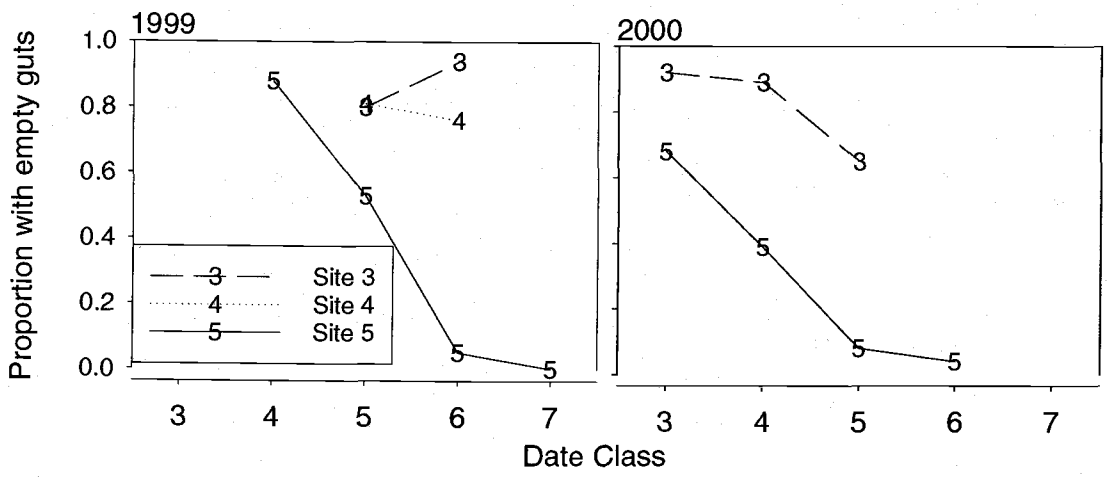


Figure 6. Proportion of suckers with empty guts collected in non-woody day popnet samples, organized by date class and sample site. Only data points calculated from >10 suckers are shown.

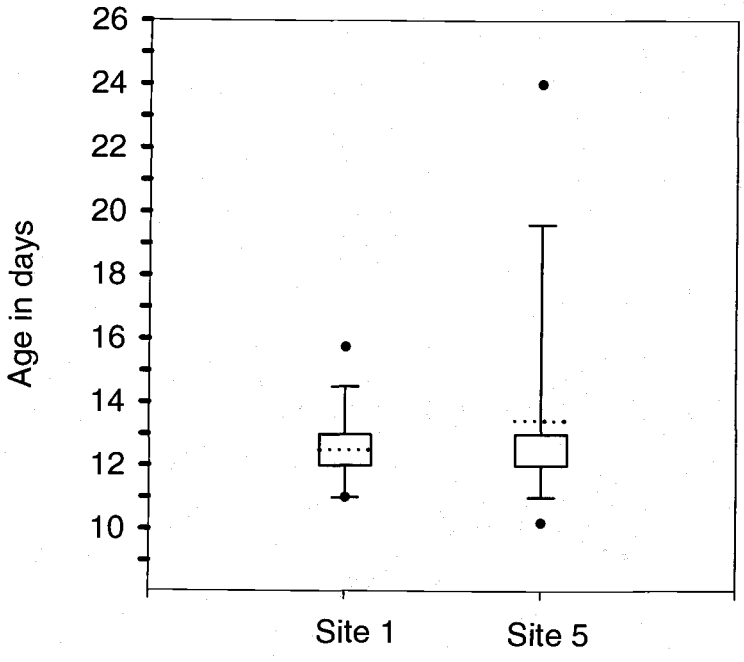


Figure 7. Age of larval suckers collected 4-5 Jun 1999 in contemporaneous drift samples at Sites 1 (n = 24) and 5 (n = 23). Bottom and top of boxes are 25th and 75th percentiles, whiskers are 10th and 90th percentiles, points are 5th and 95th percentiles, and dotted horizontal lines are mean age.

The ages of three individuals collected at Site 5 were statistical outliers (19, 20, and 25 days post-hatch). These individuals were indistinguishable from other specimens in terms of developmental stage and standard length. Exclusion of the three outliers yielded Site 5 mean age (95% CI) of 12.25 (0.54) (t-test for difference in ages, $p = 0.760$).

Day-night patterns

On two of the three sample dates, larval suckers were present in the drift when sampling of Site 1 began at 2100 hours (Figure 8). More than half of the larvae moving past Site 1 did so between 2100 and 0000 hours. After midnight, drift density at Site 1 fell to low levels for the remainder of the evenings.

No suckers were collected in the 2100 drift samples at Site 3. The first suckers were collected at 2200. Relative densities remained near 5% between 2200 and midnight. From 0100 till 0500, relative densities were consistently near 20%.

Relative density of sucker drift at Site 5 had a uni-modal distribution. No larvae were collected in the 2100 sample. Between 2200 and midnight, relative densities were near 8%. The largest relative density values were observed at 0100, followed by 0200. After 0200, relative densities dropped consistently, eventually falling to less than 10% by 0500.

Daytime popnetting in the slackwater areas of Site 5 captured numerous suckers in both 1999 and 2000 (1999: 67 popnets, 529 suckers collected; 2000: 83 popnets, 697 suckers collected). Conversely, nighttime popnetting in the same locations captured very few suckers (1999: 28 popnets, 2 suckers; 2000: 46 popnets, 3 suckers). Differences in diel utilization of lower river slackwaters were significantly different ($p = 0.016$ and 0.035, 1999 and 2000 respectively; Table 2). Drift sampling at the surface of the middle of the channel at Site 5 showed the inverse pattern. Day samples caught very few suckers (1999: 7 samples, 17 suckers; 2000: 3 samples, 0 suckers) and night samples caught large numbers (1999: 26 samples, 558 suckers; 2000: 23 samples, 1967 suckers).

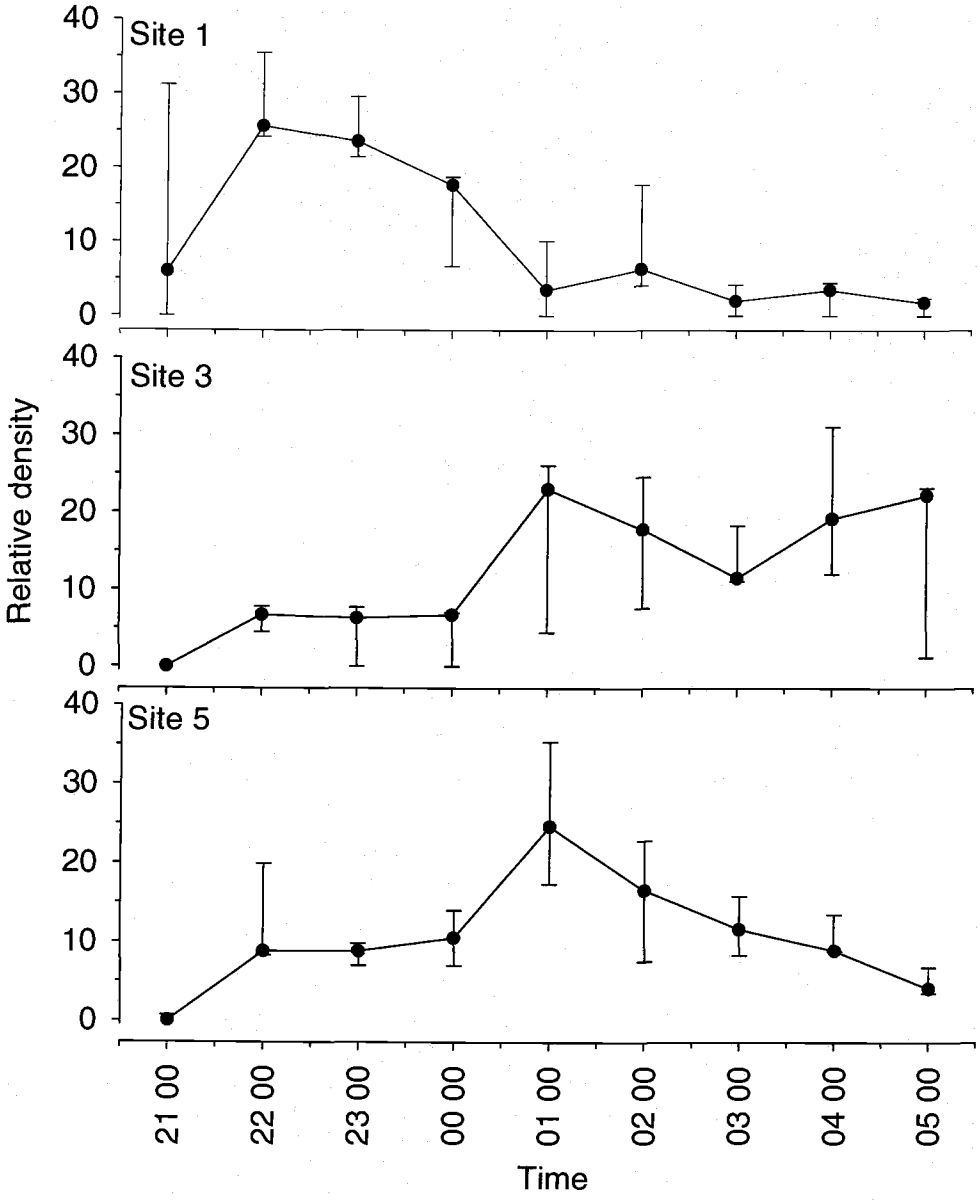


Figure 8. Relative density of larval suckers in hourly surface drift samples from upstream (site 1) to river mouth (site 5) observed during sampling on 4-5 Jun 1999, 28-29 Jun 1999, and 1-2 Jun 2000. Data points are the medium value observed, high and low whiskers are the high and low values. Trend line is added to assist visual comparisons. See text for definition of relative density.

Table 2. Multifactor ANOVA of number of suckers caught during diel popnetting of the slackwaters of the lower Williamson River in 1999 and 2000.

1999.

	df	F-ratio	p value	Mean difference
Covariate				
Date Class	1	0.62	0.4340	
Main effect				
Day or night	1	5.94	0.0164	8.02

2000.

	df	F-ratio	p value	Mean difference
Covariate				
Date Class	1	0.00	0.9471	
Main effect				
Day or night	1	4.53	0.0352	8.36

River-lake comparisons

Between 1998 and 2000, we collected 3,062 YOY suckers in 414 daytime popnets in the Williamson R and 2,343 YOY suckers in 461 daytime popnets in Upper Klamath Lake. Only 1.5% of river captured suckers were larger than 13.99 mm standard length (SL) while 46.5% of suckers collected in the lake were larger than 13.99 mm SL (Figure 9).

In 1999 and 2000, water temperatures at upper river, lower river, and lake sites were significantly different (1999: Mean temperatures (^{o}C)(1 standard error), UKL = 19.4 (0.18), lower river = 18.6(0.17), upper river = 18.2(0.20). Year = 2000: UKL = 18.5(0.12), lower river = 17.9(0.20), upper river = 17.9(0.29). Year = 1999 MF ANOVA 'location,' F ratio 41.8, p = 0.0001; Year = 2000: F ratio 37.2, p = 0.0158). Covariates 'Date Class' and 'Time Class' were also statistically significant ('Date Class' 1999: F ratio 625.4, p = 0.000; 2000: F ratio 825.3, p = 0.0000. 'Time Class'1999: F ratio 26.4, p = 0.0170; 2000: F ratio 18.64, p = 0.0000). Multiple range tests between locations indicate lake water temperatures were significantly warmer than either the upper or lower river segments, after accounting for effects of date and time (Table 3).

Floodplain utilization

In all three years of the study, YOY suckers first appeared in the river system on the falling limb of the annual hydrograph, as measured by weekly drift samples at Site 3 (Figure 10). In 1998 and 1999, larvae first appeared when river discharge exceeded estimates of bankfull discharge, however, the majority (72% in 1998, 98% in 1999) of suckers moved through the system when discharge was less than bankfull. In 2000, all suckers moved through the river system after discharge fell below bankfull volume.

Discussion

Young-of-year Lost River and shortnose suckers move from natal gravels in the Williamson and Sprague rivers to rearing grounds in Upper Klamath Lake rapidly. The mean standard length of preflexion suckers captured at Sites 1 and 2, a measure of size at swim-up from natal gravels, was 11.42 (0.48 st. dev., n=1,058) and the mean

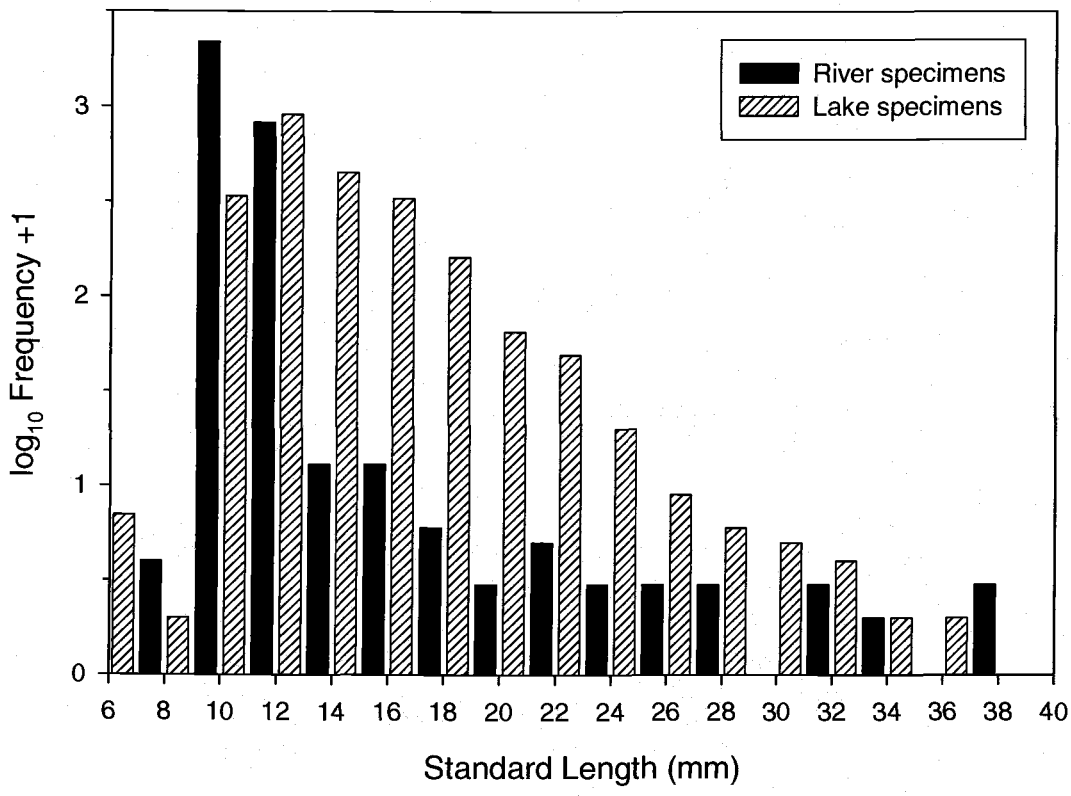


Figure 9. Log frequency size distribution of suckers collected in daytime popnets from the Williamson River (N=3,062) and Upper Klamath Lake (N=2,343), 1998-2000.

Table 3. Multiple range tests for different groups of water temperature by location.

1999.

Location pairs	Difference	+/- Limits	Homogeneous groups
Upper river - Lower river	- 0.385	0.300	Upper X
Lake - Upper river	1.148	0.563	Lower X
Lake - Lower river	0.762	0.379	Lake X

2000.

Location pairs	Difference	+/- Limits	Homogeneous groups
Upper river - Lower River	0.018	0.279	Lower river X
Lake - Upper River	0.587	0.494	Upper river X
Lake - Lower river	0.605	0.303	Lake X

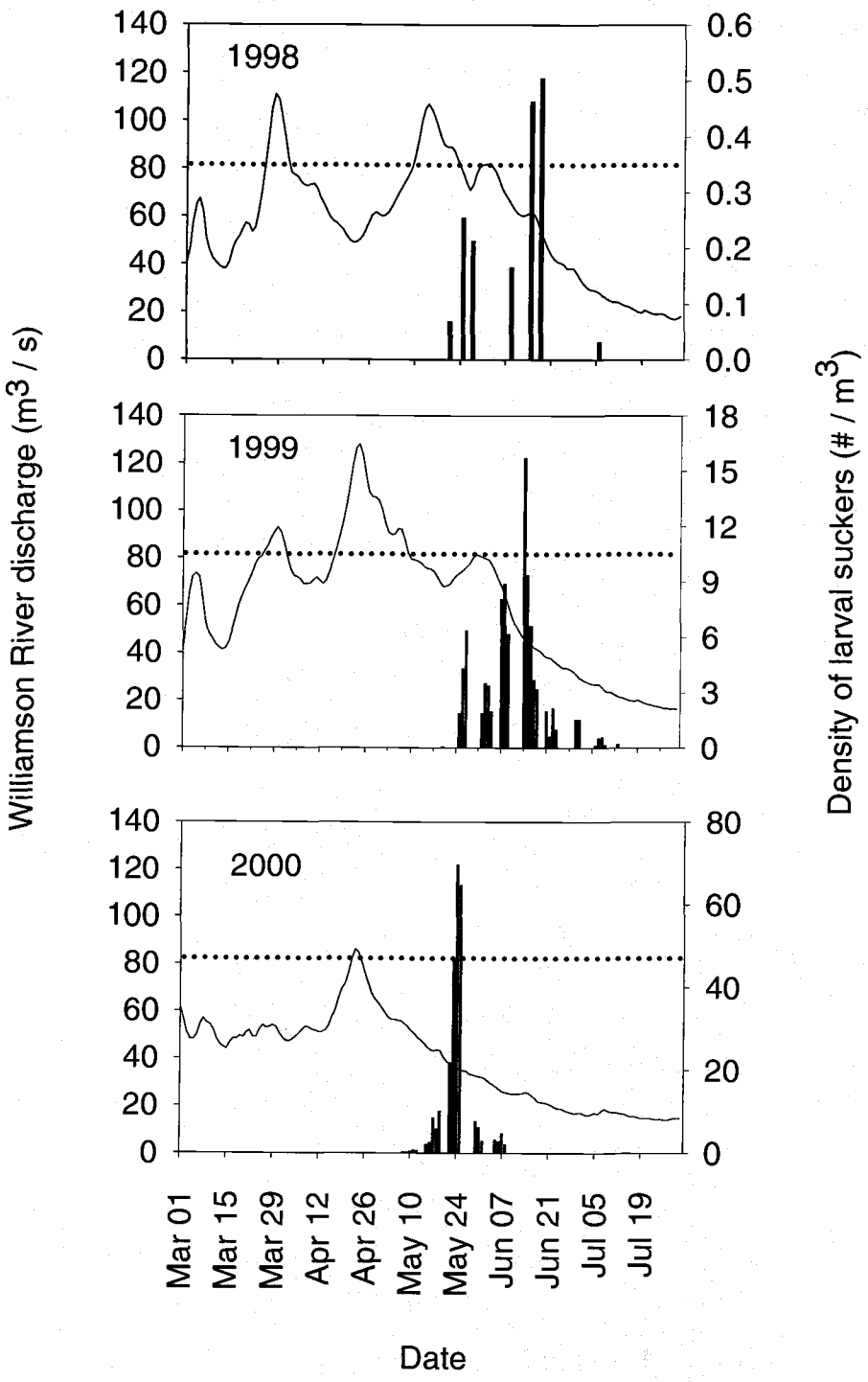


Figure 10. Relationship between Williamson River discharge (solid line) and density of larval suckers (bars) in surface drift samples collected between 2200 and 0000 hours at Site 3, 1998-2000. Dotted line represents calculated bankfull discharge volume (80 m^3 s^1). Sucker density data for 1999 and 2000 provided by Rip Shively, USGS, Klamath Falls office.

standard length of larvae entering Upper Klamath Lake from the Williamson R in our weekly samples was consistently between 11.0 and 12.0 mm (Figure 4). Ninety-three percent of suckers captured in the rivers were either preflexion or in the earliest stage of the flexion process while only 0.008% had completed flexion, with about two-thirds of these likely to be Klamath largescale suckers based on vertebral counts and morphological characteristics (D. Markle, personal communication). Age data demonstrate young suckers can travel from spawning beds in the Sprague R to Upper Klamath Lake in a single day, and on 4-5 Jun 1999, one day was the mean travel time (Figure 7). Lake elevation on 4-5 Jun 1999 was 1262.7 m (4142.96 ft) msl, indicating that even near the full pool volume of 1262.8 m (4143.3 ft) backwater effects related to intrusion of lake water into the lower Williamson R did not slow the outmigration of larval suckers.

Lost River and shortnose suckers have evolved behaviors that promote a rapid outmigration. We observed high densities of larvae shortly after sunset at Site 1, while densities remained low at downriver locations until later in the evening (Figure 8). As the night progressed, peak larval densities progressively moved downriver, reaching the mouth of the river four or five hours later. This pattern suggests larval suckers outmigrate as a nightly pulse, where large numbers of larvae enter the river's current at a synchronized time from a localized source such as up-river spawning beds, followed by downstream movement as a more-or-less cohesive unit. At least a part of each nightly pulse reached Upper Klamath Lake by morning. In a laboratory study, night and flowing water stimulated downstream movement in young Colorado pikeminnow *Ptychocheilus lucius* and razorback suckers (Tyus et al. 2000), and similar patterns of synchronized nocturnal drift have been described for other species of riverine fishes and invertebrates, with predator avoidance as a commonly suggested selection pressure (Waters 1972; Pavlov 1994). Dunsmoor (Klamath Tribes, unpublished data), Buettner and Scoppetonne (1990) and Cooperman (unpublished data) have observed that larval suckers do not drift at the surface of the channel during daytime and drifting in the benthic drift zone (Figure 2) is rare during both day and night (M.S. Cooperman, unpublished data). Presumably, larvae still in the river at the

end of each evening move to the edge of the river to hold in patches of near-shore vegetation (M.S. Cooperman, unpublished data). Larvae holding over in the lower Williamson R could explain the presence of larvae early each evening (e.g., 2200) at Sites 3 and 5 if hold-over larvae re-enter the current during a second evening of downstream drift (Figure 8).

Our diel drift and popnet sampling in the lower Williamson R supports the conclusion larval suckers control their entry and exit from slackwaters of the lower river (Table 2). During the day, larvae held near the bank where no current existed, while at night, they abandoned nearshore areas and entered the surface drift in the channel. Larvae apparently are not purely passive particles and have synchronized drift behaviors that control their movements between nearshore and mid-channel. The mechanism(s) involved in their entry and exit from the icthyoplankton drift could be loss of orientation related to lower light intensities and subsequent unintentional entrainment in the current, drift as a response to insufficient food availability, and drift as an evolved downstream dispersal behavior (Tyus et al. 2000).

We found no evidence that significant growth, advancement in developmental stage, or aging occurs within the rivers, or that food resources were abundant in the river. We also found no evidence to support the idea that 'normal' YOY shortnose or Lost River suckers maintain themselves upriver. While some larvae were collected in upriver popnet samples, indicating at least some suitable habitats for larval suckers exists upriver, significant numbers of larvae did not accumulate in these habitats. Curiously, in both 1999 and 2000 larval suckers were first captured in popnets downriver (Sites 4 and 5) a week earlier than they were captured upriver (Sites 2 or 3), suggesting that rapid outmigration rather than upriver accumulation is normal.

Although modifications of the lower Williamson R may have had other effects, they do not appear to have delayed larval entry to nursery areas in Upper Klamath Lake. Large numbers of larval suckers reached Upper Klamath Lake within one or two days of emergence from natal gravels (Figure 7). Based on a series of laboratory experiments, Dunsmoor (Fisheries biologist, Klamath Tribe, unpublished data) has suggested the critical period for first feeding of larval suckers prior to irreversible starvation is 3 to 5 days post swim-up (e.g., emergence from natal gravels). The

dynamics of first feeding appear to be critical to these larvae. One aspect of first feeding is quickly getting to a habitat where feeding is successful. Suckers collected at the river mouth (Site 5) were more likely to have material in their guts than at any other river site (Figure 6). Because ages (Figure 7) and sizes (Figure 4) were similar, it is unlikely that larvae at Site 5 had greater foraging ability. Site 5 is more strongly influenced by intrusion of lake water and preliminary analyses (M.S. Cooperman, unpublished data) show lake larvae are significantly better fed than river larvae of the same developmental stage collected on the same date.

The dichotomy in standard lengths (Figure 9) and gut fullness of young suckers collected from the Williamson R and Upper Klamath Lake suggests rapid entry to the lake may be beneficial. Differences in water temperature and food availability are two potential benefits of rapid entry to Upper Klamath Lake. Water temperatures, measured at locations where larvae accumulated, were significantly warmer in the lake than in the river (Table 3). At temperatures below lethal levels (30°C; Saiki et al. (1999); YOY Lost River and shortnose suckers grow faster with warmer temperatures (Terwilliger et al., in review). Larger size is associated with a host of fitness advantages including enhanced predator avoidance (Houde 1987; Post and Prankevicius 1987; Cargnelli and Gross 1996), improved foraging ability and starvation resistance (Miller et al. 1988; Bestgen 1996), and better over-winter survival (Sogard 1997; Schindler 1999).

Assessing the potential importance of floodplain habitats for larval suckers in this system is difficult because no such habitat presently exists and it is impossible to conclusively determine if present day behaviors are comparable to historic ones or are new behaviors in response to altered system conditions. However, available information suggests historic floodplain use by outmigrating Lost River and shortnose sucker larvae was not a common strategy. Adult Lost River and shortnose suckers spawn in the Williamson and Sprague rivers during or after peaks in discharge (Perkins et al. 2000; Cunningham and Shively 2001). Most fish species that rely on floodplains as rearing grounds for their young typically spawn on the rising limb of the hydrograph, ensuring larvae will be in the river system at the peak of discharge and therefore have the greatest possibility of accessing the floodplain (Welcomme

1979; Lowe-McConnell 1987; Petry 2000). Adult spawning is likely cued by changing water temperatures, photo-period, and discharge, and is unlikely to have been affected by modifications to the lower Williamson R. Additionally, adults of both species spawn in Upper Klamath Lake at lakeshore springs. It is unlikely that this reproductive strategy would persist if floodplains were a critical habitat for young.

The timing of adult spawning directly affects the timing of larval sucker entry to the system. During the three years of our study, the outmigration of larval suckers occurred almost entirely on the falling limb of the annual hydrographs and at discharges less then the bankfull volume of the premodification channel (Figure 10). Based on river discharge, the maximum amount of time a larva would have been able to reside on the floodplain was three weeks (for larvae in the river on 19 May 1998), although backwater effects associated with high lake elevations may have expanded the time of river-floodplain connectivity. Risley and Lanean (1999) found that water yield from the Williamson-Sprague watershed, adjusted for precipitation inputs, has increased between 1950-1996 relative to the water yields between 1920-1949. Risley and Lanean's findings suggest our interpretation of the potential for past floodplain use is conservative and support our conclusion that floodplain use was not a typical tactic for outmigrating young suckers. These data do not reflect the potential contribution of backwater effects, which could have expanded the duration of river-floodplain connectivity. Also, a multi-incised braided delta unconfined by artificial levees, as existed prior to channel modifications of the 1950's, might have provided important river-mouth delta habitat such as inundated floodplains, natural berms and islands.

Research on the balance between river residency, floodplain use, and rapid outmigration to lakes in related species is consistent with our findings. June suckers *Chasmistes liorus*, spawn in the Provo River of Utah from late May through late June (Radant and Hickman 1985; Modde and Muirhead 1994). Modde and Muirhead (1994) found June sucker larvae emigrate immediately to downstream lakes. Cui-ui suckers *Chasmistes cujus* spawn in the lower Truckee River of Nevada, and outmigrating larvae move directly to Pyramid Lake without prolonged residence in the Truckee R (Scoppettone et al. 1986, 1993). There are no reported cases of larval

Chasmistes rearing on floodplains. East of the Klamath Basin, Warner suckers *Catostomus warnerensis* inhabit streams and small shallow lakes in the Warner Valley. Unlike Chasmistes, Warner sucker larvae actively work against downstream displacement by holding in slack water areas of the river and avoiding the strong currents in the middle of the river channel (Kennedy and Vinyard 1997). Kennedy and Vineyard (1997) suggest Warner suckers have evolved to resist downstream displacement due to the ephemeral nature of lakes in the arid Warner Valley. In contrast, Upper Klamath Lake has been present since at least the Pleistocene and there is no record of the lake drying up.

If more spawning occurred upstream of the Sprague R Dam, we might expect more river residency and more larval use of the lower Williamson R, as it would take longer for the young to move to the lake. However, some sucker spawning does occur upstream of the Sprague R Dam, but we collected very few larger outmigrants. It is possible: (*a*) larvae moved downstream rapidly and reached the lower river without significant growth and therefore appeared no different than larvae hatched below the dam; (*b*) larvae hatched above the dam did not reach the lower river until after our sampling efforts were finished; and/or (*c*) larvae hatched above the dam did not survive the journey to the lower river. We can not evaluate the first possibility with our data. The second possibility is difficult to test but considered unlikely since there is little evidence of juveniles of either species in the Sprague R. The third possibility would mean the three years of our study had inappropriate conditions for successful reproduction by long upriver-migrating suckers.

If, as we suggest, quick entry to Upper Klamath Lake is important and in-river rearing is not, it seems inconsistent for adult suckers to make energetically demanding spawning runs of 30 km or more, when spawning can successfully occur within 15 km of the lake or within the lake. However, in-lake, short river migration and long river migration might have been evolutionary stable, or 'risk sharing' strategies. Each reproductive tactic would experience variable levels of annual reproductive success depending on the vagarities of weather and other factors. With a long lived and iteroparous life history, multiple strategies might have stabilized long-term trends. At present, we have no means of determining whether survivors of each year class

followed in-lake, short river migration, or long river migration life strategies. It is possible that a few "river holding" larvae could be important to the success of some year classes. The absence of larger outmigrating YOY suckers suggests either conditions between 1998 and 2000 were not appropriate for survival of up-river spawned progeny and/or that very few long-migration suckers passed the Sprague R Dam and successfully spawned. Research addressing whether there is 'river residency' larval behavior associated with long-migration tactics in these species would help to better understand the relative importance of upper Sprague R spawning.

In total, our results strongly indicate shortnose and Lost River suckers have evolved behaviors to promote a rapid outmigration from up-river spawning beds to in-lake rearing grounds and that river channel modifications have not had a measurable negative effect on the outmigration process. Our results also indicate levee construction, which isolated the lower Williamson R from its floodplain, may not have eliminated access to a preferred larval habitat. As such, channel modifications are not likely to have been a primary contributor to the recruitment problem in these species by their affect on larval habitat use. The isolation of the floodplain or river channel may however have had other effects on water quality or produced other stressors beyond the scope of this study, modifications that have negatively impacted YOY suckers (e.g., increased nutrient supply and resulting poor water quality; Bortleson and Fretwell 1993; Kann and Walker 1999).

Other anthropogenic factors, both related and unrelated to tributary modifications, have been cited as contributing to the species' endangerment. Restoration of the Williamson River's channel and the river-lake delta ecosystem will address some of these factors, including moderating water temperatures, filtering sediments and nutrients from over-bank flow, and halting the decomposition of peat soils that comprise the floodplain wetlands that have been converted to agriculture. Restoration of floodplains and riverine wetlands may create patches of warmer, highly productive habitats that could promote rearing and growth prior to entry to Upper Klamath Lake, and thereby improve YOY suckers ability to avoid predators and survivor episodes of stressful water quality. Restoration is also unlikely to have a negative impact on larval outmigration, especially if delta habitats become more lake-

like. Finally, these results suggest the root cause of year class failure is likely to lie within Upper Klamath Lake.

Acknowledgments

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CHAPTER 3

ABUNDANCE, SIZE, AND FEEDING SUCCESS OF LARVAL SHORTNOSE SUCKERS AND LOST RIVER SUCKERS FROM DIFFERENT HABITATS OF THE LITTORAL ZONE OF UPPER KLAMATH LAKE

Michael S. Cooperman and Douglas F. Markle

Abstract

Shortnose suckers and Lost River suckers are endangered species endemic to the shallow lakes of the upper Klamath River watershed. We examined habitat use by larval suckers in the near-shore portions of the lower Williamson River and Upper Klamath Lake during spring and summer, 1998-2000. Emergent macrophytes, including *Scirpus* sp., *Sparganium* sp., and *Polygonum* sp. supported significantly higher abundances, larger mean sizes, and better-fed larvae than submergent macrophytes, woody vegetation, or open water habitat types. There were no significant differences in abundance, size or gut fullness of sucker larvae collected from different emergent macrophytes. We found no evidence of density dependant effects or changes in habitat types during the larval stage. Ranked catch per unit effort data indicated predators were also more likely to be in emergent macrophytes, but ordination indicated larval fishes and potential predators were differentially distributed along a vegetation structure - water depth gradient with larvae in shallow vegetated areas. Between-habitat differences in larval suckers appear to be due to selection for, or better survival in, emergent macrophytes, not differential access or exclusion from other habitat types. The mechanism mostly likely to account for the importance of emergent macrophytes is increased foraging success. The resultant size and gut fullness advantages for larvae in emergent macrophytes could have a positive effect on sucker year class success. Whether or not the advantages transfer to recruitment to the adult population 3-7 years later is unknown. Our results suggest larval sucker access to emergent macrophytes may be necessary, but perhaps not sufficient, for promoting year class formation.

Introduction

Habitat selection by young-of-year (YOY) fishes during their first growing season is typically described as a balancing act between maximizing growth rate and minimizing predation risk (Werner and Gilliam 1984; Werner 2002). In many ecosystems, submerged and emergent macrophytes, floating algae, and other aquatic vegetation provide YOY fish with elevated concentrations of prey items and increased protection from predators (Crowder and Cooper 1979; Heck and Crowder 1991; Dibble et al. 1996; Weaver et al. 1996). Not surprisingly, many YOY fishes preferentially utilize vegetated habitats relative to other available habitats (Heck and Crowder 1991; Dibble et al. 1996). Several other factors may also influence YOY fish distribution, growth, and survival. These include physical processes that prevent individuals from accessing or using potential habitats (Sinclair 1988; Sogard 1994), physiological constraints related to differences between habitat types (such as temperature, dissolved oxygen, and pH)(Kerr 1980; Jackson et al. 2001), and biotic interactions such as competitive exclusion (Sogard 1994; Bystrom et al. 1998; Jackson et al. 2001).

Regardless of the mechanisms responsible for YOY fish habitat utilization patterns, survival of young fish is typically greatest for those with the highest growth rates, as these individuals pass through the most starvation-prone and predation-vulnerable life stages more quickly than slower growing con-specifics (Houde 1987; Schindler 1999; Houde 2002). Rapid early life growth is also important because YOY of most species need to attain a critical size by the end of the first growing season or face an increased probability of over-winter mortality (Quinn and Peterson 1996; Schindler 1999).

Despite strong causal connections between YOY habitat use, growth, and survival, and between YOY survival and adult population dynamics, detailed studies of YOY fish habitat utilization patterns and the potential fitness consequence at the scale of the immediate habitat surrounding the individual fish (the contingent habitat, *sensu* Werner 2002) are uncommon (Dibble et al. 1996).

Shortnose suckers and Lost River suckers are long-lived, highly fecund endemics (Perkins et al. 2000) of the large shallow lakes of the upper portions of the

Klamath River watershed (Figure 1). Both species were listed as endangered under the Federal Endangered Species Act in 1988, and the largest remaining populations of both species are in Upper Klamath Lake (UKL). UKL's suckers spawn in the spring, and the majority run up the Williamson River. Preflexion protolarvae (10-12 mm standard length; SL) (Snyder 1983) make a rapid outmigration from the Williamson River and enter UKL (Cooperman and Markle 2003). The larval stage ends approximately 45-60 days post-hatch, at about 22 mm SL, commensurate with absorption of the anal fin-fold and development of the full complement of fin rays (Cooperman, unpublished data). There is limited information on ontogenetic habitat change in larval suckers, mechanisms responsible for larval sucker habitat selection, or how fluctuations in lake surface elevation may affect habitat dynamics.

In this paper, we describe larval shortnose and Lost River sucker habitat utilization patterns within the littoral areas of the lower Williamson River and UKL. Specifically, we address the questions: 1) Are there differences in abundance, size, and/or gut fullness of larval suckers between different habitat types; 2) Do larval suckers display any evidence of niche shifting during ontogeny; 3) What abiotic factors affect larval sucker distributions; and 4) What other species of fishes make up the larval sucker fish assemblage. We discuss our results in context of potential mechanisms structuring observed patterns and comment on management implications for these endangered species.

Study Location

Our study occurred in the northeastern portion of UKL in the Williamson River Delta ecosystem, which includes the near-shore portions of UKL between Agency Straits and Goose Bay and the lower four km of the Williamson River (Figure 2). The delta ecosystem is the primary early nursery area for larval shortnose and Lost River suckers spawned in the Williamson River and the site of a large restoration effort by The Nature Conservancy, the Klamath Indian Tribe, government agencies and private organizations.

Upper Klamath Lake is a large, shallow, natural lake lying in the rain-shadow east of the Cascade Mountains. Link River Dam, completed in 1921 as part of the US

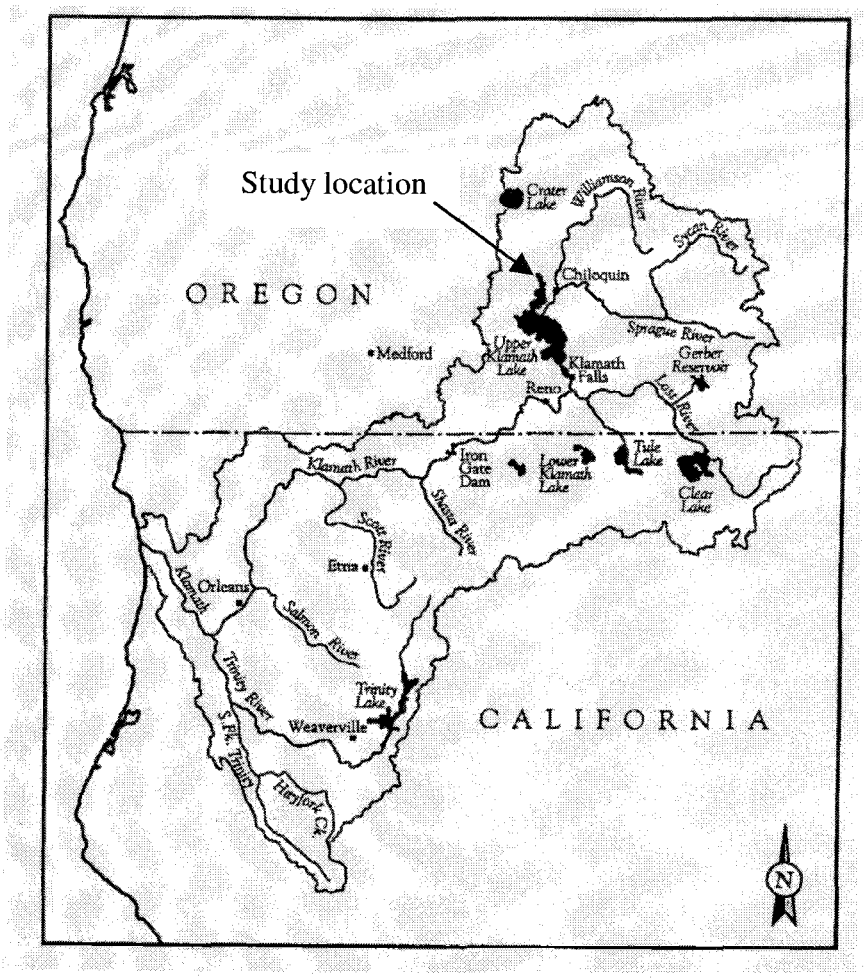

Figure 1. Klamath River watershed, south-central Oregon and Northern California. Map reproduced from National Research Council 2002.

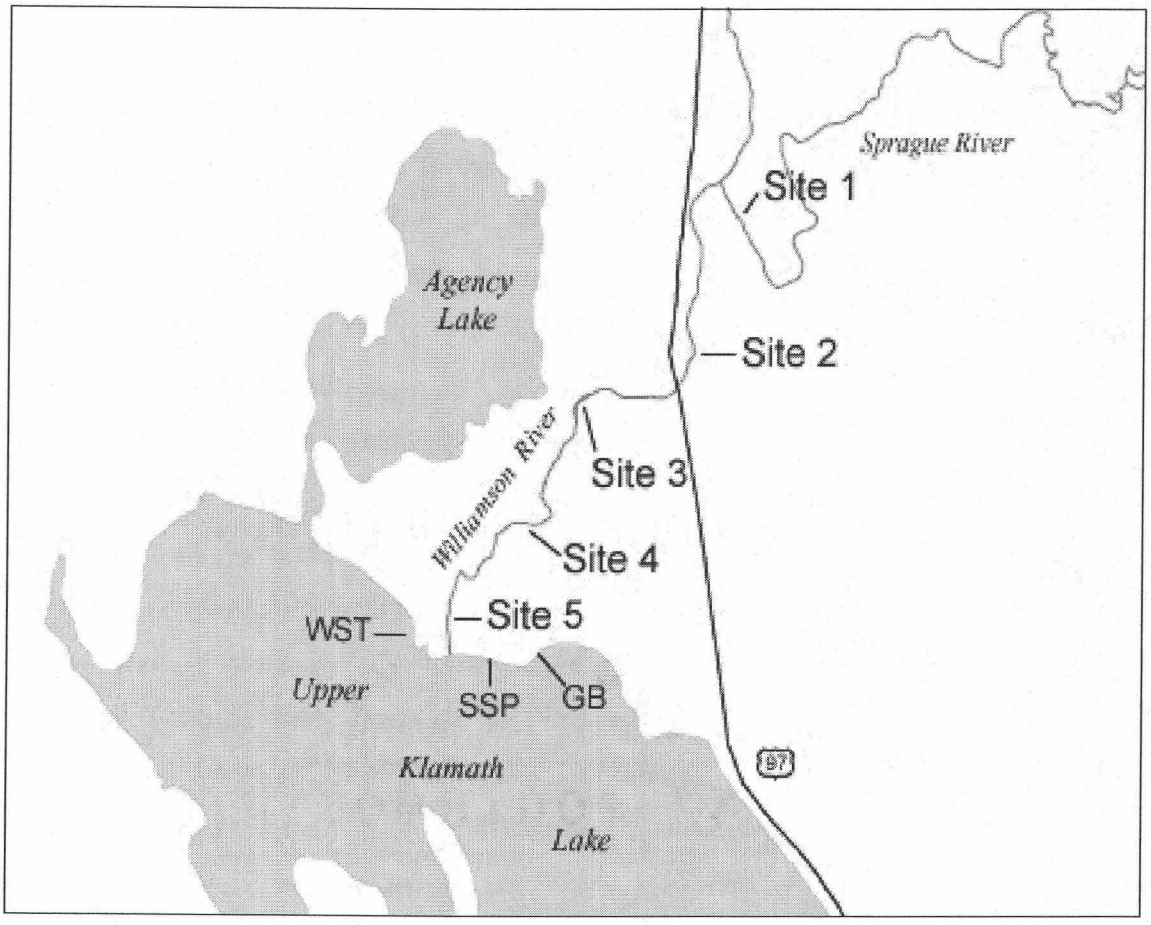

Figure 2. Sample site locations. Site 1 is 0.5 km below Sprague River Dam. Sucker spawning occurs between Sites 1 and 2.

Bureau of Reclamation's Klamath Irrigation Project, regulates outflow from UKL, expanded the range of lake elevations, and changed the timing of annual high and low water levels (Markle and Cooperman 2002). Pre-project water surface elevations (n=17) ranged between 4,140.0 - 4,143.1 ft mean sea level (msl) and post-project elevations (n=81) range between 4,136.6 - 4,143.3 ft msl (Markle and Cooperman 2002). At lake surface elevation 4,139.0, mean depth of the lake is approximately 2m. UKL suffers from cultural eutrophication (Bortleson and Fretwell 1993; Snyder and Morace 1997), is hypereutrophic (Kann 1997; Welch and Burke 2001), and during annual summer alga blooms lake water quality can be extreme (e.g., ph>10.0, dissolved oxygen <2 mg l^{-1}) (Martin and Saiki 1999; Saiki et al. 1999). The city of Klamath Falls, Oregon is at the outlet of the lake, which is the source of the Klamath River, and approximately 25 km north of the California-Oregon border.

The Williamson River is the largest tributary to the lake, contributing approximately 50% of the annual inflow (Philip Williams & Associates 2001; Rykbost and Todd 2002). In the 1950's, the lower 4 km of the Williamson were extensively dredged, straightened, and contained within levees (Cooperman and Markle 2003). Those modifications created near-shore slackwater zones with a concomitant increase in the abundance of aquatic macrophytes (Cooperman and Markle 2003).

Within the delta ecosystem, three emergent aquatic macropytes (e.g., rooted aquatic plants that extend to or above the water surface) are common: *Scirpus acutus* (hardstem bulrush), *Polygonum coccineum* (smart weed), and *Sparganium eurycarpum* (river burr reed) (Dunsmoor 2000). One submergent macrophyte (e.g., rooted aquatic plant that does not approach the water surface) *Potomogeton sp.* (Dunsmoor 2000), was present but rare during our sampling. For simplicity, reference to these plants will be by genus name.

Material and Methods

Sample gear, sample sites, and sample protocol

Sample equipment and methodologies, sample sites, effort, and protocols were described in Cooperman and Markle (2003). Salient points are reviewed below. Only

results of daytime samples collected between 08:00 and 16:30 were used in analyses herein.

We used 1 m^2, 100 *u*m mesh, remote releasing popnet samplers (Larson et al. 1986; Cooperman and Markle 2003) to sample the larval fish community within 20 m of shoreline and water depths of 7 to 110 cm in the Williamson River delta ecosystem during spring-summer of 1998 through 2000.

We collected popnet samples from four locations in the Williamson River (Figure 2), numbered sequentially from upriver to down, starting with Site 2. Site 1, below Sprague River dam, was established for related sampling and was not a part of this study. Site 2 was approximately 0.5 km upstream of US Highway 97 bridge. Pockets of still water 10-100 cm deep exist where river banks have slumped into the channel. Still waters were a mixture of unvegetated areas and patches of aquatic/semi-aquatic plants including *Scirpus* and other rushes, reed canary grass, and/or submerged macrophytes. Site 3 was downstream of Modoc Point Rd. bridge. Near-shore areas were shallow with little or no current. Patches of reed canary grass, assorted rushes, and filamentous green algae were common and interspaced with unvegetated areas. Near-shore areas of Site 4, located half-way between Site 3 and the mouth of the river, were similar to those of Site 5, located 100 m upstream of the mouth of the river. These sites had a 3-8 m wide zone of slackwater, containing intermingled patches of willows, emergent macropytes and unvegetated shoreline. By mid July of each year, submergent macrophytes became established along the outer edge of the slackwater zone.

We also collected popnet samples from three locations in UKL (Figure 2). West-shore Tulana Farms (WST) had an organic muck bottom with extensive stands of *Sparganium* and *Scirpus* mixed with patches of open water. South-Shore Delta preserve (SSP) and Goose Bay (GB) had sandy bottoms and intermingled patches of open water, emergent macrophytes, and willows.

Sample effort differed each year (Table 1). A sample event was one visit to a location, and included multiple popnet samples, typically six distributed between habitat types in proportion to habitat availability. Actual number of samples per sample event varied based on habitat availability and logistics. Each popnet sample

Table 1. Date classes, popnet sample effort and number of larval suckers caught, 1998-2000.

Year	Dates	DateClass	# Samples - # Larval suckers						
			Site 2	Site 3	Site 4	Site 5	WST	SSP	GB
1998	May 12 - May 18	3		4 - 0		6 - 0	2 - 0		5 - 0
	Jun 1 - Jun 5	4		5 - 1		6 - 6	7 - 4		9 - 9
	Jun 11 - Jun 16	5		0 - 0		0 - 0	8 - 195		8 - 5
	Jun 22 - Jun 27	6		8 - 40		9 - 39	6 - 283		9 - 93
	Jul 6 - Jul 16	7		7 - 0		8 - 4	18 - 3		25 - 7
1999	Apr 28 - May 8	2	6 - 0	3 - 0	3 - 0	10 - 0	7 - 0		6 - 1
	May 11 - May 21	3	9 - 0	7 - 0	6 - 0	9 - 0	9 - 4		12 - 2
	May 25 - Jun 3	4	12 - 0	9 - 0	12 - 3	12 - 16	12 - 59		12 - 136
	Jun 8 - Jun 18	5	11 - 5	12 - 243	12 - 661	12 - 466	12 - 215		12 - 290
	Jun 19 - Jul 1	6	10 - 3	6 - 188	12 - 45	12 - 21	6 - 20		12 - 115
	Jul 6 - Jul 16	7	6 - 0	2 - 0	9 - 0	12 - 17	12 - 30		12 - 138
2000	Apr 19 - Apr 27	1		6 - 0		12 - 1	12 - 1	12 - 6	12 - 1
	May 1 - May 12	2		12 - 0		12 - 1	11 - 2	9 - 0	12 - 2
	May 13 - May 26	3		12 - 38		12 - 111	12 - 12	12 - 14	12 - 13
	May 30 - Jun 9	4		11 - 83		12 - 499	12 - 38	12 - 118	12 - 26
	Jun 13 - Jun 22	5		9 - 476		12 - 49	12 - 69	11 - 105	12 - 91
	Jun 26 - Jul 7	6		8 - 0		12 - 28	12 - 1	12 - 9	12 - 110
	Jul 10 - Jul 20	7		6 - 2		11 - 6	9 - 0	8 - 0	12 - 40

was assigned a habitat type of non-woody, woody, or open water based on vegetation within 1 m of the center of the popnet. When two or three habitat types were present, components were listed in descending order of importance. For example, "non-woody + woody" meant non-woody vegetation was dominant and woody vegetation a subordinate component of the habitat. If all three habitats were present in equal amounts, habitat was recorded as "All 3." Vegetation type within the non-woody habitats was further classified as *Scirpus*, *Sparganium*, *Polygonum*, submergents, or combinations thereof.

We measured water temperature and pH, and estimated wind speed and direction, wave height, amount of cloud cover and precipitation intensity at the time each popnet sample was collected. Upon collection, the contents of each popnet were preserved in 10% formalin solution and stained with rose bengal. Within 72 hours of collection, samples were sorted and all fishes removed and preserved in 70% EtOH. At the end of the field season, all collected fishes were identified to lowest possible taxon, and standard length, developmental stage, and gut fullness were recorded (Cooperman and Markle 2003).

Data Analysis

Popnet samples were assigned to a "date class" based on date of collection (Table 1). Typically, a date class was an 8-12 day period during which two sample events took place at each location (typically, N=12 popnets per date class per location). Because many habitat types had low numbers of samples, such as woody + non-woody, we used the dominant habitat (DOMHAB) of mixed habitat samples as a variable. Samples with habitat type = All 3 were assigned DOMHAB = Mix.

At present, we can not differentiate larvae of the three upper basin sucker species (Lost River, shortnose, and Klamath largescale *Catostomus snyderi*), so we analyzed all sucker larvae together. Based on other work with identifiable juveniles, we assumed most were Lost River or shortnose suckers. Abundances of preflexion and early-, middle-, and late-flexion mesolarvae were highly correlated in popnet samples (all pair-wise p values <0.0002; Cooperman, unpublished data) and these lifestages were combined into "early larvae" and subsequently analyzed as a single unit.

Abundances of post-flexion mesolarvae and metalarvae were also highly correlated ($p = 0.001$), and were aggregated into "late larvae" and subsequently analyzed as a single group. Abundances of preflexion and early flexion larvae and post-flexion mesolarvae and metalarvae were not significantly correlated (all p values > 0.44). We conducted separate analyses for river and lake samples because the Williamson River is primarily a transit corridor (Cooperman and Markle 2003) and UKL is the nursery area.

Habitat effect on larval sucker abundance, length, and gut fullness

To examine habitat use it was necessary to remove confounding inter-annual, location and seasonal effects. For each analysis of habitat relationship to abundance, size, and gut fullness, we used residuals from Year-Location-Date class (YLD) means. YLD means were calculated as:

$$(1) \qquad \overline{X}_{ijk} = \sum_{m=1}^{n} \frac{X_{ijkm}}{n}$$

where i = year of collection, j = location of collection, k = date class of collection, and $\overline{X}$ = the YLD mean. For residual abundance, n = number of samples collected in each YLD combination, m = sample number with the YLD combination, and X_{ijkm} = number of individuals collected in a sample. For residual length and residual gut fullness, n = number of individuals collected in each YLD combination, m = individual number, and X_{ijkm} was the length or gut fullness of each individual collected during each YLD combination.

Residuals were calculated as:

$$(2) \qquad R_x = X_{ijkm} - \overline{X}_{ijk}$$

where R_x was the residual of sample X. For residual abundance, X_{ijkm} was the number of individuals collected in sample m of each YLD combination. For residual length

and gut fullness, X_{ijkm} was the mean length or gut fullness of all individuals collected in sample m of each YLD combination. When early and late larvae were collected in the same sample, residual abundance and gut fullness calculations used only individuals of the appropriate population. No partitioning by stage occurred for residual length calculations. YLD residuals were similarly calculated using the four non-woody vegetation types.

Essentially, one-way ANOVA analysis of YLD residuals between habitat types or vegetation types yield the same results as multifactor ANOVA, in that the analysis determines the influence of one factor (i.e., habitat type) on another (i.e., abundance) after factoring out the influence of other factors (i.e., year, location, and date of collection). We choose YLD residuals over multi-factor ANOVA for consistency of inputs between complementary analyses (i.e., graphic displays and community ordination were enhanced by use of residuals). For each ANOVA analysis we limited inputs to samples collected during YLD combinations when 10 or more larval suckers were collected and when at least one sample was collected from each of the three most common habitat types (non-woody, open water, woody). We refer to these analyses as 'three-habitat' comparisons. Because woody habitat was less common than the others, we repeated each analysis by restricting inputs to only non-woody and open water samples collected during YLD combinations when 10 or greater larvae were collected and both non-woody and open water habitats were sampled two or more times. We refer to these analyses as 'two-habitat' comparisons. We present results of the three habitat analyses in tables and describe results of two-habitat comparisons in the text. Several analyses had unequal sample sizes and/or unequal variances, thus, we report Kruskal-Wallace test of ranks and p values and Levene's test for homogeneity of variance for all ANOVA analyses. In all cases, we excluded a habitat type from statistical analysis if less than 5 samples from that habitat met selection criteria.

To examine seasonal trends we calculated mean residuals and standard errors for each habitat type per date class. For example, if 15 samples were collected in non-woody habitats in Upper Klamath Lake during date class 5 of any year, we used the 15 residual abundance values to calculate a mean and standard error.

Abundance

Residual abundance was compared based on dominant habitat type. Late larvae were rare in the river (Cooperman and Markle 2003) and not analyzed. We tested for differences in larval sucker abundance as a function of vegetation type by repeating the above methods for only non-woody samples (i.e., residuals were recalculated using only non-woody samples) and vegetation type equal to *Scirpus, Sparganium, Polygonum,* or submergent macrophytes. When a non-woody sample included two or more species of plant, the sample was placed in the category of the dominant species (i.e., *Scirpus* + *Polygonum* = *Scirpus*).

Length

Length residuals were examined across dominant habitat types and across non-woody vegetation types. Samples that did not collect larval suckers were excluded from residual calculation and analysis.

Gut Fullness

Larvae were qualitatively assigned to one of five gut fullness levels (Cooperman and Markle, in press). Residual gut fullness was examined across dominant habitat type, but the analysis was restricted to samples with positive catches. The analysis excluded all metalarvae and specimens with yolk or gut fullness levels "not visible" or "damaged." All samples were collected between 08:00 and 16:30 and gut fullness was not correlated to time of day ($p=0.466$). Gut fullness residuals were examined across dominant habitat types and across non-woody vegetation types. Trend analyses were done for both differences between habitat types and within non-woody vegetation types.

Habitat - predator relationships

Juvenile chubs (blue chubs *Klamathella coerulea* and tui chubs *Siphateles bicolor*) and juvenile sculpins (*Cottus klamathensis*, *C. princeps*, and *C. tenuis*) were common in popnet samples and are potential predators of larval suckers. We calculated year-location-DOMHAB specific catch-per-unit-effort ranks (1 = highest, 2

= middle, 3 = lowest) and visually inspected results for trends in predator abundance between habitat types. Chubs and sculpins were analyzed separately.

Predator relationships to larval sucker abundance and gut fullness

We examined linear relationships between late larval residual abundance or late larval gut fullness and log transformed abundance (x+1) of juvenile chubs. Abundance of juvenile chubs and late larval suckers had maximum overlap in non-woody habitats between date classes 5 to 7, so we restricted analyses to these conditions.

Community Ordination

We used non-metric multi-dimensional scaling (PC-Ord version 4.0; Mather 1976) to relate abundance of fishes in lake popnet samples to sample conditions. The first matrix used residual abundance of six fish groups: early suckers, late suckers, early cyprinids, late cyprinids, juvenile cyprinids, and juvenile *Cottus* sp. Cyprinids included blue and tui chubs and fat-head minnows (*Pimephales promelas*). *Cottus* included the previously mentioned three species. Larval (n = 6) and adult (n = 1) *Cottus*, juvenile rainbow trout (*Oncorhynchus mykiss newberrii* = 2), and larval yellow perch (n = 18, *Perca flavescens*) were the only other fishes collected in these samples, but were rare and not included.

The second matrix contained 10 quantitative descriptors including: DOMHAB, water depth, distance to shore, water temperature, wave action, and edge effect. DOMHAB was split into its component parts (DOMHAB = non-woody, woody, open water, all 3) with each part coded as a binary variable (0 = no, 1 = yes). Wave action was converted to binary data (no waves, low waves (height < 5 cm), medium waves (5-10 cm), and high waves (> 10 cm)). Edge effect, determined by the presence/absence of a different habitat type within 1.5 m of the center of the popnet was coded as 0 = no, 1 = yes. To avoid parameters being linear combinations summing to 1, DOMHAB = all 3, wave action = medium, and edge effect = no were removed from the analysis. Only samples with data values for all parameters were included in the analysis, resulting in 381 samples entering the analysis. Water pH was

routinely measured, but deleted from analysis due to missing values caused by equipment failure.

We compared results of three independent runs using "slow and thorough" autopilot setting with random start configurations (McCune and Grace 2002) to ensure we obtained consistent results. We used 30 runs per tested dimension Monte Carlo simulation with randomized data to determine number of dimensions (axes) to use in the final solution (McCune and Grace 2002). Three samples were identified as multivariate outliers (>2 standard deviations from the multivariate mean of fish residual abundances). Results of analyses with and without outliers were similar, so only results with outliers included are presented.

Results

During three years of study, we collected 414 daytime popnet samples in the Williamson River and 461 daytime popnets in Upper Klamath Lake (Table 1). River popnets collected 3,052 larval suckers (98.9% early) and lake popnets collected 2,267 larval suckers (54.6% early; Table 1, Figure 3). The timing of peak abundance of larval suckers progressed as a function of location and developmental stage (Figure 3). In the river, 98.9% of larval suckers were collected between May 11 - July 7 (date class 3 through 6), while in the lake, 95.2% of early larvae were collected between May 25 and July 7 (date class 4 through 6) and 93.0% of late larvae were collected between June 8 and July 20 (date classes 5 through 7).

Habitat relationships with abundance, length and gut fullness

Larval suckers were significantly more abundant in non-woody emergent macrophytes than any other habitat (Table 2), and this distribution pattern was consistent throughout the course of the study (Figure 3). In general, the abundance of larval suckers in open water and woody habitats was similar, although abundance in woody habitats was more variable (Table 2, Figure 3). The two-habitat comparison of abundance in non-woody and open water habitats produced similar results, although all p values were less than 0.001. There was no significant difference in the abundance of larval suckers amongst different emergent non-woody vegetation types (Table 2).

Submergent macrophytes were rare at the locations and dates sampled. In total, we collected eight submergent macrophyte popnet samples from the lake during date class 6 or 7, with a Catch Per Unit Effort (CPUE) of 0.50 larvae sample^{-1}. In contrast, emergent macrophyte CPUE for this same time frame and location was 9.24 larvae sample^{-1} (N=68 samples, 628 larvae).

The length of larval suckers between habitat types was not significantly different between the three most common habitat types (Table 3) and there was no seasonal trend in size differences between habitats (Figure 4). However, the two habitat comparisons identified a significant length differences between non-woody and open water samples in the river and a marginal difference between these habitats in the lake (River: non-woody n = 81, mean residual length (MRL) = -0.08; open water n = 29, MRL = -0.21, Kruskal-Wallace (KW) p = 0.027. Lake: non-woody n = 80, MRL = -0.08, open water n = 37, MRL = -0.34, KW p = 0.084). There was no evidence of size differences between larvae from different non-woody vegetation types (Table 3).

Residual gut fullness in the Williamson River was marginally different between habitat types, and larvae in non-woody habitats had the highest gut fullness levels (Table 4). There was a trend of increasing gut fullness over time for larvae collected from non-woody habitats, while the reverse pattern was observed in open water areas (Figure 5). In UKL, residual gut fullness of early larvae was not significantly different between the three habitat types (Table 4), and small sample size prevented statistical comparison of gut fullness for late larvae. In woody habitats, gut fullness was dependant upon developmental stage. Early larvae had low residuals while late larvae had the highest residual gut fullness. However, only 24 late larvae were collected in woody lake samples. Larvae collected in open water consistently had low residual gut fullness (Table 4), and this was most pronounced at times of peak larval abundance (Figure 5). Two-habitat comparisons yielded somewhat different results, as gut fullness was significantly different for early larvae in the lake (non-woody: n = 48, mean residual gut fullness (MGF) = 0.21; open water: n = 20, MGF = -0.37, KW p = 0.051). Although late larvae from non-woody habitats in the lake had larger mean residual gut fullness (n = 31, MGF = 0.11) than late larvae from open water (n = 15, MRGF = -0.40), the differences were not statistically significant

Table 2. Differences in the abundance of larval suckers as a function of habitat type based on YLD residuals. N = number of samples. SE = pooled s standard error. KW = Kruskal-Wallace test of ranks. Leven's = Levene's test for equality of variance. * Denotes habitat type included in calculation of residuals but excluded from statistical analysis due to small sample size (n<5). Comparisons of non-woody and open water habitats based on larger sample sizes are described in the text.

DOMHAB	N	Mean Residual Abundance	SE	Mean Rank	KW test statistic	KW p value	Levene's p value
River, early larvae							
Non-woody	26	0.21	0.07	34.0	12.1	0.002	0.008
Open water	17	-0.22	0.09	19.8			
Woody	8	-0.14	0.13	18.9			
Mix*	1	-0.43	0.38	6.0			
Lake, early larvae							
Non-woody	40	0.21	0.06	52.3	18.1	0.0001	0.035
Open water	24	-0.17	0.08	30.3			
Woody	17	-0.24	0.10	29.7			
Lake, late larvae							
Non-woody	23	0.16	0.10	27.4	5.8	0.055	0.271
Open water	13	-0.20	0.13	16.8			
Woody	9	-0.17	0.16	20.7			
Lake, late larvae, Non-woody samples only							
Polygonum	49	-0.02	0.05	86.6	1.34	0.511	0.315
Scirpus	77	-0.02	0.04	85.5			
Sparganium	43	0.06	0.06	96.2			
submergents*	8	< -0.01	0.13	99.3			

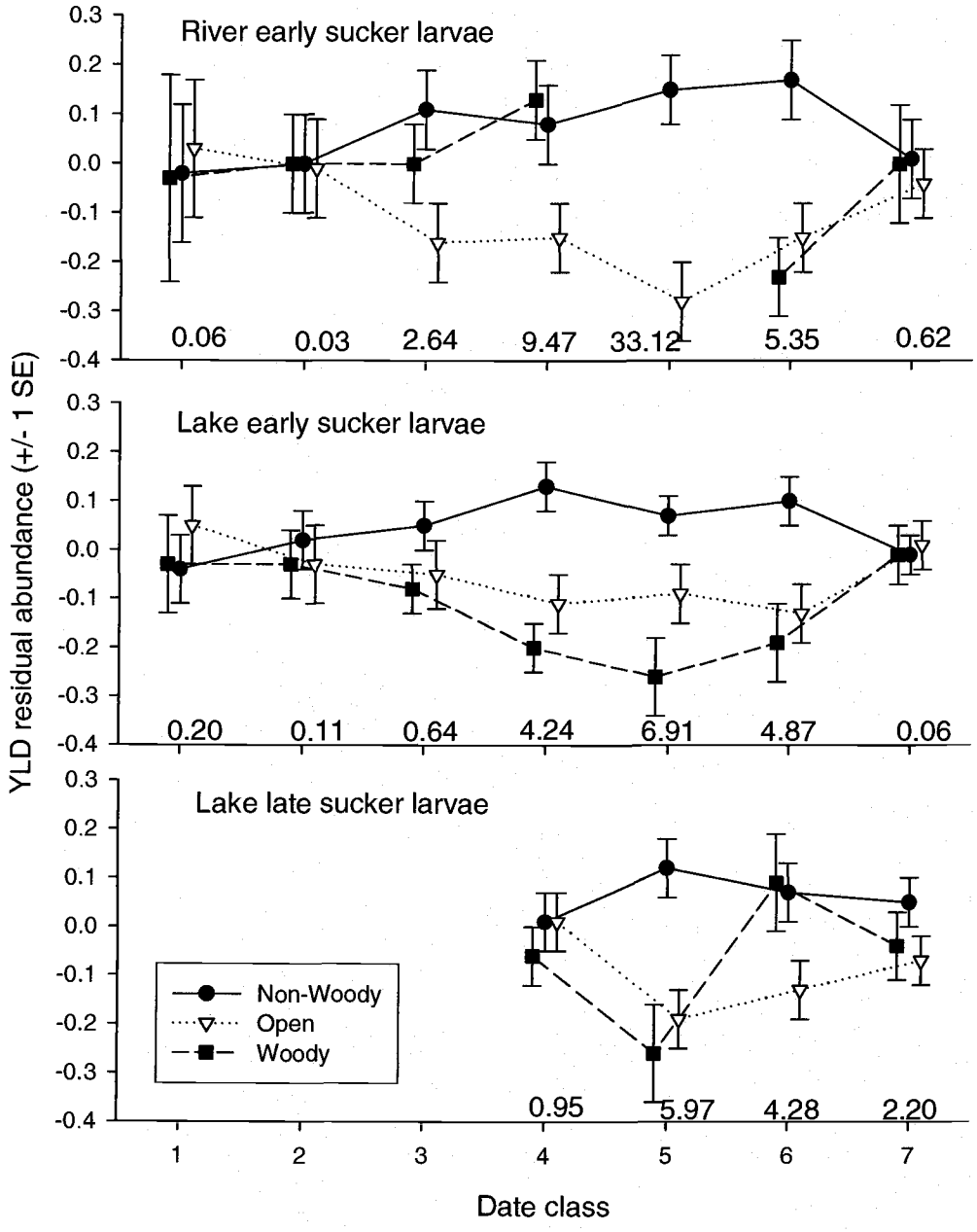

Figure 3. YLD residual abundance (+/- 1 standard error) of larval suckers in the three most common habitat types. Legend in lower panel is the same for all panels. No "Woody" samples were collected from the river during DateClass 5. No late larvae were collected during DateClass 1 through 3. Numbers given above X-axes are the average number of sucker larvae collected per sample during that DateClass.

Table 3. Differences in the length of larval sucker as a function of habitat type based on YLD residuals. N = number of samples. SE = pooled s standard error. KW = Kruskal-Wallace test of ranks. Levene's = Levene's test of equality of variance. * Denotes habitat type included in calculation of residuals but excluded from statistical analysis due to small sample size (n<5). Comparisons of non-woody and open water habitats based on larger sample sizes are described in the text.

DOMHAB	N	Mean residual length	SE	Mean rank	KW test statistic	KW p value	Levene's p value
River							
Non-woody	18	0.09	0.10	13.5	0.55	0.452	0.03
Open water	5	-0.03	0.20	10.8			
Woody*	3	0.32	0.25	17.8			
Lake							
Non-woody	34	-0.21	0.24	29.9	2.12	0.346	0.836
Open water	14	0.27	0.37	36.3			
Woody	12	-0.47	0.40	26.4			
Mix*	1	0.99	1.40	50.0			
Lake, non-woody samples only							
Polygonum	43	-0.33	0.24	59.4	2.04	0.361	0.002
Scirpus	58	0.17	0.21	68.2			
Sparganium	30	0.04	0.29	71.2			
submergents*	2	1.09	1.10	82.0			

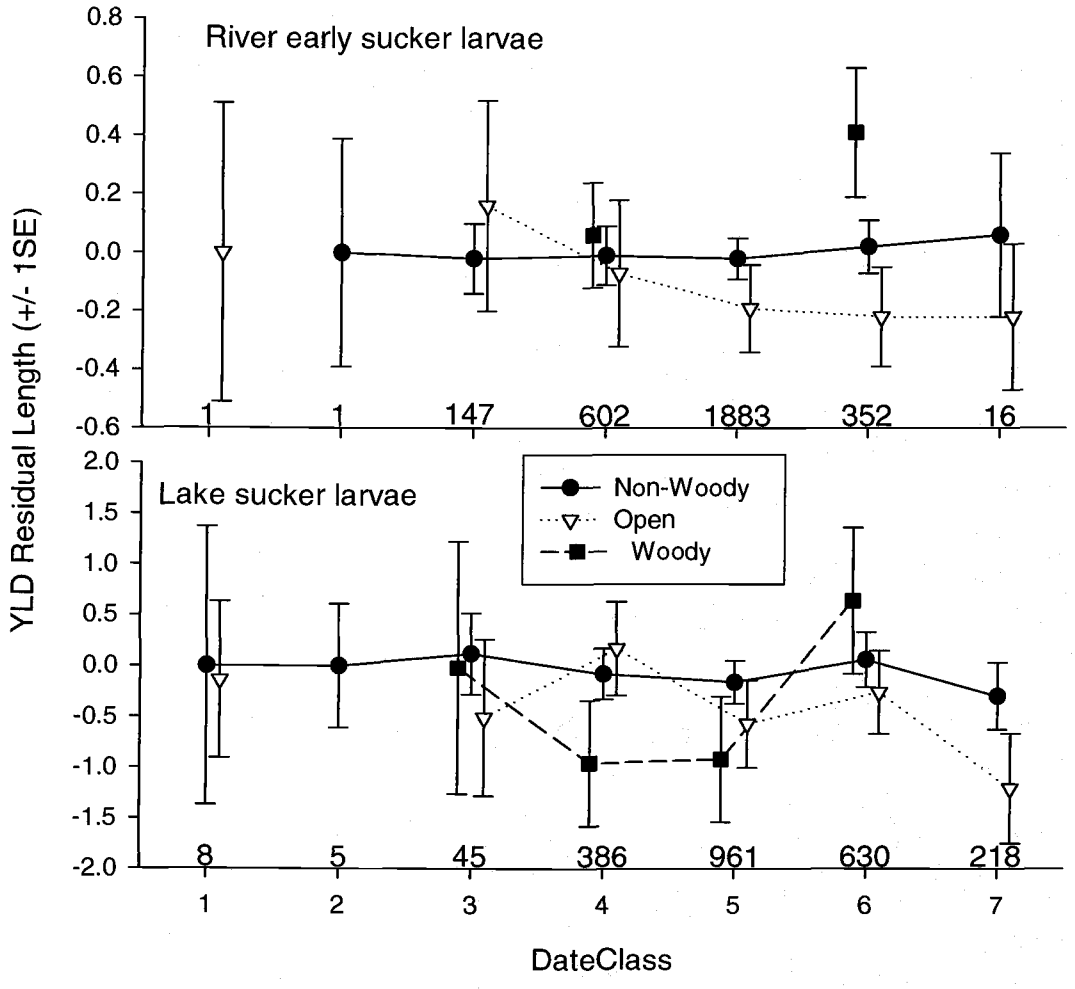

Figure 4. YLD residual length (+/- 1 standard error) of larval suckers collected from three habitat types of the Williamson River and Upper Klamath Lake. Note the different Y-axes. Legend given is the same for both panels. DateClasses missing habitat types indicate no suckers were collected in that habitat type during that DateClass. Numbers given above X-axes are the number of individuals collected during that DateClass.

(KW p = 0.128). There were no significant differences in gut fullness between different types of non-woody macrophytes, although larvae collected in *Scirpus* had lower mean residual gut fullness than those observed in other non-woody macrophytes (Table 4). Except for a late season drop in *Scirpus*, residual gut fullness did not change significantly over the season for early sucker larvae in non-woody vegetation in UKL (Figure 6).

Community organization

Near-shore fish community ordination

We selected a 3 dimensional solution as the best fit for our community data (Figure 7A & B). We used 200 iterations with real data to produce a solution with final stress of 10.37 and instability of 0.011. Axis 1 explained 55.7% of the variance, axis 2 explained 29.9% and axis 3 explained 10.5% (96.2% cumulative). Monte Carlo test results indicate our 3-D solution produced significantly lower stress than expected by chance when compared to 30 runs with randomized data (p = 0.032).

NMS axis 1 and axis 2 were defined by gradients of vegetation structure and these axes combined to produce a cluster of larval fishes and a cluster of juvenile-adult fishes (Figure 7A). Larval fishes were associated with non-woody vegetation and juvenile-adult fishes were associated with open water. The strongest observed association between fish group and environmental parameter were for early larval suckers, which were strongly positively associated with axis 1 (the prevalence of non-woody vegetation) and juvenile-adult cyprinids, which were positively associated with axis 2 (prevalence of open water). No other measured environmental parameters had correlation values stronger than +/- 0.100 on axes 1 or 2. Axis 3 explained a gradient of water depth-distance from shore and wave action (Figure 7B). Early larval suckers were highly associated with the combination of shallow water, close to shore, and high wave action. Late larval suckers also followed this gradient, but less strongly. Juvenile-adult cyprinids were associated with deeper water and greater distances from shore and lower wave action. Cyprinid larvae and juvenile *Cottus* were not strongly associated with axis 3.

Table 4. Gut fullness as a function of habitat type based on YLD residuals. N = number of samples. SE = pooled s standard error. KW = Kruskal-Wallace test of ranks. Levene's = Levene's test of equality of variance. * Denotes habitat type included in calculation of residuals but excluded from statistical analysis due to small sample size (n<5). Comparisons of non-woody and open water habitats based on larger sample sizes are described in the text.

DOMHAB	N	Mean Residual Abundance	SE	Mean Rank	KW test statistic	KW p value	Levene's p value
River, early larvae							
Non-woody	9	0.19	0.24	11.3	3.58	0.058	0.472
Open water	6	-0.73	0.30	5.6			
Woody*	3	0.12	0.42	11.7			
Lake, early larvae							
Non-woody	22	0.17	0.81	23.8	4.07	0.13	0.070
Open water	8	-0.24	0.17	17.5			
Woody	10	-0.41	0.29	15.6			
Mix*	1	0.11	0.26	27.0			
Lake, late larvae							
Non-woody	15	0.38	0.21	13.7			
Open water*	4	-0.121	0.41	3.3			
Woody*	4	0.55	0.41	14.3			
Lake, late larvae, non-woody samples only							
Polygonum	21	0.11	0.17	49.2	3.70	0.157	0.069
Scirpus	43	-0.15	0.12	39.6			
Sparganium	25	0.17	0.16	50.8			

Figure 5. YLD residual gut fullness (+/- 1 standard error) of larval suckers in the three most common habitat types. Legend in the lower panel is the same for all panels. Missing data points indicate no applicable larvae were collected in that habitat type during that date class. Numbers given above the X-axes are the number of larvae collected during that date class.

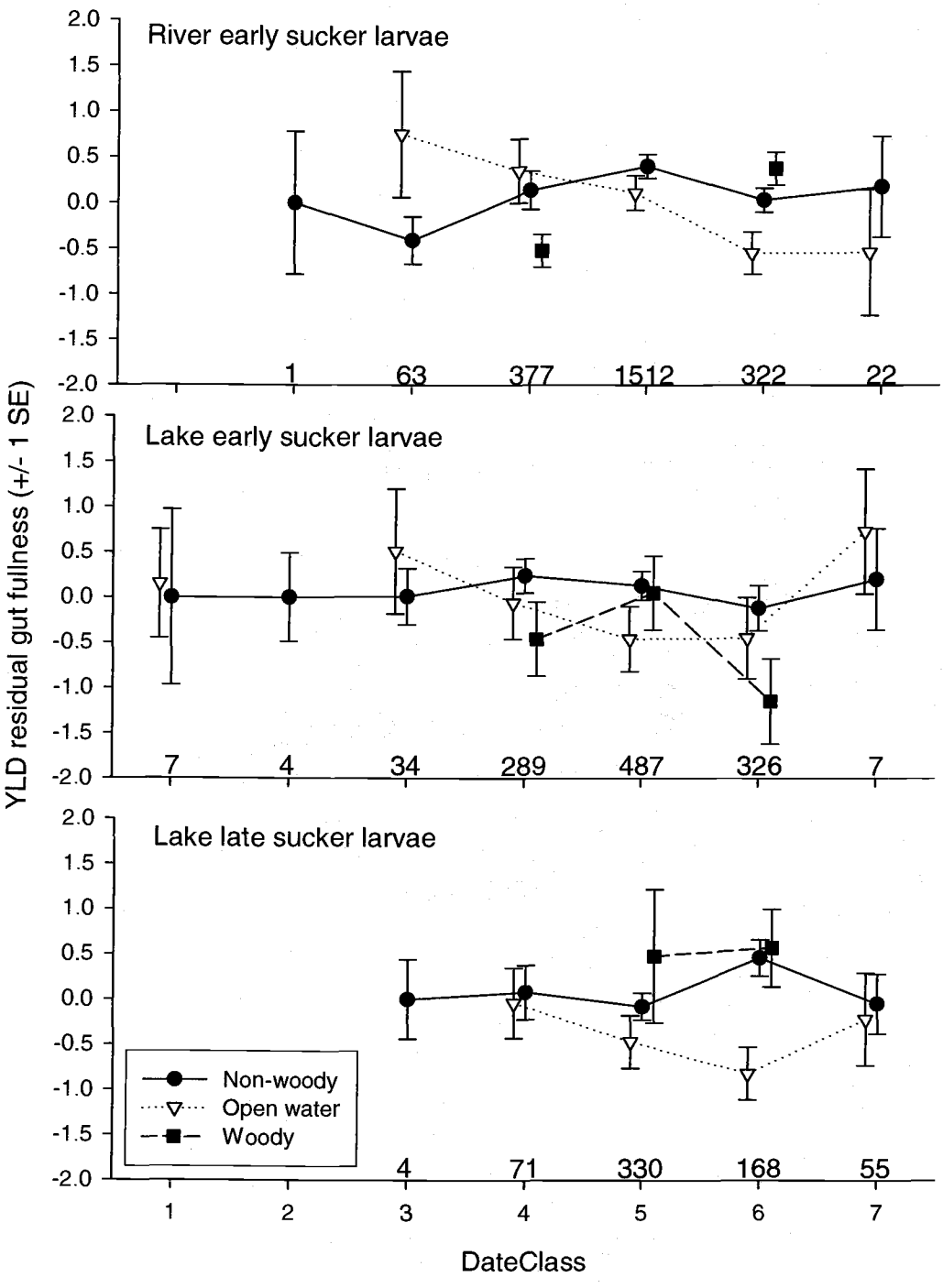
River early sucker larvae
Lake early sucker larvae
Lake late sucker larvae
YLD residual gut fullness (+/- 1 SE)
DateClass
Non-woody
Open water
Woody
1
63
377
1512
322
22
7
4
34
289
487
326
7
4
71
330
168
55

Figure 5.

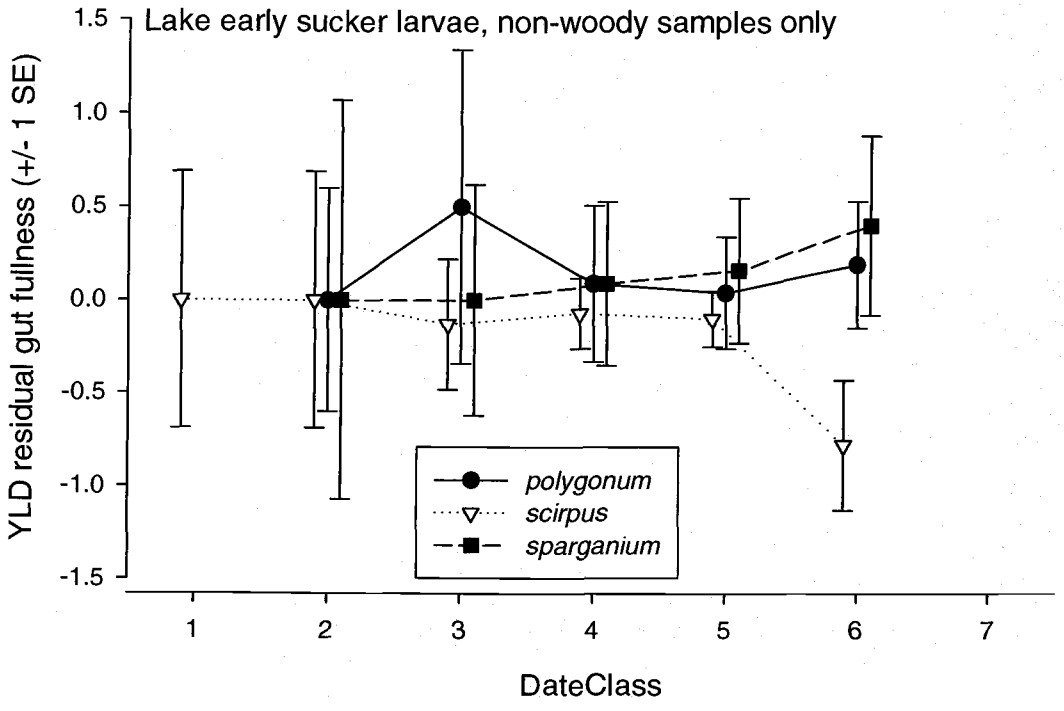

Figure 6. Mean (+/- 1 standard error) YLD residual gut fullness levels of pre-caudal sucker larvae collected in day time non-woody popnet samples from Upper Klamath Lake. Results of samples collected during date class 7 are excluded from figure because only 2 late larvae were collected within this time period over the three years of the study.

Figure 7 A and B. Three dimensional non-metric multi-dimensional scaling ordination of the near-shore fish community of Upper Klamath Lake. Fish data are YLD residual abundance values. Axis notations identify parameters with correlation scores > +/- 0.100. Arrows point in direction of increasing values for each parameter. Juv. = juvenile. A - Axis 1 and 2. Axis 1 explains 55.7% of the variance in the data and Axis 2 explains 29.9%. B - Axis 1 and Axis 3. Axis 3 explains 10.5% of variance.

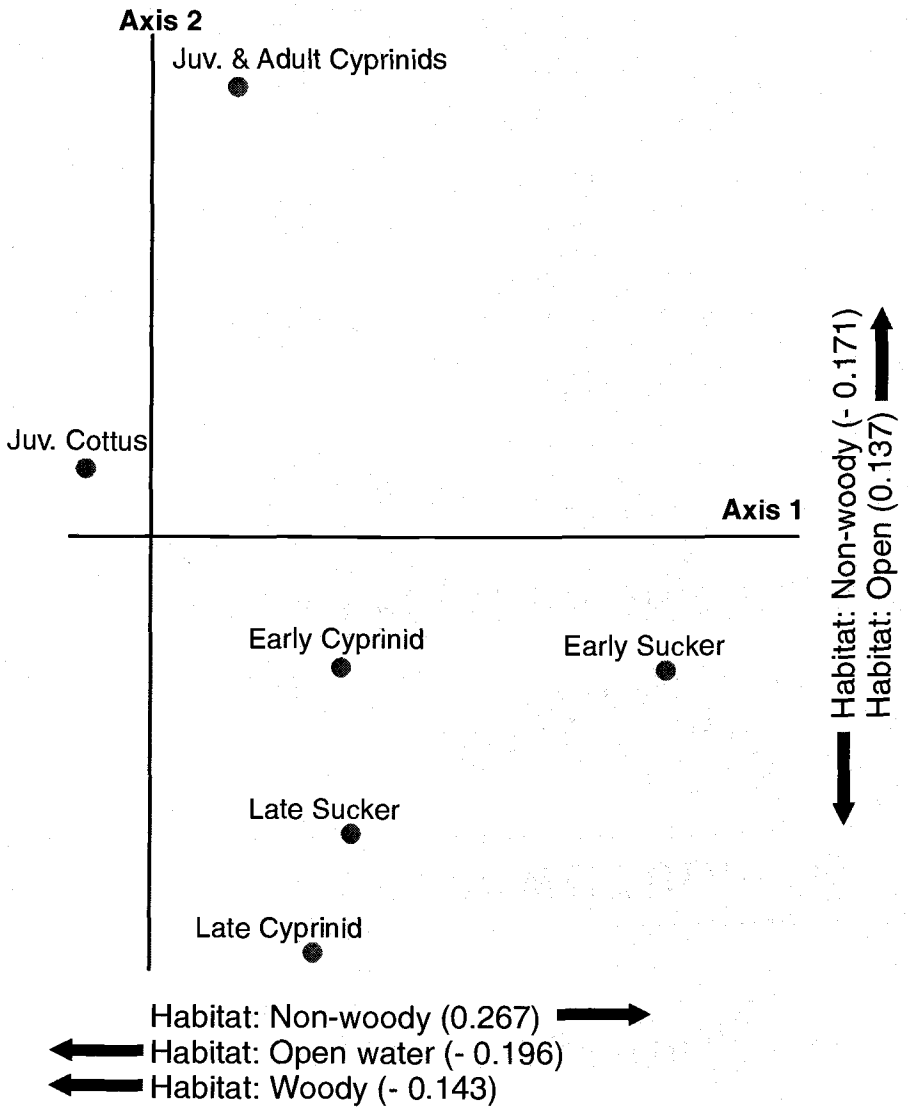
Axis 2
Juv. & Adult Cyprinids
Juv. Cottus
Axis 1
Habitat: Non-woody (- 0.171)
Habitat: Open (0.137)
Early Cyprinid
Early Sucker
Late Sucker
Late Cyprinid
Habitat: Non-woody (0.267)
Habitat: Open water (- 0.196)
Habitat: Woody (- 0.143)

Figure 7A.

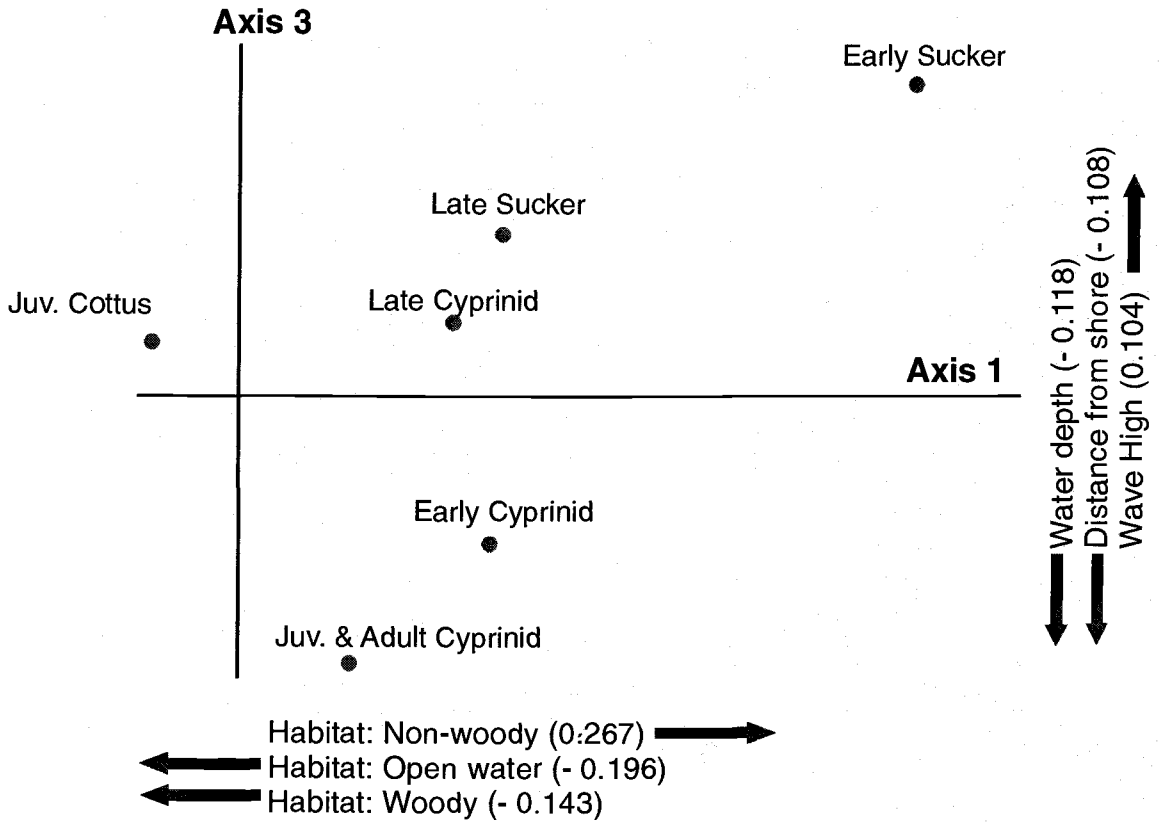
Axis 3
Early Sucker
Late Sucker
Juv. Cottus
Late Cyprinid
Axis 1
Early Cyprinid
Juv. & Adult Cyprinid
Water depth (- 0.118)
Distance from shore (- 0.108)
Wave High (0.104)
Habitat: Non-woody (0.267)
Habitat: Open water (- 0.196)
Habitat: Woody (- 0.143)

Figure 7B.

Habitat use by potential predators

The 461 daytime lake popnet samples collected 269 juvenile chubs. Juvenile chubs were present at all locations sampled and in all three years of the study. CPUE ranged from a low of 0.06 chubs sample^{-1} at WST in 2000 to a high value of 1.58 chubs sample^{-1} at GB in 2000. CPUE was less variable in other years (1998: WST - 0.54, GB - 0.23; 1999: WST- 0.72, GB - 0.64). CPUE at SSP in 2000 was 0.16. The three year combined juvenile chub CPUE at Site 5 within the Williamson River, the river location with the highest chub catch rates, was 0.10. Within UKL, juvenile chubs were most abundant in non-woody samples and least abundant in woody samples (Table 5).

We collected 83 juvenile or adult sculpins, and juvenile or adults were present at all locations in all years of the study. CPUE ranged from a low of 0.07 sculpins sample^{-1} at WST in 1999 to a high of 0.29 at GB in 2000. CPUE for the other five year-location combinations were all between 0.15 and 0.21. The three year CPUE for Site 5 within the Williamson River was 0.39. Within UKL, *Cottus* were most abundant in non-woody samples and least abundant in woody samples (Table 5).

Relationship between juvenile cyprinid abundance and sucker abundance and feeding

Late larval sucker abundance was weakly but significantly positively correlated with juvenile cyprinid abundance (late larval residual abundance = -0.028 + 0.221 log (# juvenile cyprinids + 1), $r^2 = 3.25\%$, $p = 0.034$). Residual gut fullness of late larvae was negatively, but non-significantly, correlated with juvenile cyprinid abundance (0.13 - 0.28 log (# juvenile cyprinid +1), $r^2 = 1.28\%$, $p = 0.322$).

Discussion

Non-woody emergent macrophytes were an important habitat for larval suckers. Emergent macrophytes supported the highest abundance of larval suckers in both the Williamson River and Upper Klamath Lake (Table 2, Figure 3), and emergent macrophytes typically hosted the largest (Table 3, Figure 4) and best fed (Table 4, Figure 5) larval suckers. In contrast, open water and woody habitats hosted significantly lower numbers, smaller mean sizes, and more poorly fed sucker larvae.

Table 5. Distribution of potential predators based on ranked CPUE by habitat type among the seven YLD combinations. Numbers beneath habitat types indicate the frequency with which a predator was most, intermediate, or least encountered based on CPUE.

Predator	Rank	Non-woody	Open water	Woody
Juvenile chubs	1	5	2	0
	2	2	5	0
	3	0	0	7
Juvenile sculpins	1	5	2	0
	2	2	4	1
	3	0	1	6

Assuming sucker larvae that had reached meta-larvae stage were well fed, differences in gut fullness between non-woody and other habitats would have been larger if meta-larvae had been included in this analysis, as 83% (276 out of 331) of all sucker meta-larvae were collected in non-woody habitats. Observed patterns in abundance, size, and gut fullness differences between habitat types were consistent regardless of developmental stage (Tables 2 and 4, Figures 3 and 5). Our results are consistent with other work documenting the importance of macrophytes to YOY fishes (Heck and Crowder 1991; Dibble et al. 1996; Weaver et al. 1996; Werner 2002).

Although it is possible the between habitat differences reflect earlier occupation of a different habitat type and are not an accurate indicator of habitat quality, this effect should be random and the energetic inefficiency of larval fish swimming (Diana 1995) combined with the large ratio of habitat patch size to larval sucker size (typically greater than 1000:1; Cooperman, unpublished data), suggest short-term movements between habitat types should be limited.

We found no evidence of differences in larval sucker demographics among different species of emergent macrophytes (Tables 2, 3, 4). Lack of vegetation specific differences supports the conclusion that habitat selection by larval suckers is based on the presence and/or abundance of physical structure, not plant specific features. At the locations we sampled, *Scirpus*, *Sparganium*, and *Polygonum* typically grew in dense single species stands, suggesting each of these species provided sufficient stem densities. A potential confounding influence to our interpretation is that species of macrophytes were non-randomly distributed within the system in response to variables such as aspect, exposure to wave action, and sediment characteristics (Dunsmoor 2000). It is possible some of these factors may also be partly responsible for controlling the distribution of larval suckers, eliminating the opportunity for suckers to reach or select among species of macrophytes. However, lack of among macrophyte differences suggests none of the variables controlling macrophyte distributions were controlling larval sucker distributions.

In contrast to the importance of emergent macrophytes, submergent macrophytes were not highly utilized (Table 2). Submergents were rarely sampled during our study because they were neither common nor readily available during the

study. Further, when submergents were available, they were not highly used by suckers. The relative non-use of available submergents may be related to larval sucker behavior. Both early and late larval suckers are strongly surface oriented (Cooperman, personal observation) and aquatic plants that do not approach the water surface may not provide appropriate physical structure.

At the densities observed during our study, there was no evidence of density dependant effects or intra-specific competition. Between habitat differences in abundance and gut fullness were generally largest when larval suckers were most numerous (Figures 3 and 5), and there was no relationship between abundance of larvae and mean gut fullness (Cooperman, unpublished data). Conversely, the magnitude of size differences between habitats was largely unaffected by abundance of suckers (Figure 4). This suggests the distribution patterns are not a result of habitat shifting in response to intra-specific interactions, as predicted by the ideal free distribution and its correlates (Fretwell and Lucas 1970). Therefore, patterns are likely a result of either better access to non-woody habitats, exclusion from habitat types other than non-woody, or post-settlement events including movement to non-woody habitats and/or increased survivorship and growth of larvae in non-woody habitats. Because non-woody, woody, and open water patches were common and intermingled throughout the study area (Cooperman, personal observation) and we found no indication of competitive exclusion of sucker larvae from one or more habitat types (Table 5, Figures 3 and 5), we believe between habitat differences are likely related to post-settlement events.

Larval suckers may accumulate in emergent macrophytes because their food is more abundant and/or accessible, as reflected in the enhanced foraging success for larvae in emergent macrophytes (Table 4, Figure 5). Multiple mechanisms, including greater productivity, better physical cover from predators, and/or better protection from wind generated waves, may explain the foraging advantage associated with occupying emergent macrophytes.

Ordination of UKL's near-shore fish community also supported the conclusion that habitat type was an important variable affecting larval sucker distribution and fish assemblage organization (Figure 7A and B). Early larval suckers were strongly

associated with non-woody vegetation and shallow water, while late larval suckers, and all cyprinid larvae, were also strongly associated with non-woody vegetation but less affected by water depth. Conversely, larval suckers and larval cyprinids had a strong negative association with open water and woody vegetation, suggesting these habitats did not provide acceptable conditions for larval fishes. Juvenile *Cottus* and juvenile and adult cyprinids were separated from larval fishes in the ordination and were associated with open water and/or woody vegetation. Juvenile and adult cyprinids were also highly associated with deeper water.

The NMS ordination suggests predation pressure may be an important mechanism structuring the fish community and that larval fishes may be using emergent macrophytes and/or shallow water as a refuge from predators (Figure 7A and B). Many investigations have documented that the physical structure provided by aquatic plants can provide small fish with protection from their predators, either because predatory fishes are excluded from vegetation or by reducing encounter rates and/or capture efficiency (Werner et al. 1983; Main 1987; Rozas and Odum 1988; Carr 1994; Weaver et al. 1997).

CPUE data describing juvenile cyprinid and *Cottus* habitat use in UKL conflicts with the ordination results. CPUE for these fishes indicate they were most frequently captured in non-woody vegetation (Table 5), the same habitat where larval fishes were most abundant, indicating potential predators of larval suckers were not excluded from macrophyte patches. There was no evidence of a negative relationship between abundance of larval suckers and abundance of potential predators in non-woody habitats, indicating sucker larvae neither vacate their patch of non-woody macrophytes when predators enter their immediate area, nor are larval suckers consumed in large enough quantities to affect the relative balance of larval sucker CPUE between habitat types. Also, we found no evidence that larval sucker foraging success suffered when juvenile cyprinids were present, suggesting larval suckers did not adjust their behavior in an effort to reduce encounter rates. To more fully evaluate the importance of emergent macrophytes as a predation refuge for larval suckers, information on differential encounter rates and capture efficiencies between habitat types would be needed.

Residual abundance, size and gut fullness data strongly indicate the importance of emergent macrophytes to larval suckers (Tables 2-4). It is possible that larval data reflect earlier occupation of a different habitat type and are not an accurate indicator of the quality of the sampled habitat. However, that effect should be random plus the energetic inefficiency of larval fish swimming (Dabrowski et al. 1986; Diana 1995) and the large ratio of habitat patch size to larval sucker size (typically greater than 1000:1; Cooperman, unpublished data), suggest short-term movements between habitat types would be limited.

The size and gut fullness advantage of sucker larvae from emergent macrophytes (Tables 2-4) may have a positive effect on survival, as even subtle differences in individual sizes or foraging success can have profound effects on larval survival (Miller et al. 1988). For example, larger, faster growing, better fed larvae are vulnerable to predators for shorter periods of time than smaller, slower growing, poorly fed con-specifics (Houde 1987; Miller et al. 1988). Also, over-winter survival tends to be highly size selective (Schindler 1999; Werner 2002).

Because survival of larval suckers through flexion appears to be partly dependant on availability of emergent macrophytes from April through mid-July, and volume of emergent macrophytes is a function of lake surface elevation (Dunsmoor 2000; Markle, unpublished data), our results indicate maintenance of lake elevations that ensure availability of emergent macrophytes should enhance early survival. Whether or not early larval survival translates into improved year class production is unknown beyond the obvious case of zero survivorship through the larval stage. However, Cowan and Shaw (2002) suggest that most evidence indicates little or no correlation and Houde (1994) theorizes that most freshwater fish year classes are determined in the juvenile stage. Because larval and juvenile cyprinids also use emergent macrophytes (Table 5, Figure 7), there may be other, positive or negative, interactions directly related to volume of emergent macrophytes. Whether or not the advantages associated with larval rearing in emergent macrophytes transfer to later lifestages, our results suggest access to emergent macrophytes during larval sucker rearing is a necessary, but perhaps not sufficient, factor for promoting year class production of endangered shortnose and Lost River suckers.

Acknowledgments

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CHAPTER 4

Seasonal and inter-annual effects of weather and habitat on survival of larval shortnose suckers and Lost River suckers in Upper Klamath Lake

Michael S. Cooperman and Douglas F. Markle

Abstract

Persistent year-class failure is a principle hurdle in the conservation and recovery of Upper Klamath Lake's endangered Lost River and shortnose suckers. We used seven years of larval sucker survey data (1995-2001) to construct tri-weekly larval production estimates for 10 mm (LPE10) and 15 mm (LPE15) larvae. LPE10 was positively related to air temperature and volume of inundated emergent macrophytes (VIEM) in the three weeks prior to collection. LPE15 was positively related to LPE10 in the preceding sample and VIEM in the three weeks prior to collection and negatively related to high wind events in the three weeks prior to collection. Survival from 10 to 15 mm was best when mean air temperature, VIEM and proportion of high wind events during the three weeks prior to collection were, respectively, 13-22°C, >15,000 m^3, and <0.28. These results are consistent with basic larval fish survival concepts, especially the stage duration and stable ocean hypotheses. We used these results to estimate larval production and 10-15 mm survival between 1960-2001 and compared the results to an estimate of annual recruitment during that time. Inter-annual variability in air temperature, VIEM and proportion of high wind events suggested a relationship to North Pacific climatic events and long-term patterns in relative larval production and survival. As expected, there was a poor relationship between larval production and survival and subsequent adult recruitment suggesting that sucker year-class strength is not established during the larval stage. However, it is important to emphasize that environmental conditions acting on larvae may set both the lower and upper limits on subsequent adult recruitment.

Introduction

Order of magnitude fluctuations in recruitment are normal for many fish species (Mills and Mann 1985, Cowan and Shaw 2002), and population fluctuations resulting from inter-annual variability in recruitment can greatly complicate management of fisheries or at-risk species (Sale 1990, Ludwig et al. 1993, Ross 1997). Environmental factors are primary determinants of recruitment success, principally through their effect on young-of-year survival (Hjort 1914, Lasker 1981, Hollowed et al. 1987, Cowan and Shaw 2002, Chavez et al. 2003), but their complex interactions and co-linearity make identifying key mechanisms difficult (Hollowed et al. 1987, Sale 1990, Megrey et al. 1995, Ludsin and DeVries 1997). Young-of-year (YOY) survival is a primary driver of population dynamics because even small changes in early life mortality rates can have profound effects on abundance of later life stages (Houde 1987, Houde 2002).

Because freshwater fishes typically have relatively high average larval survival rates, year-class strength for freshwater fishes is commonly established during the juvenile stage (Houde 1994) and freshwater fish recruitment dynamics may only be sensitive to episodic events that eliminate most or all larvae (Houde 1994, Ludsin and DeVries 1997). However, there are examples of freshwater fish year-classes being established during the larval stage (Freeberg et al. 1990, Mion et al. 1998, Sammons and Bettoli 1998, Bremigan and Stein 1999). Typically, those freshwater species are more similar to marine teleosts with high fecundity, small egg size, limited pre- and post-fertilization parental investment in reproduction, and higher than average larval mortality rates (Diana 1995, Ludsin and DeVries 1997).

Lost River suckers (*Deltistes luxatus*; LRS) and shortnose suckers (*Chasmistes brevirostris*; SNS) are endemics of upper Klamath River basin (Figure 1), and abundances of both species are greatly reduced from historic levels. Both species were listed as "endangered" under the federal Endangered Species Act in 1988 (USFWS 1993). The largest remaining populations of both species are in Upper Klamath Lake (UKL) and age data derived from a fish kills in the 1980s and 1990s indicate there was limited recruitment during the 1970's and 1980's (Scoppettone and Vinyard 1991, Cunningham and Shively 2001, Markle and Cooperman 2002; Figure 2). Typically,

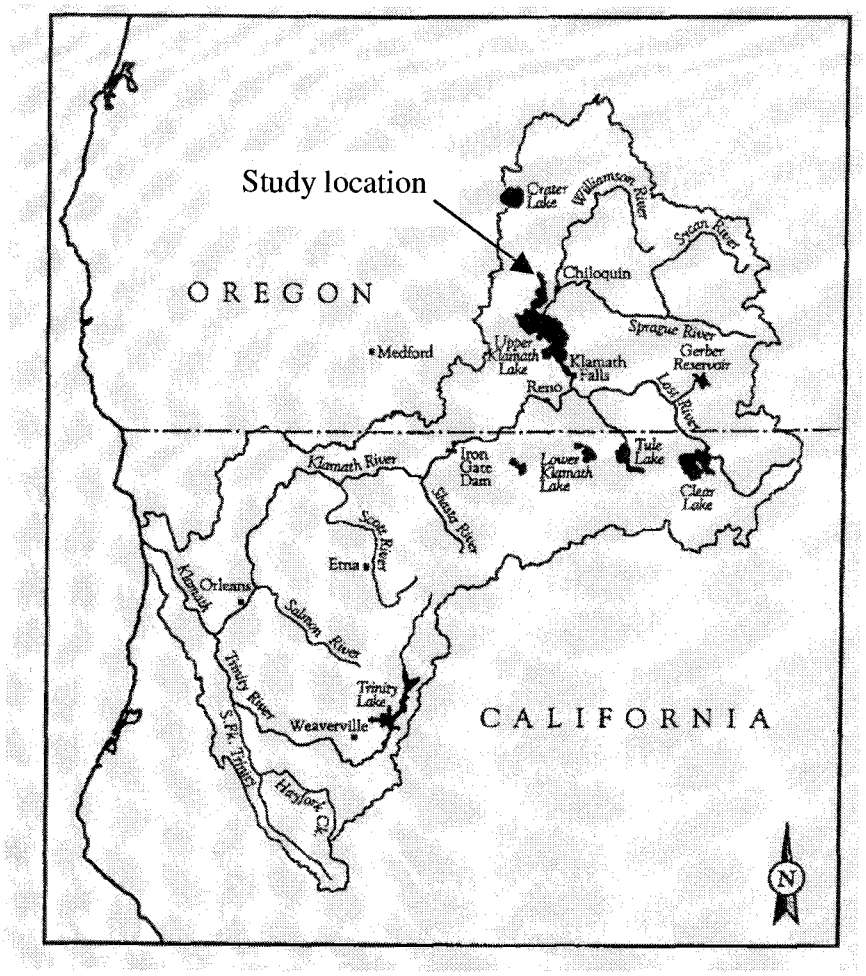

Figure 1. Map of the Klamath River watershed, south-central Oregon and Northern California (reproduced from National research Council 2002).

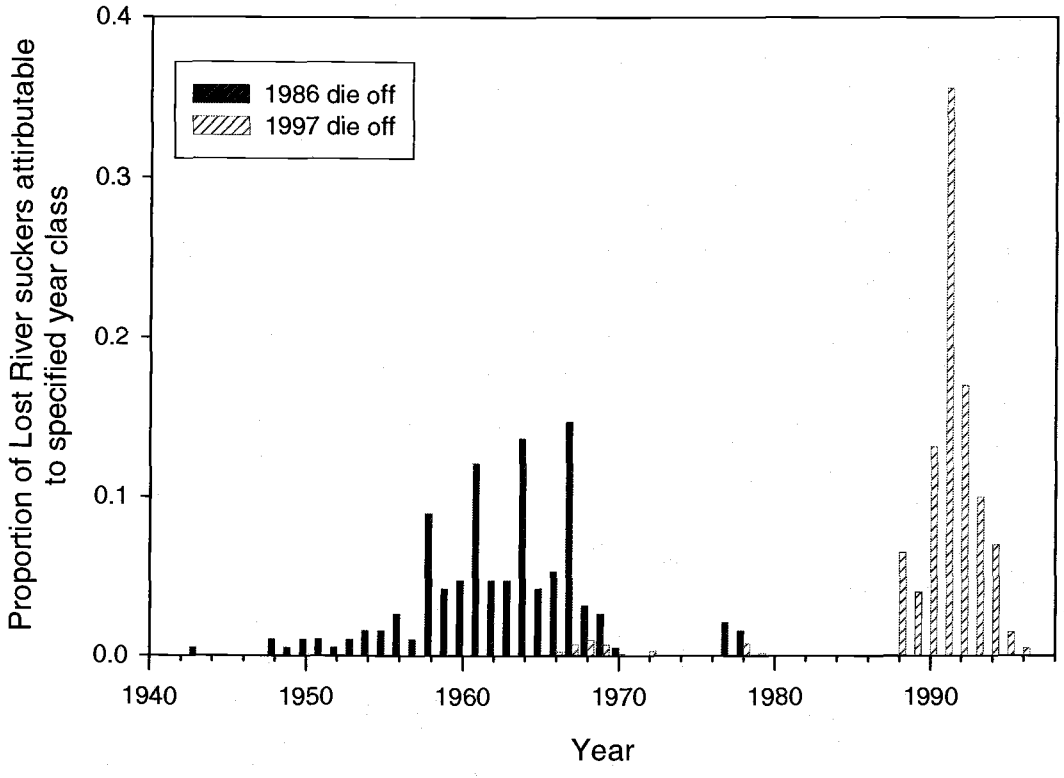

Figure 2. Age structure of Upper Klamath Lake suckers inferred from 1986 and 1997 die-offs; 1986 data from Scoppettone and Vineyard (1991), 1997 data provided by R. Shively, USGS.

large numbers of sucker larvae can be found each spring-summer, but many fewer seem to survive through the first winter (Simon and Markle 2001). Persistent year-class failure is considered a principle hindrance to recovery of these suckers (USFWS 1993, 2001), but the specific conditions that affect year-class success are unknown, as is whether year-class strength is determined during the larval or juvenile stage.

Factors hypothesized to adversely affect YOY sucker survival include blocked access to historic Sprague River spawning grounds caused by Chiloquin Dam, dredging and channelization of the lower Williamson River, loss of riverine and lake wetland nursery areas, degraded water quality related to cultural eutrophication of UKL, loss of in-lake nursery areas caused by draw-down of the lake to met irrigation and downstream flow demands, and competition-predation due to exotic species (USFWS 1993, 2001). Cooperman and Markle (2003b) present evidence that modifications of the lower Williamson River do not adversely affect movement of larval suckers from upriver spawning beds to in-lake rearing grounds and question the role of Chiloquin Dam and loss of riverine wetlands in limiting larval sucker survival. Terwilliger et al. (2003) found sublethal effects of low dissolved oxygen on larval sucker growth when water temperatures exceeded 22 C, but no effects due to high pH or unionized ammonia concentrations. Cooperman and Markle (*in review*) document the importance of emergent macrophyte habitats to larval suckers, and suggest limited access to this habitat type caused by low lake elevations may have a negative effect on larval sucker survival. However, larval survival is not expected to be highly correlated with year class success (Cowan and Shaw 2002) and correlations between year-class strength and lake elevation are not strong (NRC 2002), suggesting more complex recruitment dynamics.

Abundance of larval and spawning adult suckers was systematically monitored in UKL from 1995-2001. Here, we use larval trawl catch data to construct larval production estimates (LPE) (Heath 1993, Pepin 2002) for each year and each survey within a year. We examine relationships between annual LPE, spawning stock size, and environmental conditions, as well as between survey LPE and recent (three week) conditions. Results of the 1995-2001 analyses were used to construct estimates of larval production and survival from 1960 - 2001. We discuss potential mechanisms by

which environmental conditions might effect larval sucker production, survival, and year-class strength, and management implications of our results.

Study Location and Species

Upper Klamath Lake (UKL) is a large (23324 ha), shallow (average depth = 2.45m), natural lake lying in the rain-shadow east of the Cascade Mountains (Figure 1). Link River Dam, completed in 1921 as part of the US Bureau of Reclamation's Klamath Irrigation Project regulates outflow from UKL, and expanded the range of lake elevations and changed the timing of annual high and low water levels Markle and Cooperman 2002). UKL suffers from cultural eutrophication (Bortleson and Fretwell 1993, Snyder and Morace 1997), and is hypereutrophic (Kann 1997, Welch and Burke 2001). During summer algal blooms, lake water pH > 10.0 and dissolved oxygen <2 mg l^{-1} (Martin and Saiki 1999, Saiki et al. 1999).

Lost River suckers and shortnose suckers are long lived (maximum observed age: LRS: 43 yrs; SNS: 33 yrs), highly fecund (LRS: 44,000 - 236,000 eggs $female^{-1}$; SNS: 18,000-72,000 eggs $female^{-1}$), and iteroparous (Perkins et al. 2000). Sexual maturity occurs between 4-9 years of age. The suckers spawn in Spring in the lake or tributaries with most spawning occurring in the Williamson and Sprague rivers. Negatively buoyant eggs (ca. 3 mm diameter, unpublished data) are laid over gravel-cobble substrates (Buettner and Scoppettone 1990) and hatch in about 10 days. At hatching, Lost River suckers are 9.6-10.4 mm standard length (SL), and shortnose suckers are 7.0-9.6 mm SL (Hoff et al. 1997). Mean dry weight at hatching is roughly 700 μg (L. Dunsmoor, Klamath Tribes fishery biologist, unpublished data), approximately twice the 339 μg average dry weight for freshwater fish larvae (Houde and Zastrow 1993). Preflexion protolarvae are10-12 mm SL at swim-up from natal gravels and outmigrate to UKL typically within 1 day of swim-up (Cooperman and Markle 2003b).

Sucker larvae typically appear in UKL near the end of April and newly emerged suckers continue to recruit to the lake through June (Cooperman and Markle 2003b). In UKL, larval suckers are surface oriented and associated with emergent macrophytes in near-shore areas (Cooperman and Markle *in review*). The larval stage

ends approximately 45-55 days post-hatch, at about 22 mm SL, with absorption of the anal fin-fold and development of the full complement of fin rays (unpublished data). Although larval sucker growth rate is affected by water temperature (Terwilliger et al. 2002), field caught larvae average 0.25 mm day^{-1} (range 0.15-0.49, n=210, st. dev.=0.05; Terwilliger, unpublished data) and showed no significant size-specific growth rate differences over the 11-19.5 mm size range. Hoff et al. (1997) reported growth rates of 0.12 – 0.16 mm per day for hatchery- reared fish, but hatchery conditions at the time were believed sub-optimal (Dunsmoor, personal communication).

Methods

Adult spawning stock assessment

Between 1995 and 2001, US Geological Survey (USGS) or we have monitored abundance of adult suckers entering the Williamson River from UKL. Based on trammel net catch per unit effort data, an annual index of spawning stock size has been constructed for each year (Cunningham and Shively 2001). Because larval suckers currently cannot be confidently identified to species, we used a combined measure of Lost River and shortnose adult spawning stock size (adult index) as our measure of relative reproductive stock size each year.

Larval sampling

Between 1995 and 2001, we used a larval trawl (0.8 x 1.5 m opening with 2.5 m of 1000 *um* Nitex mesh netting and 15 m ropes attached to frame; La Bolle et al. 1985) to collect larval fishes from ten sites along the shoreline of Upper Klamath Lake (Figure 3). Each survey typically lasted four days with two samples collected per site. In 1995, surveys were two to three weeks apart beginning the first week of April and ending the last week of June (six surveys and 120 samples). From 1996 through 2001, surveys were consistently three weeks apart beginning the first ten days of April and ending the last ten days of July (six surveys and 120 samples). At each site, we set the trawl in water about 1 m deep, 3-13 m (avg. 6.2 m) off-shore, waited at least 15

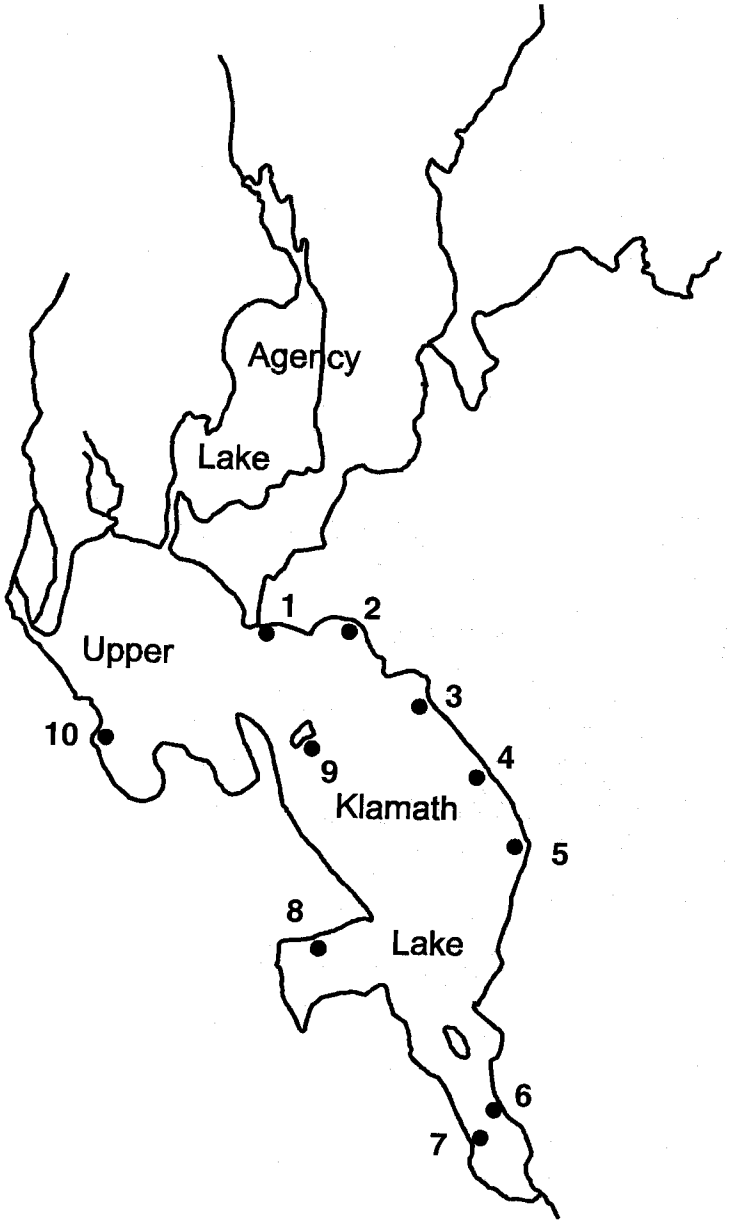

Figure 3. Larval trawl survey sites in Upper Klamath Lake.

minutes, and pulled the trawl to shore. When vegetated and unvegetated habitats were present, one sample was collected from each habitat. During each survey, sites were sampled in a variable order depending on logistic considerations such as wind direction and speed. All samples were collected during daylight hours, contents immediately preserved in 5-10% formalin, and transferred to 50% isopropanol, usually within 72 hours. Samples were sorted, and all larval suckers measured to nearest mm, usually within 1 to 4 weeks of collection.

Larval production estimate

Because larval mortality rates are so high, larval survey abundance estimates must be corrected for mortality. We constructed a larval production estimate (LPE) following the approach of Heath (1993) and Pepin (2002) and estimated larval mortality using the declining limb of the combined 1995-2001 larval length-frequency distribution (Figure 4). The LPE is an attempt to determine the number of 10 and 15 mm suckers required to produce a given size frequency distribution. For each size class, we back-calculated the number of 10 or 15 mm larvae required to produce the number in that size class given the estimated mortality rates, as: $\log(N_o) = \Sigma(\log(N_x) + MZ)$, where $\log(N_o)$ = estimated production of 10 or 15 mm larvae, $\log(N_x)$ = number of larvae in a mm size class, M = mortality rate of size group and Z = number of size classes between size class N_x and N_o. Mortality rate was based on linear regression of log transformed abundance for each size group, except that abundance of 10 mm larvae was not used in the regression of the smaller group. For 11-14 mm sucker larvae, the log-linear regression estimate of mortality per mm was 0.408 ($p = 0.0541$, $r^2 = 89.5\%$; Figure 4). For 15-19mm suckers, the log-linear regression estimate of mortality per mm was 0.316 ($p=0.0037$, $r^2 = 95.8\%$; Figure 4).

Results were back-transformed and summed to produce LPE10 and LPE15 for each sampling survey. We calculated a survival probability for a "cohort" as $LPE15_t/LPE10_{t-1}$, where t represents a survey and t-1 represents the prior survey, three weeks earlier. Survival probability was not calculated when $LPE10_{t-1}$ equaled zero. Graphical and text reference to data use an identification number based on the last two

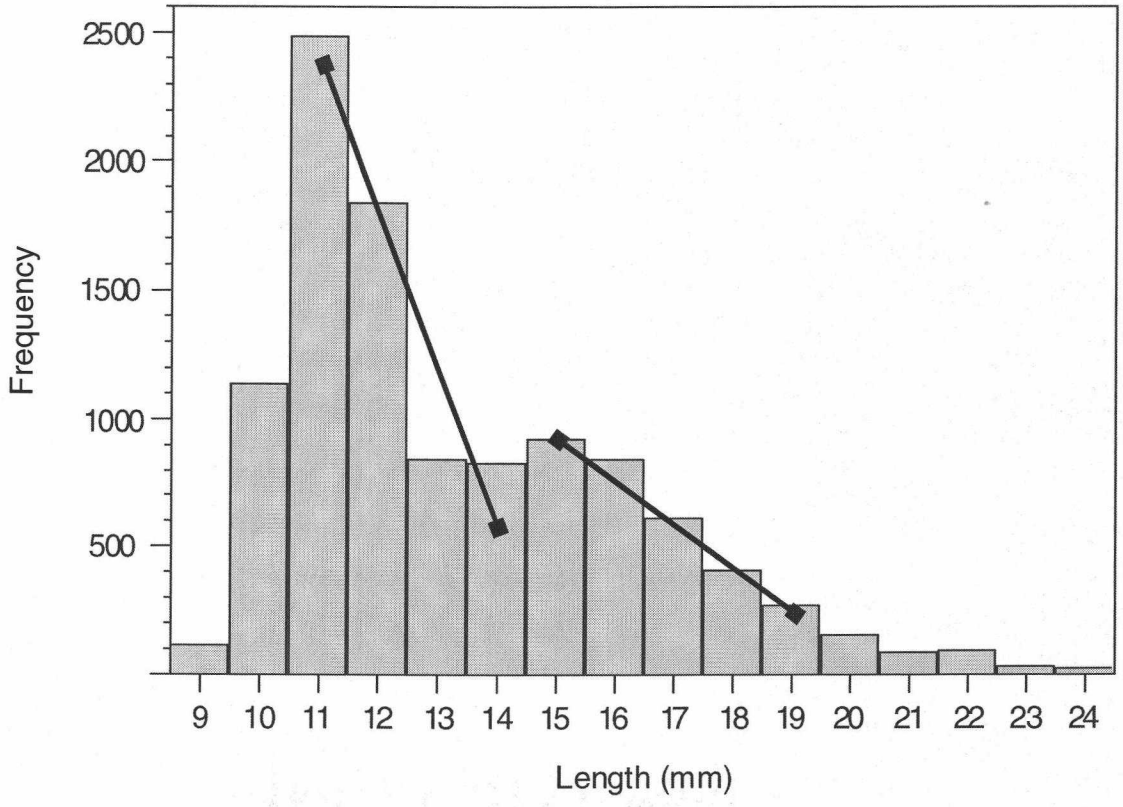

Figure 4. Size distribution of larval suckers from Upper Klamath Lake, 1995-2001. Lines illustrate regressions used to calculate mortality rates between 11-14mm (log Y = 12.297 - 0.408*X) and 15-19 mm (log Y = 11.685 - 0.316*X).

digits of the year of collection and the Julian day of collection, or, for survival probability, the midpoint Julian day of the two collections.

LPE assumes constant gear efficiency across the size range of targeted organisms, but confirmation of this assumption is often difficult to obtain (Pepin 2002). Concurrent sampling with a beach seine showed that size-specific densities were similar in each gear at 20 mm, suggesting that the larval trawl efficiency did not decline until sizes larger than 20 mm. Based on our three-week sampling interval and an estimated daily growth rate of about 0.25 mm (see above), we could estimate production of 10 mm larvae (LPE10) using the catch of 10-14 mm larvae and the production of 15 mm larvae (LPE15) using the catch of 15-19 mm larvae. Unless growth rates were dramatically different for a cohort, cohorts should not have been double-counted or missed using this approach.

Environmental variables

We obtained Williamson River daily mean discharge data for 1960-2001 from USGS river gage # 11502500, located in the Williamson River below the confluence with the Sprague River. All data had been internally reviewed and accepted by USGS (USGS data management personnel, personal communication).

We obtained hourly air temperature and wind speed for 1960-2001 for Kingsley Air Field, Klamath Falls, Oregon, from the National Climatic Data Center, Asheville, North Carolina. Kingsley Air Field is approximately five miles south of the southern terminus of UKL. Data were collected using the same methodologies from 1960-2001 and recorded as the mean during the first two minutes of each hour. We only used data collected between 1500 -2000 hrs, times corresponding to the hottest and windiest periods of the day (Cooperman, unpublished data). For air temperature, we used means and for wind speed we used means and proportions of low and high wind speed events. Proportion of low and high wind events were used because it is extreme events that are most likely to affect young fishes (Houde 1994, Ludsin and DeVries 1997). A low wind event was an hourly value of 0 km h^{-1} and a high wind event was an hourly value >16.1 km h^{-1} (10 m h^{-1}). Laenen and Letourneau (1996) report wind speeds of 10 m h^{-1} are sufficient to produce bottom shear stresses

sufficient to resuspend bottom sediments in UKL. Proportions were calculated as the number of high or low wind events relative to the total number of observations during a given time period. No air temperature or wind speed data were available for 1971 or 1972, so these years were excluded.

Volume of inundated emergent macrophytes (VIEM) is a function of lake elevation, but more directly tracks important habitat for larval suckers (Cooperman and Markle *in review*) than does lake elevation. VIEM (ft^3) was related to lake elevation (LE, in ft) from macrophyte distribution data from three areas near the mouth of the Williamson River (Tulana Farms, Goose Bay and lower Williamson, data in Dunsmoor, et al., 2000). The polynomial regression was

$$VIEM = 8.77995x10^{11} - 4.214247x10^{8}*LE + 51249.1*LE^2 \ (df = 43, p < 0.0001, r^2 = 99.9\%).$$

For 1995-2001 analyses, VIEM was calculated from daily mean lake elevation. For 1960-2001 analyses, VIEM was calculated from the daily mean lake elevation recorded every fifth day. US Bureau of Reclamation provided all lake elevation data and VIEM was converted to m^3 for subsequent analyses.

Analyses

We used analyses of 1995-2001 LPE data to determine the importance of environmental variables on larval sucker production and survival. The environmental matrix was Williamson River discharge, volume of inundated emergent vegetation, air temperature, proportion low wind events, and proportion high wind events. Environmental variables identified in those analyses were then used to project estimated larval sucker production and survival for 1960-2001.

1995-2001. We examined the relationship between larval sucker production or survival and environmental conditions during the three weeks prior to a survey using non-metric multi-dimensional scaling (PC-Ord version 4.0; Mather 1976). Because ordination of all surveys (n=42) and ordination of those in which survival probability could be calculated (n=29) were highly similar, we only present the later. Prior to ordination we tested for outliers in environmental space and removed cases greater than 2.0 standard deviations from the multivariate mean (McCune and Grace 2002).

The ordination incorporated Euclidean distance and the slow and through auto-pilot setting with random start configurations and 40 iterations. We compared results with real data to 40 runs per tested dimension with randomized data via Monte Carlo simulation to determine the best dimensionality for the final solution. We used survival probability as an overlay to illustrate patterns in the ordination. We also show a graphical relationship between survival probability and date. Summary statistics were calculated for four visually delineated groups and group differences evaluated using Bonferroni's multiple comparison (α=0.10).

We used backward, stepwise multiple linear regression (F = 3.0 to exit) to evaluate relationships between larval sucker production and survival and environmental variables. Data with leverages greater than three times the average were removed. We did not test for interactions. The first analysis was by annual LPE_{10} because adult monitoring determines the relative annual abundance of adult suckers that enter the Williamson River to spawn during each year, but does not determine the specific timing of spawning by individual adults. Independent variables were adult index, mean wind speed, mean air temperature, and VIEM. Environmental values were the mean condition between April 1 and June 30, representing the time immediately proceeding and during peak 10mm abundance.

Because adult index was not retained in the first analysis, we removed adult index and examined relationships between survey-specific LPE10 and Williamson River discharge, VIEM, air temperature, proportion low wind events, and proportion high wind events. Environmental parameters were averages calculated for the three week period prior to the last day of each LPE10 survey. We also related LPE15 to LPE10 of the prior survey, Williamson River discharge, air temperature, VIEM, and proportion low and high wind events. The latter analysis was restricted to comparisons where LPE10 was greater than zero. Environmental parameters were averages calculated for the three week period prior to the last day of each LPE15 survey. We also examined relationships of survival probability of a cohort ($LPE15_t/LPE10_{t-1}$) and the abundance of older larvae during the earlier survey ($LPE15_{t-1}$), VIEM, air temperature, proportion low and high wind events. Environmental conditions were the mean value observed during the three week period prior to the $LPE15_t$ survey.

Survival probability of a cohort was also examined with a discriminant function. Because mean survival probability was 0.18, we made two survival classes, those with survival probabilities <0.18 = '0' and survival probability ≥ 0.18 = '1.' Independent variables were mean air temperature, VIEM, proportion high and low wind events, Williamson River discharge and the abundance of older larvae during the survey ($LPE15_{t-1}$).

Trends in production and survival, 1960-2001. We used results from the 1995-2001 regressions and discriminant function to construct time series plots of predicted annual LPE10, LPE15 and survival probability for the period, 1960-2001. We used mean April - June conditions for environmental parameters affecting LPE10, mean June-July conditions for parameters affecting LPE15, and mean May-July conditions for parameters affecting survival probability. Annual residuals from the 40 year grand mean for each response variable (1960-2001, excluding 1971 and 1972) were smoothed with a five year moving average to identify long-term patterns.

Results

During April-July 1995-2001, we collected 10,181 larval suckers between 10-20 mm SL in 840 larval trawl samples during 42 surveys. The first survey each year, except 2000, collected zero 10-14 mm larvae. Twenty surveys collected zero 15-19 mm larvae. In no case was a positive LPE15 followed by a zero LPE15 later in the same year. There were 29 cases where a positive LPE10 was followed by a LPE15 survey three weeks later, yielding 29 three-week periods when survival of 10 mm larvae could be calculated. Mean three-week survival probability was 0.18, median was 0.04, and ranged from 0 (6 times) to 0.92 (7 Jun 00).

Larval production estimates, 1995-2001

The earliest positive LPE10 was 5 Apr 00 (Julian day 86; Figure 5), and LPE10 was consistently positive between Julian days 100 to 200 (Figure 5). The earliest positive LPE15 was 6 Jun 01 (Julian day 147; Figure 5), and LPE15 was consistently positive between Julian days 150-200 (Figure 5).

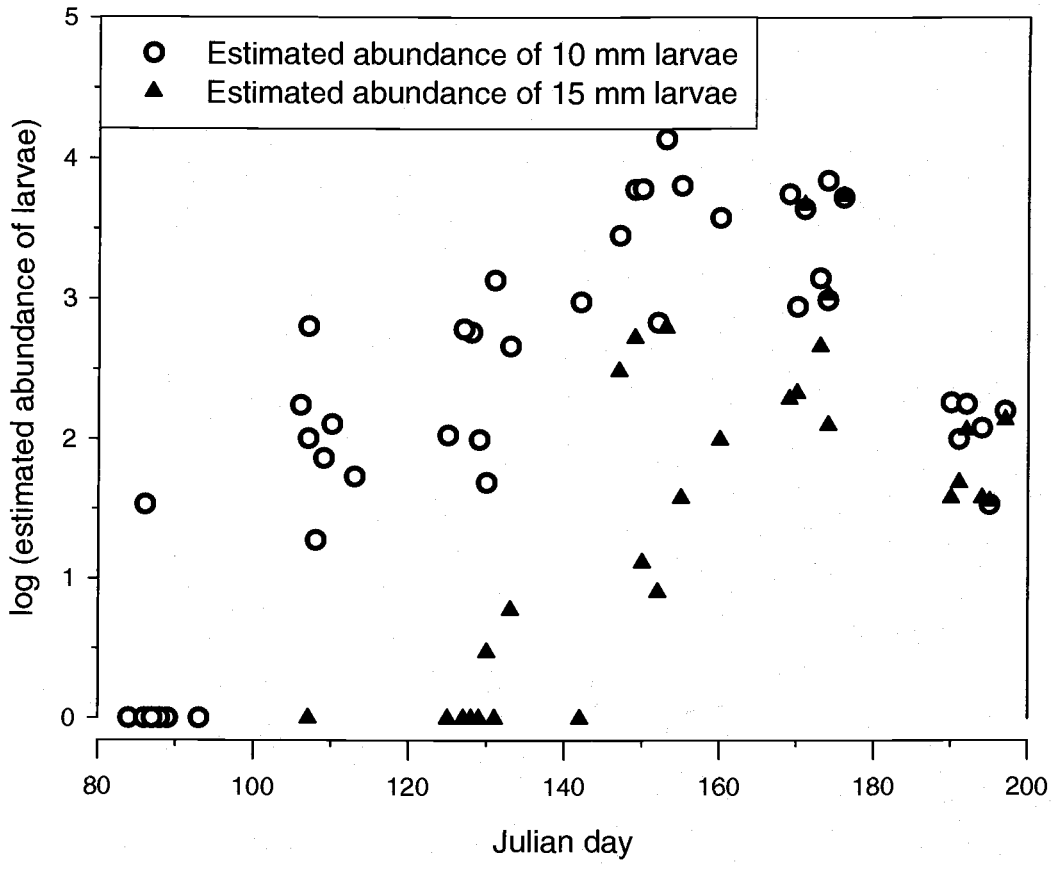

Figure 5. Estimated log abundance of 10 mm and 15 mm sucker larvae arranged by Julian day of survey for larval trawl samples collected 1995-2001.

Ordination

We selected a two dimensional non-metric multidimensional scaling ordination as the best fit for our survival probability data (Figure 6). One sample (ID 00-191; 3.75 standard deviations from multivariate mean) was removed as an outlier. The model required 67 iterations to produce a stable solution with final stress of 8.11 and final instability of 0.008. For ecological data, these values are highly acceptable (McCune and Grace 2002). Monte Carlo test results indicate our 2-D solution produced significantly less stress than expected by chance when compared to 40 runs with randomized data ($p = 0.0244$). The NMS solution had a relatively uniform distribution of data in each quadrant (Figure 6), indicating no unusually influential observations and relatively robust inference about the influence of environmental conditions on the production and survival of larval suckers in UKL.

Because the first axis was dominated by an early season to late season progression, we rotated the solution to maximize correlation of air temperature along the first axis. After rotation, axis 1 explained 66.2% of variance and maintained the seasonal progression. The left side of the first axis represented high Williamson River discharges, abundant emergent macrophytes, high winds and low air temperatures while the right end of the axis represented low river discharges, less emergent macrophytes, fewer high wind events, and higher air temperatures. Axis 2 explained 29.7% of the variance and was dominated by proportion low wind events. Survival probability was weakly correlated with both axes (axis 1: $r^2 = 0.213$; axis 2: $r^2 = -0.212$).

The relationship between survival probability and date indicated four groups (three with low survival in any season and one with high survival in mid-season; Figure 7). All seven surveys with survival probabilities >0.18 occurred between May 20 (Julian day 140) and June 29 (day180), but 8 surveys that fell within this range had values <0.18. All samples collected outside the 140-180 Julian day range had survival probabilities <0.18. None of the measured environmental parameters were significantly different between the middle season-low survival and middle season-high survival groups (Table 1), although statistical power for these comparisons was low, ranging from 0.182 to detect a difference of 1000 m^3 in volume of emergents

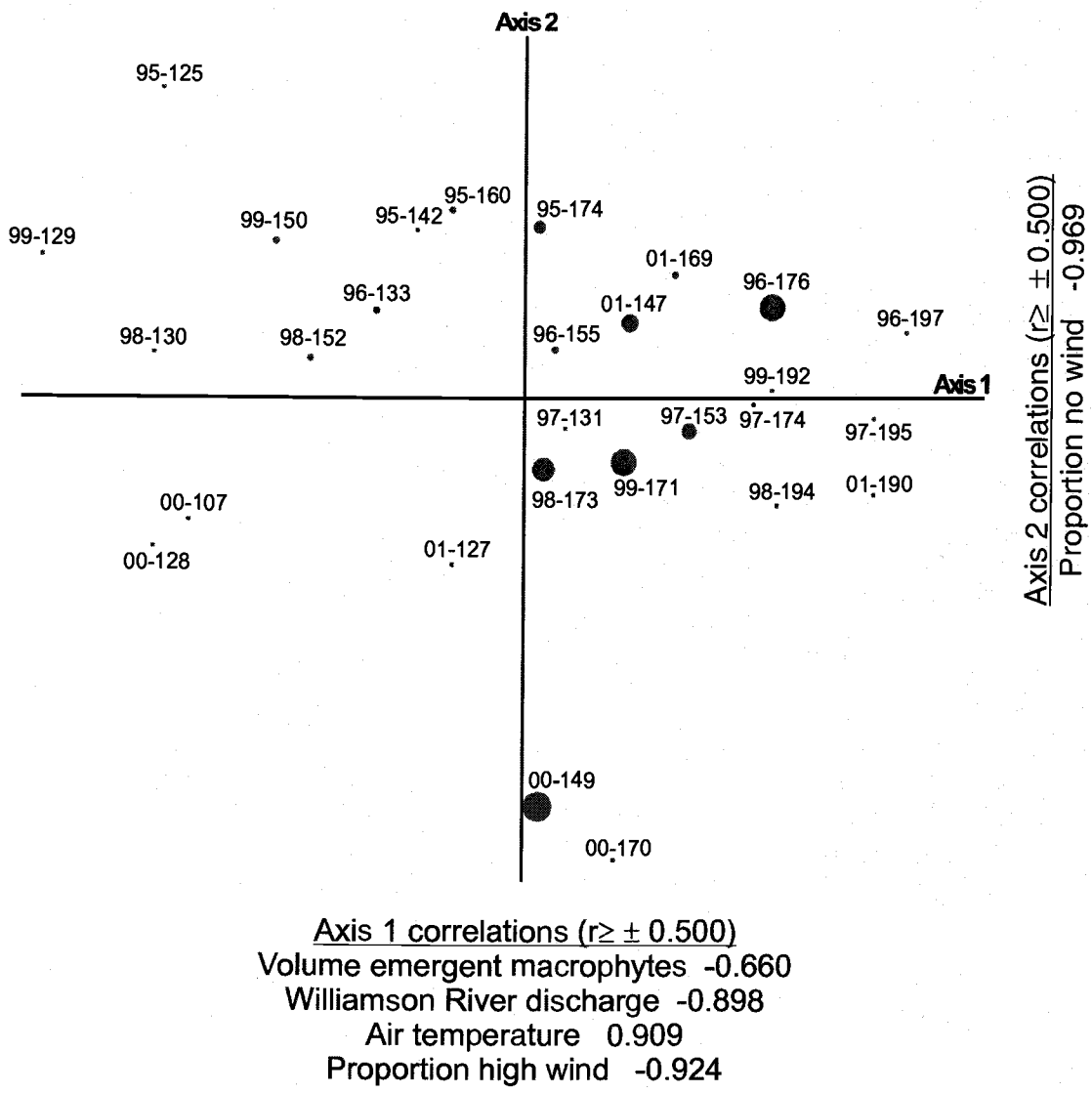

Figure 6. Two dimensional non-metric multidimensional scaling ordination of 28 larval trawl surveys based on mean environmental conditions during the three week period ending on date of sample collection. Solution was rotated to maximize correlation of air temperature along the first axis. First two digits of labels are year sample was collected, last three digits are the mean Julian day of the three week period. Symbol size is proportional to survival probability. Survival probability correlation on axis 1 was 0.213 and for axis 2 was –0.212. Axis 1 depicts an early season to late season gradient and explains 66.2% of variance. Axis 2 is dominated by a proportion no wind gradient and explains 29.7% of variance.

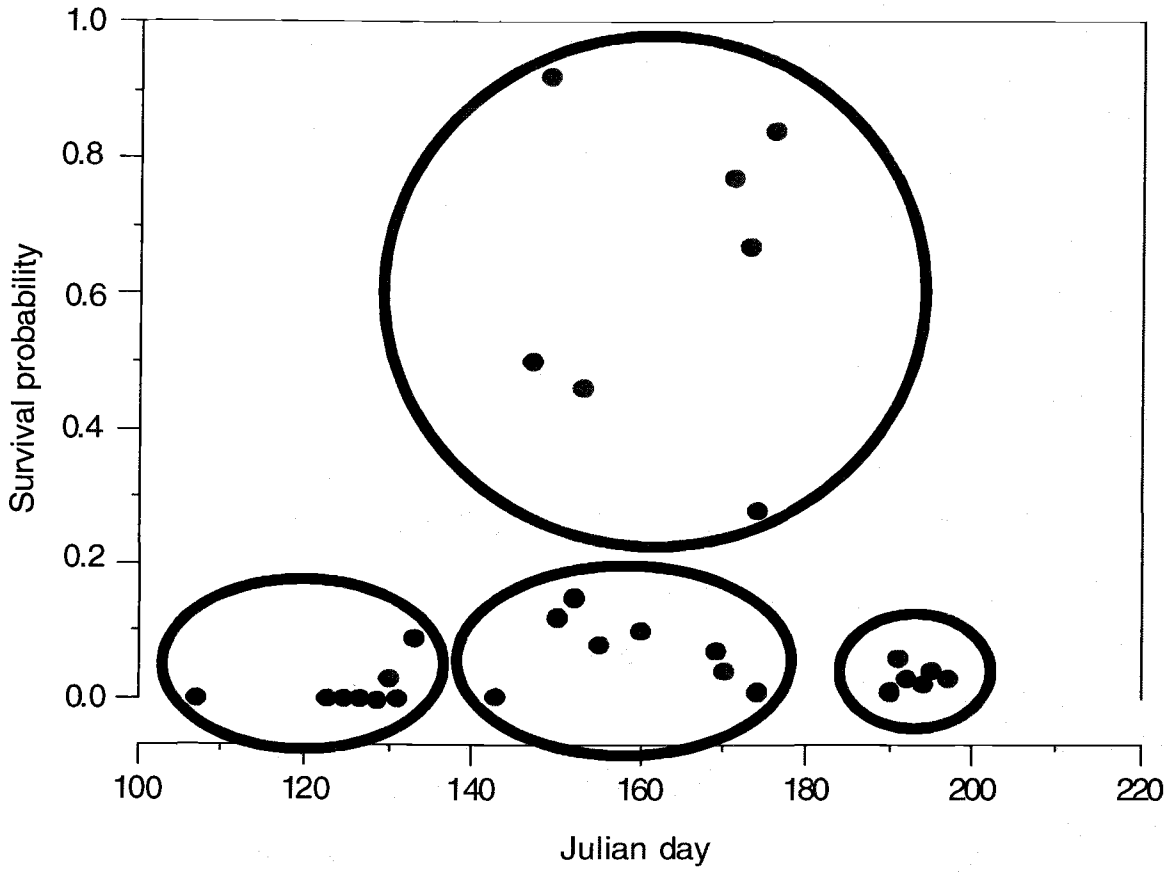

Figure 7. Proportion of 10 mm sucker larvae surviving to 15 mm, arranged by the mean Julian day of the three week window between $LPE10_{t-1}$ and LPE15 surveys (n=29 samples). Four groups (early season-low survival, middle season-low survival, middle season-high survival, late season-low survival) are circled and summary statistics for each group are presented in Table 1.

Table 1. Mean and standard deviation of measured parameters partitioned by season-survival cluster. Superscripts depict statistically different groups identified by Bonferroni's multiple comparison procedure ($\alpha = 0.10$).

Parameter	Early season - low survival (n=8)	Middle season - low survival (n=8)	Middle season - high survival (n=7)	Late season - low survival (n=6)
Julian day	126.3^{A}	159.0^{B}	163.3^{B}	193.2^{C}
$LPE10_{t-1}$	$151\ (201)^{A}$	$3023\ (4779)^{A}$	$2778\ (2608)^{A}$	$3062\ (2210)^{A}$
$LPE15_{t-1}$		$183.1\ (265.8)^{A}$	$22.0\ (36.0)^{A}$	
LPE15	$1\ (2)^{A}$	$86\ (85)^{A}$	$1863\ (2185)^{B}$	$68\ (46)^{A}$
Proportion surviving	$0.02\ (0.03)^{A}$	$0.07\ (0.05)^{A}$	$0.64\ (0.23)^{B}$	$0.03(0.02)^{A}$
UKL elevation (m)	$1263.61\ (0.07)^{A}$	$1263.54\ (0.13)^{A}$	$1263.58\ (0.09)^{A}$	$1263.28\ (0.14)^{B}$
Volume emergent macrophytes inundated (m^3)	$22212\ (2674)^{A}$	$19968\ (4259)^{A}$	$20997\ (3101)^{A}$	$11750\ (3904)^{B}$
Williamson River discharge ($m^3\ s^{-1}$)	$59.5\ (19.6)^{A}$	$41.5\ (24.0)^{AB}$	$31.4\ (10.2)^{B}$	$17.6\ (4.9)^{B}$
Air temperature (^{o}C)	$10.8\ (3.1)^{A}$	$16.0\ (2.2)^{B}$	$17.4\ (1.8)^{B}$	$21.8\ (1.9)^{C}$
Wind speed ($km\ h^{-1}$)	$13.0\ (2.7)^{A}$	$11.2\ (2.1)^{AB}$	$9.4\ (1.6)^{BC}$	$7.2\ (1.5)^{C}$
Proportion no wind	$0.14\ (0.08)^{A}$	$0.12\ (0.12)^{A}$	$0.15\ (0.11)^{A}$	$0.21\ (0.18)^{A}$
Proportion high wind	$0.38\ (0.13)^{A}$	$0.24\ (0.09)^{B}$	$0.16\ (0.08)^{BC}$	$0.05\ (0.03)^{C}$

inundated, to 0.592 to detect an air temperature difference of 1.5 °C. A regression analysis of samples within the 140-180 day range was very different from the analysis with all data (eq. 5), but equally noisy:

1) Survival probability = 0.89 - 0.13*log($LPE15_{t-1}$+1) - 2.10 proportion high wind events (n = 15, F = 3.50, p = 0.0634, r^2adj = 26.3%).

Regression analyses, 1995-2001

Annual LPE10 was positively related to air temperature and VIEM:

2) log(LPE10+1) = -1.50 + 0.25*air temperature + 0.00008*VIEM (n = 7, F = 21.6, p = 0.0072, r^2adj = 87.3%)

The spawning stock size (adult index) had no influence on LPE10 (component p = 0.90). Two unusually influential years, 1998 and 2001, were not excluded due to small sample size. Unusually low April-June air temperatures characterized 1998 and unusually low April-June VIEM characterized 2001. The last parameter excluded was mean wind speed (F = 0.008), and its exclusion did not affect r^2.

Survey LPE10 was also positively related to air temperature and VIEM:

3) log(LPE10+1) = -2.91 + 0.18*air temperature + 0.00015*VIEM (n = 38, F = 46.2, p < 0.0001, r^2adj = 70.9%)

Four surveys were unusually influential (ID: 97-195, 98-194, 99-87, 01-169), and were excluded. Their inclusion did not change the parameters included in the model nor the p value, but reduced r^2adj to 60.6%. The last parameter excluded was proportion high wind events (F = 0.30), and its exclusion did not affect r^2.

Survey LPE15 was positively related to prior survey LPE10 and VIEM and negatively related to high wind events:

4) log(LPE15+1) = -3.18 + 1.27*log($LPE10_{t-1}$+1) + 0.0001*VIEM - 2.42*proportion high wind events (n = 25, F = 22.15, p < 0.0001, r^2adj = 72.6%)

Four surveys were unusually influential (ID: 97-131, 97-174, 99-129, 00-128) and were excluded. Their inclusion simplified the model by removing VIEM and proportion high wind events and left $LPE10_{t-1}$ as the only parameter (p = <0.0001, r^2adj = 58.8%).

Survival probability was positively related to VIEM and air temperature but the relationship was very noisy:

5) Survival probability = -0.65 + 0.000021*VIEM + 0.023*air temperature (n = 26, F = 3.24, p = 0.0569, r^2adj = 14.7)

Three-week survival probability ranged from 0 – 92% and average annual three-week survival ranged from 6-10% (1995, 1997, 2001) to 15-17% (1996, 1998, 1999, 2000). Two surveys were unusually influential (ID: 96-176 and 00-149) and were removed. They had the highest survival probabilities observed (84 and 92%, respectively), intermediate VIEM values and air temperature, and below average proportion high wind events. Log($LPE15_{t-1}$) was the last parameter excluded from the solution (F to remove = 0.74), but its inclusion did not affect solution r^2adj. Inclusion of the two influential samples modified the model by removing the effects of VIEM and air temperature and yielding a positive relationship with $LPE15_{t-1}$ and a negative relationship with proportion high wind, although the relationship remained noisy (p=0.0428, r^2adj = 21.5%).

Discriminant function analysis

A single discriminant function indicated that survival probability was positively associated with VIEM and negatively associated with high wind events:

6) 1.173*VIEM - 1.187 proportion high wind events (Wilks lambda = 0.79, p = 0.0472)

The function correctly classified 72.4% of the 29 cases (low survival class 0: 16 of 22 correct and high survival class 1: 5 of 7 correct).

Time series analysis, 1960-2001

Early season (April - June) air temperatures were lower than the long-term average from 1960 to 1984 and above average from 1984 to 2001(Figure 8a). The hottest early seasons were 1987 and 1992 and the coolest were 1964, 1968, and 1991. Early season volume of emergents was below the long-term average through the 1960's and early 1970's, near average in the late 1970s, and consistently above average in the 1980s (Figure 8b). Emergent volume was more variable in the 1990s,

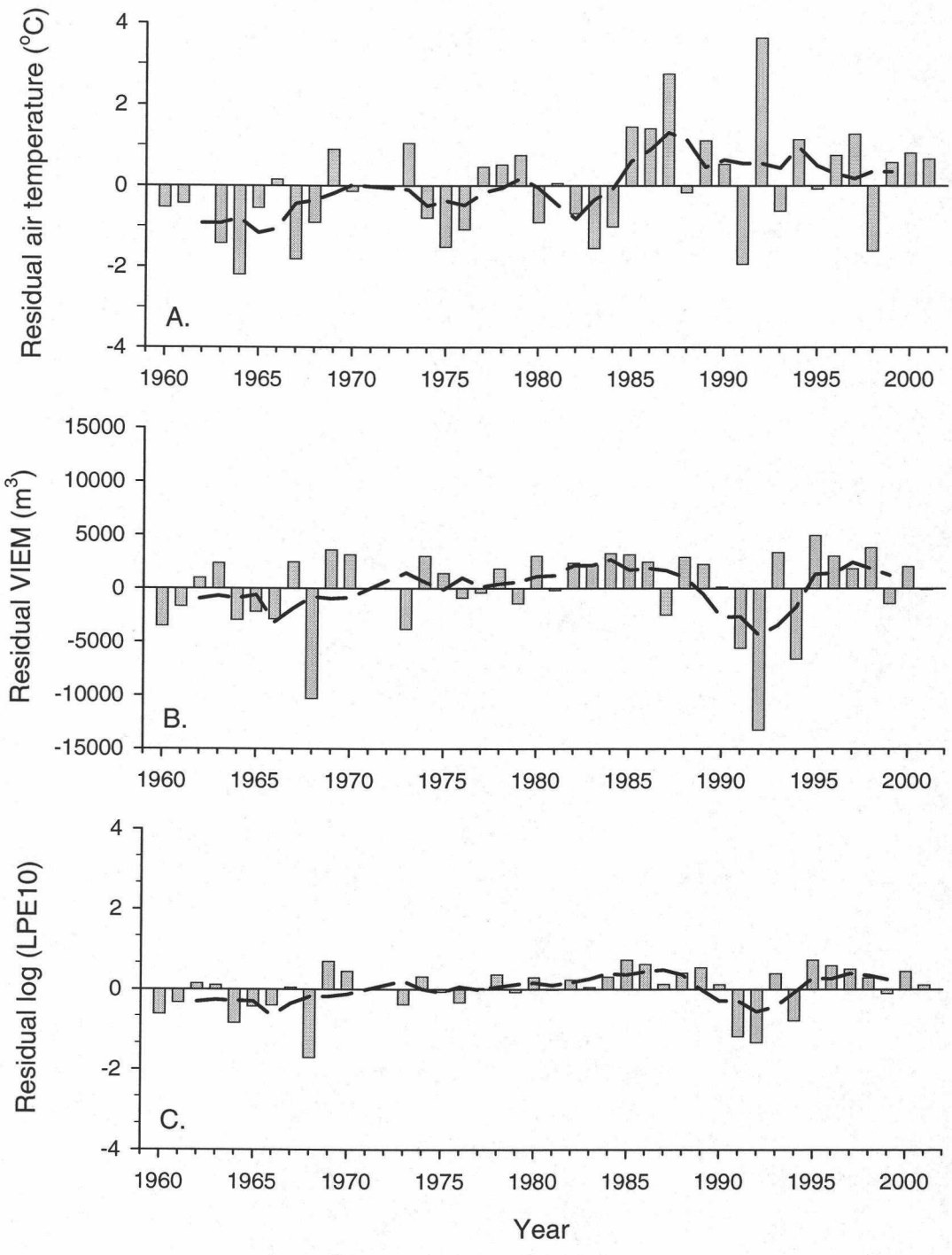

Figure 8. Forty year (1960-2001, excluding 1971-2) plots of residual April-June conditions for parameters that influenced LPE10. Panel A is air temperature, Panel B is VIEM, and Panel C is LPE10 based on regression equation log(LPE10) = -2.91 + 0.18 air temperature + 0.00015 VIEM. Dashed lines are 5 point moving average smoothes.

with the lowest levels observed during the 41-year period occurring in the first half of the 1990s and above average values between 1995 and 2001. The early season volume of emergents was lowest in 1968 and 1992. Somewhat distinctive transitions between below and above average trends occurred in 1974-5, 1990-91, and 1994-5.

Annual LPE10 projections, based on equation 3, followed the same pattern as early season VIEM (Figure 8c). Projections were below average in the 1960s, near average in the 1970s, and above average in the 1980s and 1990s except for a large dip in the early 1990s. The lowest projected LPE10 occurred in 1968, closely followed by 1991, 1992, and 1994. There were no unusually high LPE10 projections.

The frequency of late season (June-July) high wind events was low in the 1960's, 1970's, and after 1995, while the period from 1980-1995 had above average frequencies of high wind events (Figure 9a). The windiest late season was 1984, while the 1960's tended to be years with the lowest winds. Late season VIEM between 1960 and 2001 was highly variable and without an obvious long term trend, although the 5-yr trend line passed through the long term mean approximately every 4-7 years (Figure 9b). Lowest late season emergent volumes occurred in 1968, 1992, and 1994, and numerous years had relatively high volumes, especially 1975 and 1982. The annual LPE15 projections, based on equation 5, were relatively constant except for the 1990's when variation increased substantially (Figure 9c).

Projected survival probability to 15 mm, based on equations 5 and 6 suggests survivorship was below average in the 1960's and early 1990's and above average in the 1970's, 1980's and late 1990's (Figures 10a and b).

Discussion

Larval production estimate

The larval production estimate method (Heath 1993, Pepin 2002) was developed for the management of commercially exploited marine fishes (Heath 1993, Liang and Bjoerke 1997), and this study appears to be the first application to at-risk freshwater fishes. The method depends on a reasonable estimated mortality rate. Our estimated mortality rates (M=0.408 for 11-14 mm; M=0.316 for 15-19 mm; Figure 4)

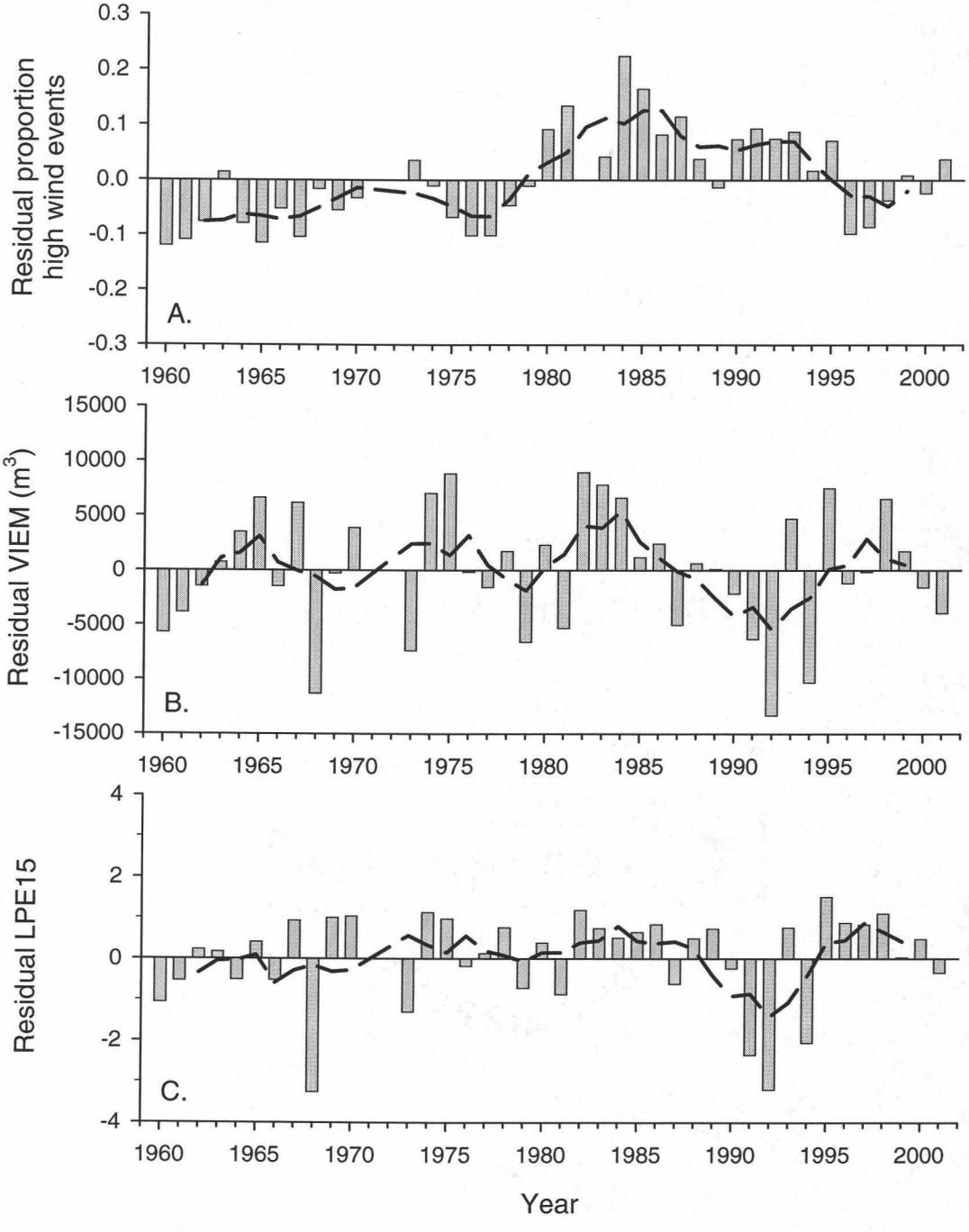

Figure 9. Forty-year plots of residual mean June-July conditions for parameters found to influence LPE15. Panel A is proportion high wind events, Panel B is VIEM, and Panel C is LPE15 based on regression equation log(LPE15+1) = -3.18 + 1.27*log(LPE10 $_{t-1}$+1) + 0.0001*VIEM – 2.42*proportion high wind events. Dashed lines are 5 point moving average smoothes.

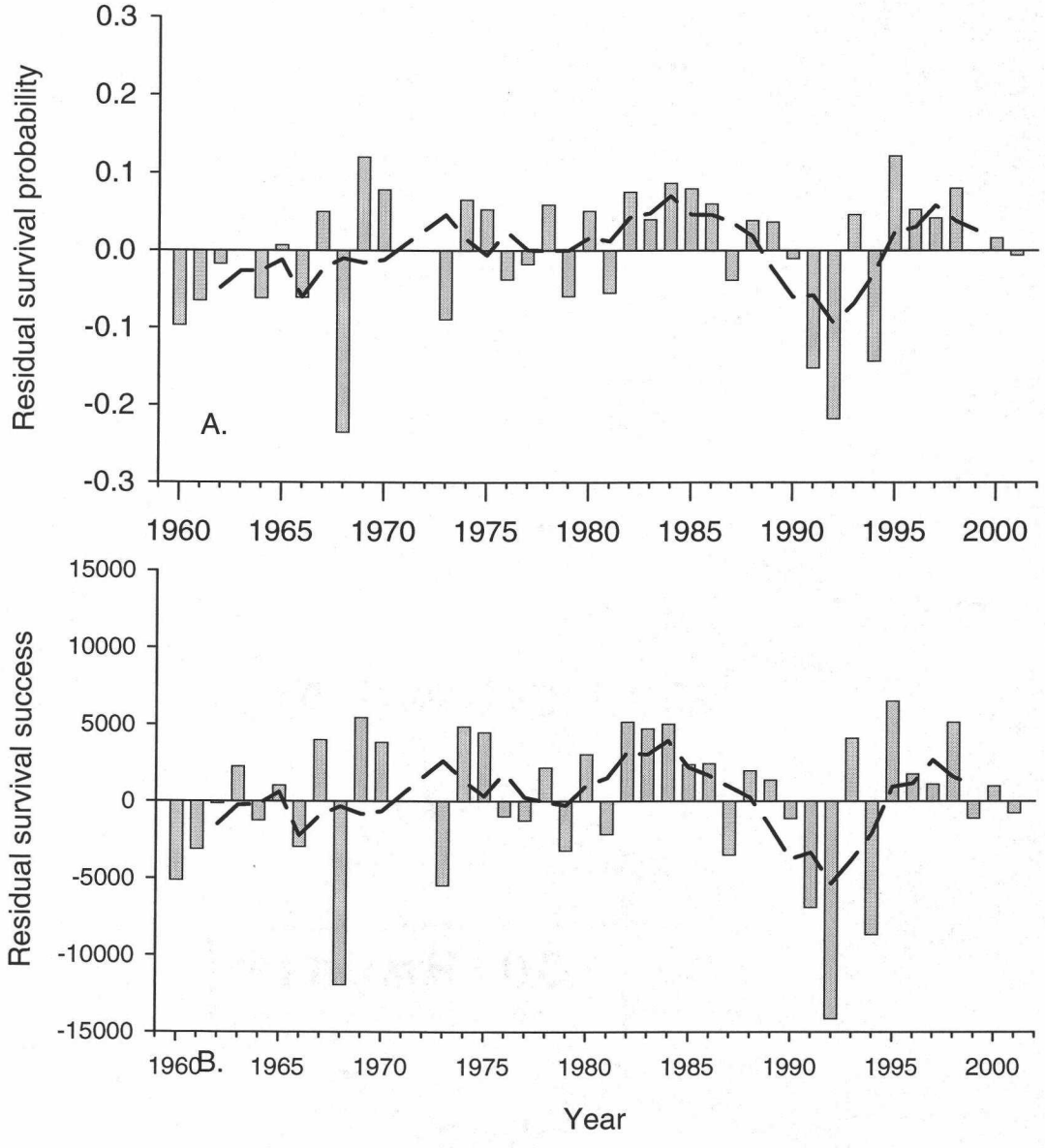

Figure 10. Forty-year trends in survival probability based on May-July mean conditions of each year. Panel A presents results of regression equation Survival probability = -0.65 + 0.000021*VIEM + 0.023*air temperature. Panel B is the estimated magnitude of survival success based on the discriminant function Survival probability = 1.173*VIEM – 1.187 proportion high wind events. Dashed lines are 5 point moving average smoothes.

equate to daily instantaneous mortality rates of 0.102 (equal to 6.2% mortality day^{-1}) for 11-14 mm suckers and 0.079 (equal to 4.8% mortality day^{-1}) for 15-19 mm suckers (assuming a growth rate of 0.25 mm/d). These mortality rates are comparable to reported values for other species (Table 2), and in-line with expectation, given the relatively large size of sucker larvae and the lower rates expected of larger larvae (Houde and Zastrow 1993, Houde 2002).

1995-2001 larval trawl samples

Unconstrained multivariate ordination, linear regression, and discriminant function analyses gave complementary results and indicated air temperature, availability of emergent macrophytes and proportion of high wind events, interacted to strongly influence the production and survival of larval suckers in Upper Klamath Lake (UKL). Larval sucker survival is unlikely to be a response to any one of these parameters working in isolation from the others, as there were no significant differences within parameters between mid-season surveys with good and bad survival (Table 1). Williamson River discharge, low wind events, and the abundance of adult suckers spawning during a year were not significant influences on larval sucker abundance or survival.

Air temperature was positively associated with LPE10 (eqs. 2 & 3). In the UKL system, sucker eggs are subjected to high levels of predation by flatworms and possibly fishes (USFWS 2001). Our data suggest warmer temperatures might accelerate egg development, shorten this window of mortality and affect initial abundance of 10 mm larvae in the lake. Warmer temperatures may reduce this mortality directly through shorter stage duration or indirectly through a correlated variable. The consistent lack of correlations between numbers of eggs and numbers of yolk sac larvae (Cowan and Shaw 2002) suggests that highly variable egg to larvae mortality may be the norm.

Air temperature was also positively associated with survival probability (eq. 5). Recently hatched sucker larvae are probably vulnerable to high levels of starvation, predation, physical damage, and/or transport away from nursery grounds (USFWS 2001, Cooperman and Markle 2003b, Cooperman and Markle *in review*). Larval

Table 1. Mean and standard deviation of measured parameters partitioned by season-survival cluster. Superscripts depict statistically different groups identified by Bonferroni's multiple comparison procedure ($\alpha = 0.10$).

Parameter	Early season - low survival (n=8)	Middle season - low survival (n=8)	Middle season - high survival (n=7)	Late season - low survival (n=6)
Julian day	126.3^{A}	159.0^{B}	163.3^{B}	193.2^{C}
$LPE10_{t-1}$	151 (201)^{A}	3023 (4779)^{A}	2778 (2608)^{A}	3062 (2210)^{A}
$LPE15_{t-1}$		183.1 (265.8)^{A}	22.0 (36.0)^{A}	
LPE15	1 (2)^{A}	86 (85)^{A}	1863 (2185)^{B}	68 (46)^{A}
Proportion surviving	0.02 (0.03)^{A}	0.07 (0.05)^{A}	0.64 (0.23)^{B}	0.03(0.02)^{A}
UKL elevation (m)	1263.61 (0.07)^{A}	1263.54 (0.13)^{A}	1263.58 (0.09)^{A}	1263.28 (0.14)^{B}
Volume emergent macrophytes inundated (m^3)	22212 (2674)^{A}	19968 (4259)^{A}	20997 (3101)^{A}	11750 (3904)^{B}
Williamson River discharge ($m^3\ s^{-1}$)	59.5 (19.6)^{A}	41.5 (24.0)^{AB}	31.4 (10.2)^{B}	17.6 (4.9)^{B}
Air temperature (^{o}C)	10.8 (3.1)^{A}	16.0 (2.2)^{B}	17.4 (1.8)^{B}	21.8 (1.9)^{C}
Wind speed ($km\ h^{-1}$)	13.0 (2.7)^{A}	11.2 (2.1)^{AB}	9.4 (1.6)^{BC}	7.2 (1.5)^{C}
Proportion no wind	0.14 (0.08)^{A}	0.12 (0.12)^{A}	0.15 (0.11)^{A}	0.21 (0.18)^{A}
Proportion high wind	0.38 (0.13)^{A}	0.24 (0.09)^{B}	0.16 (0.08)^{BC}	0.05 (0.03)^{C}

sucker growth rate is highly correlated with water temperature (Terwilliger et al. 2003), and water temperature in UKL is highly correlated with air temperature (Markle, unpublished data). Again our data suggest warmer temperatures reduce stage duration and increase probability of surviving.

Air temperature was not positively associated with LPE15 (eq. 5), except indirectly through the influence of LPE10. Terwilliger et al. (2003) found non-linear growth - temperature relationships with young-of-year suckers showing reduced growth above 22°C when dissolved oxygen was below 4mg L^{-1}. Although LPE15 was not strongly related to air temperature over the full range of temperatures experienced ($df = 21$, $p = 0.091$, $r^2adj = 13.6\%$) (unpublished data), at air temperatures <21°C, LPE15 was positively related to air temperature ($df = 15$, $p = 0.003$, $r^2adj = 44.2\%$), suggesting decoupling of the temperature – growth relationship may partly explain the absence of a stronger relationship. The interaction or cross-correlation of other variables with the temperature-growth relationship may also have affected our results. For example, when air temperatures were highest, VIEM was at its lowest, and limited habitat availability may restrict LPE15 values (Eq. 4, Figure 11). In total, most of our analyses are consistent with the stage duration hypothesis (Houde 1987, Cowan and Shaw 2002), which postulates subtle changes in the growth rates of early life stages can result in large changes in abundance because faster growing individuals more quickly progress out of the size range with the highest mortality rate. Our expectation is that warm water temperatures up to about 22°C have benefits for larval suckers through increased growth, reduced stage duration and subsequent reduced mortality.

Emergent macrophytes are the primary habitat for larval suckers within UKL (Cooperman and Markle *in review*), and VIEM was positively related to LPE10, LPE15, and survival probability. Larval suckers in emergent macrophytes are larger and better fed than those in other habitats (Cooperman and Markle *in review*), and may experience protection from predators and protection from physical harm or displacement (Heck and Thoman 1981, Dibble et al. 1996, Weaver et al. 1997). The positive association between habitat volume, and abundance and survival might suggest a density-dependant relationship. In partial support, analysis (eq. 1) of samples collected during peak larval abundance (days 140 to 180) indicated a negative

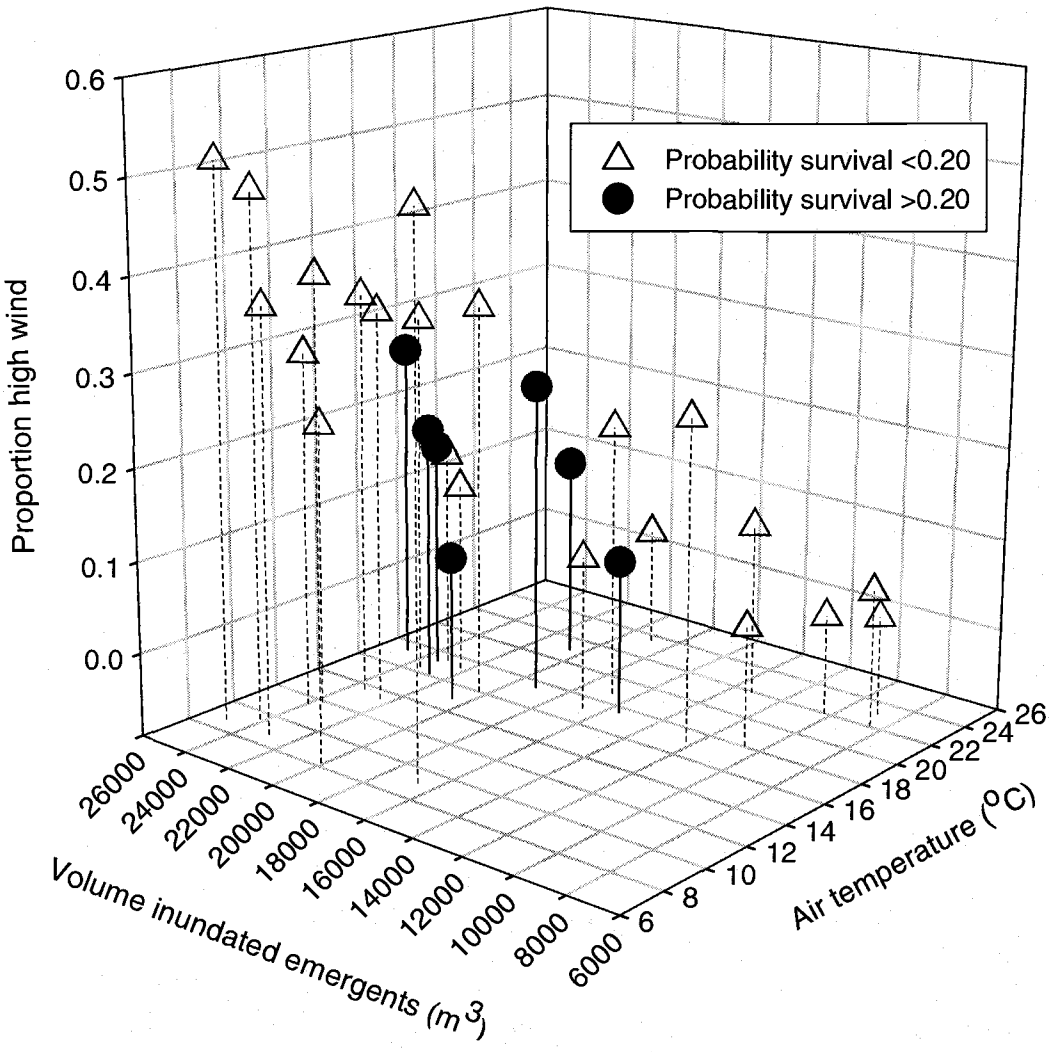

Figure 11. Three-dimensional plot of larval sucker survival probability organized by VIEM, air temperature, and proportion of high wind events.

relationship between survival and $LPE15_{t-1}$, suggesting the abundance of older larvae had a negative influence on survivorship of younger larvae. However, Cooperman and Markle (*in review*) found no evidence of density dependant effects in a more detailed study of habitat use.

Proportion high wind events was negatively associated with LPE15 and survival probability. High wind speeds produce turbulence and wind speeds of 16.1 km hr^{-1} (10 m hr^{-1}), our definition for a high wind event, are sufficient to suspend bottom sediments from 75% of the UKL bed at a lake elevation of 1261.87 m (4140.00 ft) (Laenen and Le Tourneau 1996). High winds and resulting wave energy can reduce larval fish survival via physical damage (Werner and Anholt 1993), dispersal from rearing grounds (Sinclair 1988), and reduce foraging success via the breakdown of prey accumulations, decreased visual acuity, or reduced capture efficiency (Lasker 1981, Wroblewski et al. 1989). Our regression restricted to the high survival period, days 140 to 180, indicated abundance of 15 mm larvae ($LPE15_{t-1}$) in the prior sample and high wind events had negative effects on survival probability. Though the relationship was not strong (r^2adj =26.3%), the negative relationship between $LPE15_{t-1}$ and survival probability suggests a density-dependant interaction, such as competition, may also limit survival even when environmental conditions are good. Our analyses are consistent with the "stable ocean" hypothesis, a key concept in understanding marine clupeid and engraulid larval dynamics. Its application to a lake and to similar-sized, elongate larvae seems logical but needs further testing.

Temperature, VIEM, and wind follow predictable seasonal patterns during the larval production cycle, as evidenced by axis 1 of the NMS ordination (Figure 6). However, the effects of the three parameters on larval suckers are not synchronized seasonally (early season: low air temperature and high winds (negative) and high VIEM (positive); late season: high air temperatures and low winds (positive) and low VIEM (negative)). The opposing seasonal trends appear to create a variable window of good survival. A three dimensional plot illustrated that survival probabilities were consistently low at air temperatures less than 13°C or above 22°C, at emergent volumes less than 15,000 m^3 (equivalent to a lake surface elevation of 1262.573 m (4142.30 ft)), or with proportion high wind events greater than 0.28 (Figure 11). When

all three parameters were simultaneously outside those values, survival probabilities were >20% in 7 of 11 cases and no survival probabilities were >20% when any one parameter was not in the acceptable range. The window of opportunity is also evident in the NMS solution, as all samples with survival probabilities >0.20 are localized in a narrow band along axis 1 slightly to the right of axis 2 (Figure 6).

Each of the seven years of the study period contained one three-week period when conditions were simultaneously within the acceptable range for good survival and survival was greater than 20%. Although our data indicate good conditions for survival appear annually, interannual variation in the best survival rate in a year is about 3-fold, 28-92% (Figure 7) as is the average annual rate (6-17%). Further, the four three-week periods within the window of good conditions but with survival below 8% (96-155 = 0.08, 97-131=0.00, 97-174=0.01, 00-170=0.04), combined with the absence of strong correlation between survival and the ordination axes (axis 1 r^2 = 0.2132, axis 2 r^2 = -0.212), suggests additional factors to those evaluated in this study may influence larval sucker survival.

Our habitat - larval relationships might be an artifact of the temporal auto-correlation between date, sucker abundance, and weather conditions. Because air temperature and high wind events are correlated with date ($p<0.00001$), there could be spurious relationships that simply reflect date. However, restricting analyses to only samples with >500 larvae, effectively reducing the influence of seasonal progression, yielded highly similar results (Cooperman, unpublished data).

Time series analysis

There were similar long term trends in air temperature and proportion high wind events with cooler and calmer weather in the 1960s and early 1970s, a transition in the mid-1970's, and warmer and windier weather in the late 1970's through early 1990's (Figures 8a and 9a). Early season VIEM was generally high in the 1970's and 1980's and more variable in the 1960's and 1990's (Figure 8b). Late season VIEM was more variable with some multi-year trends such as the high volumes in the early 1980's and low volumes in the early 1990's (Figure 9b). Complex, long-term trends in VIEM might be expected given the added variability of irrigation needs. However,

Williamson River discharge data showed similar multi-year trends such as high discharge in the early 1980's and lower discharge in the late 1980's and early 1990's (Figure 12a).

These weather patterns, particularly transitions around 1975-6 and 1995-6 and anomalies around 1982-3, are similar in timing to events in the northeast Pacific Ocean. Ocean regime shifts are thought to have occurred in 1975-6 and 1995-6, and a strong ENSO event in 1982-3 (Zebdi and Collie 1995, Koslow et al. 2002, Chavez et al. 2003). The relationship between Klamath basin weather, particularly wind speed, and northeast Pacific Ocean conditions is illustrated by the similarities between forty year trends in Klamath Basin weather and the Bakun Index, a measure of upwelling strength off the coast of Oregon (Figures 8, 9, and 12). Additionally, for 1995-2000, the May-July mean Bakun Index was positively correlated with annual larval sucker survival probability (i.e., the mean of the three-week survival probabilities within a year; $n = 6$, $r^2adj = 80.3\%$, $p = 0.0156$) (Cooperman, unpublished data). Only 2001 did not fit the pattern, with the highest Bakun Index value of the seven years but the third lowest annual survival (Bakun Index = 149.0, mean survival probability = 0.15).

Predicted LPE10, LPE15, and survival probability trends were below the long-term average in the 1960s and 1990s and above average during the 1970s and 1980s (Figures 8c, 9c, 10a and b), but, the age structure of adult UKL suckers indicates strong year classes in the 1960's and early 1990s and weak year classes in the 1970's and 1980's (Figure 2), years when inter-annual variability was lower (Figures 8c and 9c). Thus, year class strength does not appear to be correlated to events during the first three weeks of larval residence in Upper Klamath Lake. Further, our data suggest a negative relationship between good larval conditions, such as warm early season temperatures, and subsequent recruitment. If Upper Klamath Lake sucker year classes are not established until the juvenile stage, it would be consistent with most freshwater fishes, particularly those with larger than average hatch sizes (Houde 1994), but somewhat atypical of highly fecund freshwater fishes that provide low levels of parental care (Diana 1995, Ludsin and DeVries 1997).

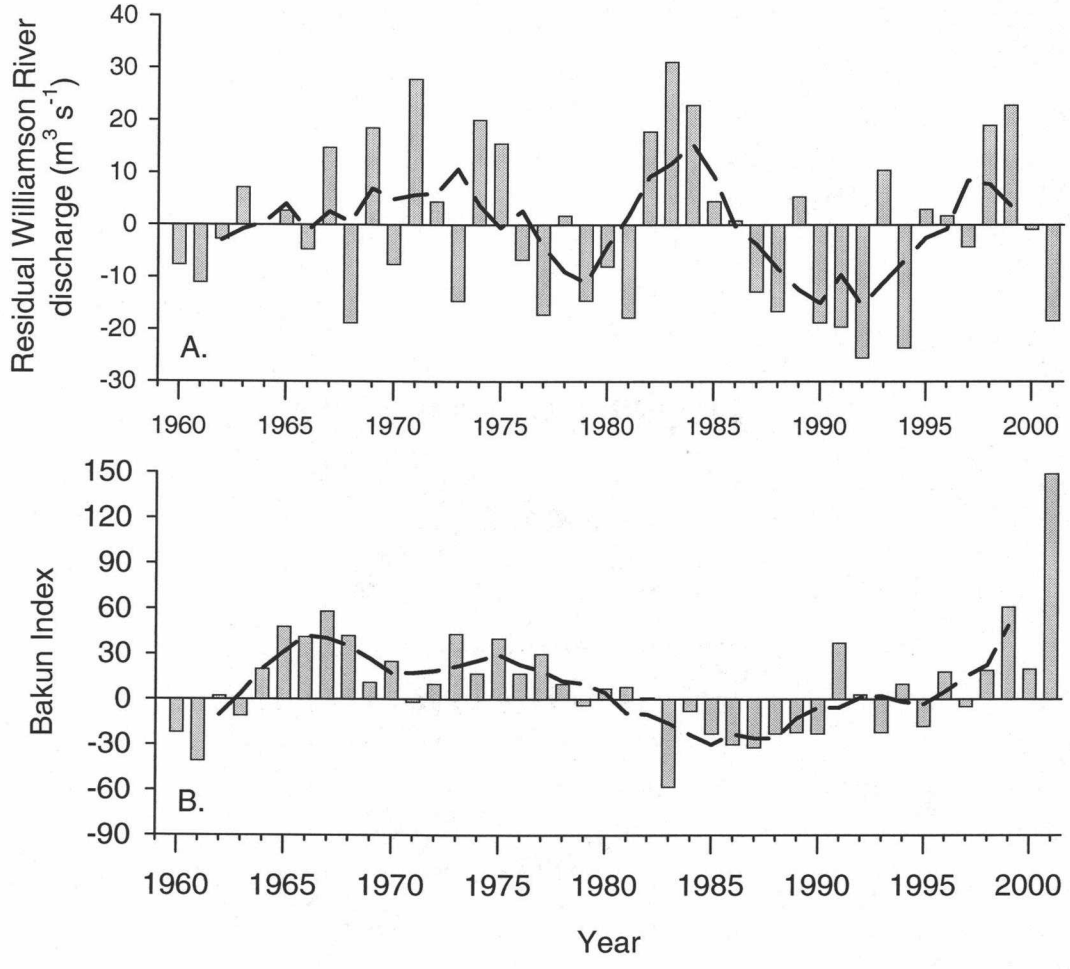

Figure 12. Panel A- Forty-year trend of Williamson River April-July mean discharge, recorded at USGS gage # 11502500. Panel B, forty-year trend in Bakun Index recorded at 42N latitude, 125W longitude. Bakun Index data provided by NOAA-Southwest fisheries science center, Pacific Fisheries Environmental Laboratory. Dashed lines are five year moving average smoothes.

The need for water allocation management for consumptive uses has created conflict in the Klamath basin (Markle and Cooperman 2002, Cooperman and Markle 2003a). It is clear that higher water volumes in the Upper Klamath Lake, coupled to weather patterns, increase the probability that early larval stages will survive. However, as is typical of most fish, there is no statistical relationship between the abundance of those survivors and subsequent recruitment to the spawning population (Cowan and Shaw 2002). This lack of statistical significance might be interpreted as a "no jeopardy" decision under the Endangered Species Act (NRC 2002). However, the literature on larval fish recruitment makes it clear that survival during the larval stage places both upper and lower limits on subsequent recruitment. Thus, although 1991 appeared to produce a good year class with a low lake volume (Markle and Cooperman 2002, NRC 2003), the management question is whether it would have been better or worse with a different lake volume. With all other variables unchanged, our data make is clear that there would have been more larvae entering the juvenile stage had there been more water.

Acknowledgements

This work is part of long-term studies of Upper Klamath Lake suckers, supported by the US Bureau of Reclamation Klamath Falls, through an Oregon Cooperative Fisheries Research Unit agreement with the Biological Resource Division of the US Geological Survey. D. Simon and M. Terwilliger conducted most of the larval trawl surveys and provided valuable advice and assistance with analyses. We are grateful to M. Buttner (USFWS), R. Larson (USFWS) and L. Dunsmoor (Klamath Tribe) for their continued interest in our work.

CHAPTER 5

CONCLUSION

Michael S. Cooperman

Our research focused on the relationship between larval suckers and their abiotic environment in the Upper Klamath Lake system, and we found little evidence that the persistent recruitment problems of the Upper Klamath Lake (UKL) populations of Lost River and shortnose suckers were directly related to events during the larval life history stage.

Larval suckers have evolved behaviors that promote rapid movement from in-river spawning beds to nursery grounds in UKL, and the dredging, diking, and channelization of the lower Williamson River does not retard the outmigration process (Chapter 2). Similarly, loss of floodplain access does not appear to present a significant survival barrier (Chapter 2). Within UKL, emergent macrophytes provided the best habitat for larval suckers (Chapter 3), and larvae were consistently able to access these habitats. Also, we found limited indications of density dependant effects, suggesting the volume of emergent macrophytes available to larval suckers was sufficient to provide habitat for all larvae reaching these habitats (Chapter 3). Finally, we found that larval sucker survival dynamics within UKL appears to be highly associated with the interaction between water temperature, wind speed, and emergent macrophyte availability, and between 1995 – 2001, at least one cohort per year was present in UKL when the three parameters were simultaneously within acceptable ranges. Although these data indicate at least one larval cohort per year should have experienced good survival into the age-0 juvenile stage (Chapter 4), only 1999 had a strong year class (Simon and Markle 2001, Markle and Cooperman 2002).

Year-class strength for UKL suckers is not established during the larval stage, as evidenced by absence of a relationship between larval sucker survival dynamics and year-class or annual recruitment patterns (Chapter 4). However, larval production and survival are important to the recovery and persistence of the species. For example, if zero or very few larvae survive in a given year, there cannot be a strong year class or subsequent strong recruitment event. Furthermore, while conditions that allow for good larval survival do not ensure good age-0 survival, conditions that promote poor larval survival, such as low lake elevations, appear to be associated with poor juvenile survival (Chapter 4, Markle and Cooperman 2002). Therefore, larval sucker success appears to be necessary, but not sufficient, to ensure year-class success.

The linkage between lake elevation, a proxy for availability of emergent macrophytes, and the success of larval suckers, but the disassociation between larval success and eventual recruitment to adult populations, produces a complex management scenario. Under the US Federal Endangered Species Act, actions that harm a protected species or its habitat are prohibited, and the US Fish and Wildlife Service (USFWS) is required to issue a jeopardy opinion for, "....any action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both survival and recovery of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species" (USFWS 2002). Our data suggest Upper Klamath Lake elevations below approximately 4139.70 ft msl (volume of inundated macrophytes = 15,000 m^3) harms larval suckers by reducing habitat availability (Chapter 3), an apparent violation of the ESA. However, because larval survival does not directly correspond to year class strength or recruitment to adult populations, the effect of low lake elevations on the larval stage may not constitute jeopardy to the species. In part, it appears to be through the disassociation of larval dynamics from adult dynamics that the USFWS (2001) and the National Research Council (2002) could both be correct while reaching different conclusions on the role of lake elevation, ESA compliance, and the welfare of the species. However, because lake elevation does not act on larval suckers in isolation from other considerations (Markle and Cooperman 2002, Cooperman and Markle 2003) the divergent opinions can't be solely explained by consideration of the larval stage.

Environmental conditions ranged widely during the four years (1998-2001) when samples were collected. Based on the four year-type classification system used by the US Bureau of Reclamation, 1998, 1999 and 2000 were above average years for total annual info to UKL, although 2000 was barely above the 500,000 acre-ft cut-off for an above average year type (1998: 716,600 acre-ft, 1999: 791,900, 2000: 508,400) and 2001 was a dry year with 230.9 acre-ft. (J. Rasmussen, USBR, personal communication). Similarly, average July wind speeds ranged widely (75 miles $24hrs^{-1}$ in 1998 to 103 miles $24hrs^{-1}$ in 2001) as did average July air temperatures (27°C in 2000 to 30°C in 1998) (Cooperman, unpublished data). Although sampling was not as comprehensive as in the other years, samples were collected (Cooperman, unpublished

data) and larval behaviors (e.g., movement, habitat use, foraging success, etc.) were consistent year to year. The high year to year consistency suggests our results are representative of the behaviors that can be expected over the full range of conditions larval sucker are likely to encounter. Additionally, because each of our findings is consistent with comparable studies on other lakesucker species (Chapters 2 and 3), we suggest our results can be used to draw inference on the natural history and ecology of other lakesuckers.

While sampling for larval suckers, we collected many larval and juvenile fathead minnows (*Pimephales promelas*), blue and tui chubs (*Gila coerulea*, *G. bicolor*), and three species of sculpins (*Cottus klamathensis*, *C. princeps*, *C. tenuis*). We found no indication of competition for space or food between larval suckers and these species (Chapter 3). However, we did not evaluate the importance of predation, a potentially significant source of mortality and a potential explanation for the poor survival of four larval cohorts despite lake elevation, wind speed, and air temperature simultaneously being within acceptable ranges (Chapter 4). Although fathead minnow are planktivorous (Helfrich 1976, Karp and Tyus 1990), Dunsmoor (Klamath Tribe, unpublished data) demonstrated they can capture and kill larval suckers. Each of the other species collected in our samples is either omnivorous or carnivorous and has high potential to prey on larval suckers. Studies evaluating the predation effect of these and other less commonly co-occurring species such as yellow perch (*Perca flavescens*) should be conducted to further resolve the causes of year-class failure and help explain recruitment dynamics of the endangered suckers.

If predation is a significant source of mortality, follow-up studies on how water management affects the population dynamics of non-suckers should be conducted. A hypothesis worth testing is whether or not a time lag effect exists. For example, management decisions made in one year to promote a strong sucker year-class (e.g., maintenance of high water levels), may have the unintended affect of also improving non-target species year-class success. If age-1 fishes are significant predators on larval or juvenile suckers, then water management of one year may harm suckers in the following year by the unintended affect of producing a large number of predators. If such a scenario is realized, a water management protocol that focuses on inter-annual

variability of lake elevations may successfully release suckers from predation pressure.

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