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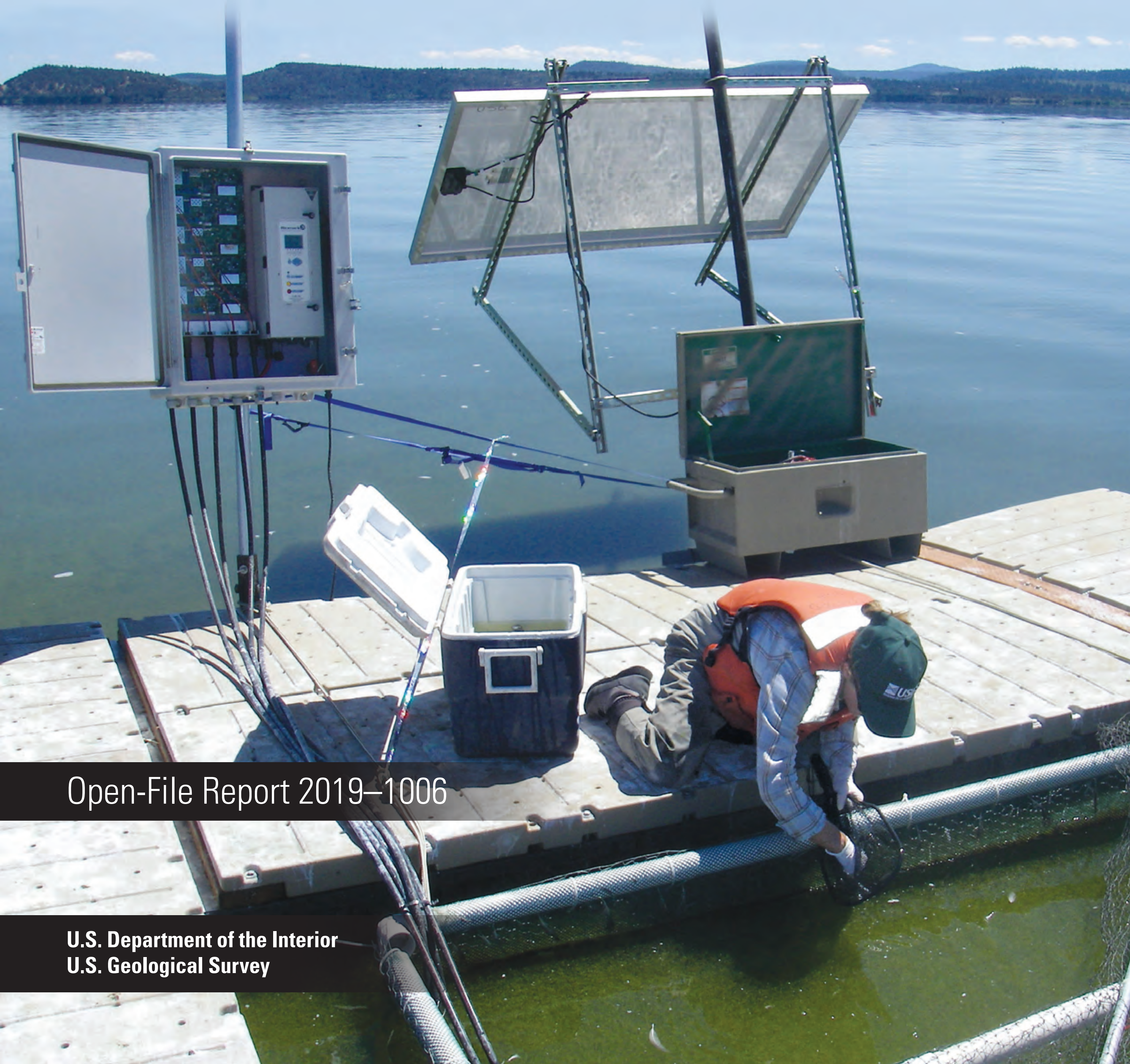
Assessing Causes of Mortality for Endangered Juvenile Lost River Suckers (*Deltistes luxatus*) in Mesocosms in Upper Klamath Lake, South-Central Oregon, 2016



Open-File Report 2019–1006

U.S. Department of the Interior
U.S. Geological Survey

Cover: Photograph showing U.S. Geological Survey employee releasing Lost River suckers at the beginning of the study into a mesocosm in Upper Klamath Lake, Oregon. Juvenile sucker movement was monitored with passive integrated transponder-tag detection equipment shown in the background. Photograph by Mark Hereford, U.S. Geological Survey, July 11, 2016.

Assessing Causes of Mortality for Endangered Juvenile Lost River Suckers (*Deltistes luxatus*) in Mesocosms in Upper Klamath Lake, South-Central Oregon, 2016

By Danielle M. Hereford, Carla M. Conway, Summer M. Burdick, Diane G. Elliott, Todd M. Perry, Amari Dolan-Caret, and Alta C. Harris

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Conversion Factors

Inch/Pound to International System of Units

Multiply	By	To obtain
	Length	
foot (ft)	0.3048	meter (m)
	Volume	
acre-foot (acre-ft)	1,233	cubic meter (m3)

International System of Units to Inch/Pound

Multiply	By	To obtain
	Length	
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
meter (m)	1.094	yard (yd)
	Area	
hectare (ha)	2.471	acre
square hectometer (hm2)	2.471	acre
square kilometer (km2)	247.1	acre
square centimeter (cm2)	0.001076	square foot (ft^2)
square centimeter (cm2)	0.1550	square inch (ft^2)
square hectometer (hm2)	0.003861	section (640 acres or 1 square mile)
square kilometer (km2)	0.3861	square mile (mi^2)
	Volume	
microliter (µL)	3.38124×10^{-5}	ounce, fluid (fl. oz)
liter (L)	33.81402	ounce, fluid (fl. oz)
liter (L)	0.2642	gallon (gal)
cubic meter (m3)	35.31	cubic foot (ft3)
cubic meter (m3)	1.308	cubic yard (yd3)
	Mass	
microgram (µg)	3.5274×10^{-8}	ounce, avoirdupois (oz)
milligram (mg)	3.5274×10^{-5}	ounce, avoirdupois (oz)
gram (g)	0.03527	ounce, avoirdupois (oz)
kilogram (kg)	2.205	pound avoirdupois (lb)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as °F = (1.8 × °C) + 32.

Datums

Vertical coordinate information is referenced to the North American Vertical Datum of 1983 (NAVD 83).
Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).
Elevation, as used in this report, refers to distance above the vertical datum.

Supplemental Information

Concentrations of chemical constituents in water are given in either milligrams per liter (mg/L) or micrograms per liter (µg/L).

Abbreviations

AIC_c	Akaike's information criterion for small sample size
DO	dissolved-oxygen
EOS	end of study
FBW	Fish Banks West
FIAB	fish introduced at beginning of study
K	body condition $K = (wt/SL^3)x10^5$
MDN	Mid North
MS-222	tricaine mesylate
nM	nanomolar; one thousand-millionth of a molar
NWIS	National Water Information System
OWSC	Oregon Water Science Center
PAS	periodic acid-Schiff
pH	negative logarithm of the effective hydrogen-ion concentration
PIT	passive integrated transponder
PVC	poly (vinyl chloride)
qPCR	quantitative Polymerase Chain Reactions
RPT	Rattlesnake Point
sd	standard deviation
SL	standard length
USGS	U.S. Geological Survey
wt	weight in grams

Assessing Causes of Mortality for Endangered Juvenile Lost River Suckers (*Deltistes luxatus*) in Mesocosms in Upper Klamath Lake, South-Central Oregon

By Danielle M. Hereford, Carla M. Conway, Summer M. Burdick, Diane G. Elliott, Todd Perry, Amari Dolan-Caret, and Alta Harris

Executive Summary

The recovery of endangered Lost River suckers (*Deltistes luxatus*) in Upper Klamath Lake, south-central Oregon, has been impeded because juveniles are not recruiting into adult spawning populations. Adult sucker populations spawn each spring but mortality of age-0 suckers during their first summer is excessively high, and recruitment of juveniles into adult populations does not occur in most years. The last significant year class to join spawning aggregations was hatched in 1991. Capture rates for age-0 Lost River suckers decrease so substantially each summer that it is thought that mortality is nearly 100 percent within the first year of life each year. Causes of mortality are not understood but poor water quality, parasites, disease, predation, and non-native species are suspected to contribute to mortality. Upper Klamath Lake is hypereutrophic and summer water-quality conditions have large diurnal and seasonal fluctuations. Photosynthesis of *Aphanizomenon flos-aquae*, the most abundant cyanobacterium in Upper Klamath Lake, is responsible for large fluctuations in dissolved-oxygen (DO) concentrations and pH.

We introduced hatchery-raised, passive integrated transponder-tagged juvenile Lost River suckers into large mesocosms located at Fish Banks, Mid North, and Rattlesnake Point in Upper Klamath Lake, Oregon, to assess sucker mortality relative to water-quality conditions. We identified the date of death for each sucker by assessing movement patterns among vertically stratified antennas. We modeled daily mortality using known fate models relative to water-quality conditions measured by sondes. Histopathology was used to understand causes of eminent mortality for moribund suckers.

Fish mortality, growth, health, and movement patterns varied among locations, but it was unclear whether this variation was due to water-quality or other factors. Seasonal mortality was 58.8 percent at Fish Banks, 27.4 percent at Mid North, and 11.5 percent at Rattlesnake Point. Growth over the 109-day study period was lowest at Fish Banks (34.5 ±10.0 millimeters [mm] standard length (SL); 18.6 ±7.7 grams [g]), intermediate at Mid North (57.5 ±13.6 mm SL; 40.1 ±15.4 g), and greatest at Rattlesnake Point (78.4 ±13.0 mm SL; 72.5 ±18.7 g). Our ability to assess causes of juvenile sucker mortality in mesocosms using our modelling approach was limited by low daily mortality. Zero to 3 mortalities occurred per day, except on July 30 at Fish Banks when 7 mortalities occurred. Relative to any other measured and tested water-quality condition, mortality was more likely to occur on days with large fluctuations in oxygen percent saturation. When we assessed the fit of the most parsimonious model, performance was poor, which suggested that other factors were contributing to mortality. Our ability to assess the relationship between seasonal patterns in water quality and fish mortality were limited by the absence of substantial differences in water quality among sites, inconsistency in the depth at which measurements were collected, and no clear pattern in conditions leading up to and during mortality events. Except for DO at Rattlesnake Point and diel temperature

variations at Fish Banks, seasonally summarized water-quality factors were similar among sites. The locations of water-quality monitors within the water column likely explain the differences in DO at Rattlesnake Point and temperature variation at Fish Banks. Furthermore, DO concentrations and other water-quality factors occurring during and prior to mortality events were inconsistent.

Microscopic assessments indicated severe gill hyperplasia, fusion of the secondary lamellae, and severe *Ichthyobodo* sp. infestations on the gills of most moribund suckers. Liver glycogen was usually depleted in suckers with severe *Ichthyobodo* sp. infestations. *Ichthyobodo* sp. infestations probably were the immediate cause of death and probably originated from the Klamath Tribes Fish Research Facility, although this parasite also is present in Upper Klamath Lake and severe water-quality conditions may have contributed to morbidity. As suckers in the mesocosms died, they were replaced with suckers from the Fish Research Facility that likely were heavily parasitized with *Ichthyobodo* sp. Therefore, it is possible that the gradient in mortality rate among sites was owing to site-varying differences in inadvertent increases in introduced parasite loads.

Introduction

Limited recruitment of juveniles into adult populations and intermittent adult mortality events limit the recovery of Lost River suckers (*Deltistes luxatus*), one of two endangered catostomids endemic to the Upper Klamath Basin in south-central Oregon and northern California. Listed as endangered in 1988 (U.S. Fish and Wildlife Service, 1988), the largest population of this long-lived sucker occupies Upper Klamath Lake, a large, hypereutrophic lake in southern Oregon. Decreases in the historically abundant populations of Lost River suckers were first documented in the mid-1960s when recreational harvests were atypically low—about 10,000 fish (Golden, 1969; Scoppettone and Vinyard, 1991). Limited recruitment was first suspected for Upper Klamath Lake suckers in 1986, when 95 percent of Lost River suckers collected during a sucker die-off event were estimated to be 19–35 years old and hatched from about 1951 to 1967 (Scoppettone, 1986). Age samples collected from suckers during massive die-off events in the mid-1990s indicated nearly all the fish had hatched around 1991. Annual mark-recapture studies done since the early 2000s indicate that there continues to be little to no recruitment to the adult Upper Klamath Lake sucker populations (Hewitt and others, 2018). The 1991 cohort, which is now older than the mean life expectancy, presently constitutes nearly all the Lost River suckers in the population (Hewitt and others, 2018). Large annual August–September decreases in capture rates of age-0 suckers and a near absence of age-1 or older juvenile suckers indicate that nearly all the mortality occurs within the first year of life (Burdick and Martin, 2017).

A direct cause of juvenile sucker mortality has not been identified. Hypotheses about causes include habitat loss and degradation; predation by or competition with abundant non-native fish; poor water quality; and cyanobacteria, parasites, disease, or some combination of these factors. In the last century, many wetlands, thought to have provided rearing habitat to juvenile suckers, were drained and converted to farmland (National Research Council, 2004). Non-native species including yellow perch (*Perca flavescens*) and fathead minnows (*Pimephales promelas*), two known predators of larval suckers, rapidly increased in abundance in Upper Klamath Lake from 1979 to 2002 (Bienz and Ziller, 1987; Scoppettone and Vineyard, 1991; Ziller, 1991; VanderKooi and others, 2006; Hereford, Ostberg, and others 2016). The nitrogen-fixing cyanobacterium *Aphanizomenon flos-aquae* (AFA) gradually became more dominant from the first observation of this species in Upper Klamath Lake in 1933 to 1957, and presently constitutes more than 90 percent of the total phytoplankton biomass in Upper Klamath Lake from May to November (Bortleson and Fretwell, 1993; Kann, 1997; Eilers and others, 2001; Eilers and others, 2004; Bradbury and others, 2004). The massive amount of AFA in Upper Klamath Lake affects the water quality by increasing pH and total ammonia during bloom cycles and decreasing dissolved-oxygen (DO) concentrations when cells die and decompose (Kann and Smith, 1999; Kann and Welch, 2005; Wood and others, 2006; Hoilman and others, 2008; Lindenberg and others, 2009; Kannarr and others, 2010). Poor water quality, associated with cyanobacteria blooms in Upper Klamath Lake, was hypothesized as the cause of widespread adult sucker mortality in 1995-1997 and 2003 and high rates of annual juvenile sucker mortality (Perkins and others, 2000; Banish and others, 2009; Eldridge, Eldridge, and others, 2012; Burdick and others, 2015).

Massive blooms of AFA and subsequent AFA cell death cause summer water quality to vary greatly both temporally and spatially across the large (305 km^2, 26,800 hectares, volume of 536 $\times 10^6$ m^3 [435,800 acre-ft]) hypereutrophic Upper Klamath Lake (Kann and Welch, 2005; Lindenberg and others, 2009; Eldridge and others, 2014). Weather conditions including sunlight, air temperature, wind speed, and wind direction directly affect the abundance and photosynthesis of AFA, which in turn affects water-quality conditions in Upper Klamath Lake (Kann and Welch, 2005; Kannarr and others, 2010; Lindenberg and others, 2009; Eldridge and others, 2014). Typical bloom conditions, which first occur in June and July when AFA is increasing and abundant, include DO concentrations that vary from supersaturated to less than 5 mg/L within 24 h and pH that can exceed 9.0 or even 10.0. During the AFA die-offs, which typically occur in late July or August, it is not uncommon to record DO concentrations of less than 2 mg/L, but concentrations of less than 1.5 mg/L are rare, even near the benthos (Helser and others, 2004). During the AFA die-off events, pH also decreases to 7–8, and total ammonia concentrations increase (Kann and Smith, 1999; Lindenberg and others, 2009; Eldridge and others, 2014). Maximum measured un-ionized ammonia concentrations vary among years and have rarely exceeded 0.48 mg/L since 2003 (Klamath Tribes, unpub. data, 2018). Rapid AFA senescence events are associated with hot air temperatures and calm wind conditions that persist for several days and prevent the lake from mixing (Kann and Smith, 1999; Wood and others, 2006; Lindenberg and others, 2009; Eldridge and others, 2014). One or two large AFA bloom and crash cycles typically occur each summer in Upper Klamath Lake (Kann, 1997; Kann and Welch, 2005; Wood and others, 2006; Hoilman and others, 2008; Lindenberg and others, 2009). Following AFA crash cycles, nitrogen becomes available for less-dominant forms of cyanobacteria and algae including *Microcystis aeruginosa*, a cyanobacterium capable of producing the hepatotoxin microcystin (Eldridge, Wood, and Echols, 2012). Cell bound concentrations of microcystin have been recorded as high as 24.4 µg/L, whereas concentrations of microcystin dissolved in the water do not exceed 4.8 µg/L (Eldridge, Wood, and Echols, 2012). Summer temperatures in Upper Klamath Lake usually are at least 20 °C but surface-water temperatures can exceed 25 °C (Wood and others, 2006; Hoilman and others, 2008; Lindenberg and others, 2009; Kannarr and others, 2010; Eldridge, Eldridge, and others, 2012) during the bloom phase.

Diurnal fluctuations of temperature, DO concentrations, and pH can be especially great during the summer in Upper Klamath Lake. *Aphanizomenon flos-aquae* photosynthesis, nocturnal respiration, and sediment decomposition are responsible for changes in DO concentrations and pH, whereas solar radiation and other weather conditions such as wind speed and direction are correlated with changes in temperature and un-ionized ammonia concentrations (Kann and Welch, 2005; Lindenberg and others, 2009). Extreme pH (>9.5) and low DO concentrations are common in Upper Klamath Lake, but conditions tend to fluctuate diurnally and do not typically persist. Because of photosynthetic activity by cyanobacteria, high pH co-occurs with high DO rather than low DO in late afternoon; stressful levels of DO and pH do not typically co-occur within 1 h. However, extreme conditions for both parameters may both occur within one day (Power, 1997; Wood and others, 2006; Hoilman and others, 2008; Lindenberg and others, 2009). Temperature also fluctuates diurnally; highest temperatures occur in late afternoon and early evening, and lowest temperatures occur around sunrise. Temperature fluctuations are greater at shallow sites than at deeper sites, and near the surface at deep sites (Lindenberg and others, 2009).

Many researchers have hypothesized that poor water quality is the primary factor contributing to low juvenile Lost River sucker survival in Upper Klamath Lake (Bortleson and Fretwell, 1993; Kann and Welch, 2005; U.S. Fish and Wildlife Service, 2008; Eldridge, Eldridge, and others 2012; Walker and others, 2012; Eldridge, and others, 2014). However, identifying specific water-quality parameters that cause or contribute to mortality has proven to be challenging. Laboratory studies found juvenile Lost River suckers to be extremely tolerant of high temperatures, low DO concentrations, high pH, and high concentrations of un-ionized ammonia when fish are exposed to one stressor at a time (Saiki and others, 1999; table 1). Young-of-year Lost River suckers have even survived anoxia for as many as 48 h by gulping air at the surface, a strategy that is energetically demanding (Burnett and Stickle, 2001; Foott and others, 2007). Microcystins are associated with decreased growth rates, altered swimming behavior, decreased immune function, tissue damage to the intestinal tracts, livers, kidneys, and gills, and death in many fishes worldwide (Fisher and Dietrich, 2000; Pavagadhi and Balasubramanian, 2013). Combinations of high pH followed by low DO did not increase mortality of juvenile suckers beyond low DO alone (Meyer and Hanson, 2002). Little is known about other synergistic effects of water-quality stressors on juvenile Lost River suckers.

It has been difficult to associate observations of juvenile sucker mortality in the wild with specific water-quality conditions. Annual juvenile sucker survival is near zero in Upper Klamath Lake, and greater than (>) 30 percent in Clear Lake Reservoir, California, where minimum DO concentrations are >5 mg/L and pH is less than or equal to (≤) 8.9 (Burdick and others, 2015). The timing of juvenile sucker mortality in Upper Klamath Lake is inferred from decreasing lakewide capture rates that occur over several months, whereas water quality can change greatly in as little as a few hours. Water quality varies spatially in Upper Klamath Lake, and juvenile suckers can move long distances (Bottcher and Burdick, 2010; Eldridge, Eldridge, and others, 2012). Lethal levels of pH, DO, un-ionized ammonia, and temperature have all been documented in Upper Klamath Lake, but the frequency and duration of these events is rarely reported (Eldridge, Eldridge, and others, 2012). It is unclear whether single water-quality factors are sufficiently extreme and of sufficient duration to cause widespread mortality of juvenile suckers in Upper Klamath Lake. Synergistic effects of multiple water-quality stressors on juvenile sucker mortality also are difficult to identify in field studies. However, this association cannot prove that diel variation in variables is a cause of mortality with field studies completed so far.

Table 1. Median lethal thresholds of stressors for Lost River suckers by life stage, as determined by Saiki and others (1999).

[All laboratory trials were done at a water temperature of 20 °C and a pH of 7.5 unless the specific factor was manipulated for a trial. Thresholds were determined for either 24- or 96-hour trials. Juveniles suckers used in the Saiki and others (1999) study weighed 0.28–0.86 grams. **Abbreviations:** °C, degrees Celsius; mg/L, milligram per liter; NA, not applicable]

Stressor	Duration (hours)	Larval	Juvenile
Temperature (°C)	24	31.93	30.76
	96	31.69	30.51
Dissolved oxygen (mg/L)	24	2.01	1.62
	96	2.10	1.58
pH	24	10.42	10.66
	96	10.35	10.30
Un-ionized ammonia (mg/L)	24	NA	1.02
	96	0.48	0.78

Fish size and life stage can affect fish tolerance for poor water quality. Larger-bodied fish, including suckers, may have lower tolerances for warmer temperatures than smaller-bodied fish (Roze and others, 2013). Lost River sucker larvae have higher median lethal thresholds for temperatures than small juveniles (Saiki and others, 1999; table 1). Based on the trend of decreasing maximum temperature tolerances with increasing size, the maximum temperature tolerance for larger suckers (such as those in our study; see description in section, "Methods") possibly is lower than the tolerances reported by Saiki and others (1999). Larger-bodied fish tend to have higher tolerances for high pH than smaller-bodied fish (Scott and Wilson, 2007), and suckers are extremely tolerant of high pH (Saiki and others, 1999; Lease and others, 2003).

The ability of a fish to tolerate hypoxic or anoxic conditions also may vary with body size, although other factors (including environmental variables, metabolism and glycogen storage levels, activity levels, and specialized adaptations that vary among species) contribute to hypoxia tolerance (Robb and Abrahams, 2003; Nilsson and Östlund-Nilsson, 2008; Dan and others, 2014). For some species such as fathead minnow and yellow perch, small individuals are more tolerant of hypoxic conditions than larger-bodied fish because they have a higher gill surface area relative to body size ratio, and gill ventilation—which is energetically expensive—is more efficient for smaller-bodied fish (Robb and Abrams, 2003). However, larger-bodied fish typically have higher glycogen stores, which can be used as an energy source during hypoxia in some species (Nilsson and Östlund-Nilsson, 2008). Studies of hypoxia tolerance for early life stage Lost River suckers noted that juveniles are more tolerant than larvae and large juveniles are more tolerant than small juveniles. Twenty-four-hour median lethal DO concentrations for Lost River suckers are 2.01 mg/L for larvae, 1.62 mg/L for small juveniles (0.28–0.86 g; table 1), and less than 1.21 mg/L for late-stage juveniles (1.7–7.3 g; Saiki and others, 1999; Meyer and Hansen, 2002).

Although juvenile Lost River suckers may be able to tolerate conditions present in Upper Klamath Lake for limited durations, chronically stressful conditions are suspected to decrease growth and contribute to mortality (Loftus, 2001). However, sublethal effects of exposure have rarely been identified for Lost River suckers in laboratory stress tests (Meyer and Hansen, 2002). Instead, Lost River suckers typically die before they show signs of compromised health (Meyer and Hansen, 2002). An exception to this is structural changes in the gills, including increased thickness of the secondary lamellae after prolonged exposure (30 d) at un-ionized ammonia concentrations as low as 370 µg/L that have been observed in juvenile Lost River suckers (Lease and others, 2003). In the absence of specific data on sublethal effects of water-quality variables on Lost River suckers, Loftus (2001) hypothesized low (4 mg/L) and high (2 mg/L) stress thresholds for suckers in Upper Klamath Lake based on available water-quality criteria for warm-water fish. Conditions more extreme than stress thresholds are expected to divert metabolic processes away from routine maintenance and growth to endurance of stressful conditions.

Fish respond to stressors, including hypoxia, by altering their behavior or physiology. Changes in behavior can make fish vulnerable to predation while physiological changes can be metabolically expensive. During hypoxia, anoxia, or elevated temperatures, fish may seek refuge and move to areas with better conditions (if possible) or they may increase their rate of buccal pumping (water movement across the gills; Sauter and others, 2001; Breau, 2012; Zhao and others, 2017). Adult Lost River suckers actively avoided areas of low DO concentrations in Upper Klamath Lake in 2003 (Banish and others, 2009). Other fishes cope with extreme conditions through modifications to gill morphology that alter their gill respiratory surface area, part of a process referred to as gill remodeling (Clarke, 2003; Sollid and others, 2003). Gill remodeling to increase the respiratory surface area has been observed during anoxic conditions or warm temperatures in many species including crucian carp (*Carassius carassius*) and goldfish (*Carassius auratus*; Sollid and others, 2003; Sollid and Nilsson, 2006). Apparent gill remodeling also has been observed, although not specifically studied, in Lost River suckers (J. Scott Foott, U.S. Fish and Wildlife, oral commun., 2017). At cool temperatures, the transition from nomoxic to hypoxic gill states can be completed in several days, but at high temperatures it can take as few as 6 h (Nilsson, 2007). Some disadvantages associated with remodeling of gills to increase respiratory surface area include substantial ion loss (also metabolically expensive), increased cardiac output, increased vulnerability to toxins (including algal toxins and un-ionized ammonia), and increased gill-parasite vulnerability (Nilsson, 2007). An increase in gill respiratory surface area may be a good strategy for fishes exposed to chronic anoxia but the risks and metabolic demands associated with gill remodeling may be too costly when environmental conditions fluctuate.

Parasites and other infectious agents in Upper Klamath Lake further complicate the effects of poor water quality on the mortality of juvenile Lost River suckers. There are many parasites and infectious agents in Upper Klamath Lake, including lampreys (*Entosphenus* sp.), *Lernaea* sp., *Ichthyobodo* sp., *Flavobacterium columnare*, *Bolbophorus* sp. (black spot trematode), and others. However, the mere presence of a parasite or pathogen is not a predictor of the occurrence of fish disease and mortality (Lafferty and Holt, 2003; Ward and Lafferty, 2004; Lafferty, 2009, 2017). Interactions among fish hosts, pathogens, and the environment are complex (Snieszko, 1974), and the frequency and severity of disease are determined in part by the infectivity and virulence of a pathogen and the susceptibility and immune competence of the host (Hedrick, 1998). Potential stressors in the Upper Klamath Lake ecosystem may have influenced the prevalence and severity of disease in the suckers. For example, in the 2014 mesocosm pilot study, Hereford, Burdick, and others (2016) reported severe *Ichthyobodo* sp. infestations on the gills of many moribund suckers. These infestations were associated with extensive epithelial hyperplasia and fusion of the lamellae. Although these histological changes seemed to be a response to the parasite, adverse water-quality conditions or the concurrent presence of toxicants may have amplified the response (Evans, 1987; Sinha and others, 2014). Others have reported increased mortality of juvenile Lost River suckers after exposure to the pathogenic bacterium *Flavobacterium columnare* (Morris and others, 2006). However, Morris and others (2006) also noted that suckers exposed to higher concentrations of sublethal un-ionized ammonia for 30 d had lower mortality from the *F. columnare* challenge than control suckers and suckers in lower un-ionized ammonia concentrations. The presence of parasites on the gills can reduce the duration or lower the threshold of low DO tolerance for common carp (Molnar, 1994). Hypoxia also can increase parasite infestation rates (Mikheev and others, 2014). Therefore, the interactions between infectious agents and water quality are complex and not easily predicted.

To examine the lethal and sub lethal effects of water quality and parasites on juvenile Lost River suckers, we used mesocosms within Upper Klamath Lake. Most laboratory studies of juvenile Lost River suckers examined water-quality parameters in isolation, whereas most previous field studies lacked the ability to accurately associate specific water-quality conditions with juvenile Lost River sucker mortality. Previous mesocosm research in Upper Klamath Lake used short-duration trials (≤7 d; Stone and others, 2017; Martin and Saiki, 1999) and were unable to determine the precise timing of mortality. We monitored the hourly movement and daily survival of juvenile Lost River suckers with passive integrated transponder (PIT) tags in mesocosms that exposed suckers to ambient environmental conditions. Moribund suckers were examined with histopathology to determine cause of death. The specific objectives of this study were to (1) assess the survival of juvenile Lost River suckers in mesocosms relative to water-quality conditions at three locations in Upper Klamath Lake, (2) assess movement patterns relative to water-quality conditions, and (3) assess changes in health, growth, and body condition among locations. In this report, we focus our quantitative analysis on water-quality conditions that co-occur with mortality and use descriptive methods to discuss events leading up to mortality.

Methods

Mesocosm Design, Fish Introduction, and Sampling the Mesocosm

Mesocosms were established at Fish Banks West (hereafter "Fish Banks" or FBW), Mid North (MDN), and Rattlesnake Point (RPT) sites in Upper Klamath Lake, south-central Oregon, in June 2016 (fig. 1). Mid North and Rattlesnake Point sites were selected for their contrasting water quality and Fish Banks was selected because of its proximity to a wetland thought to provide beneficial habitat to suckers. Mesocosms were about 2.7 m long and 2.9 m wide and varied in total height from 2.7 m at Fish Banks to 4.6 m at Mid North. Mesocosm frames were constructed using 7.62-cm poly vinyl chloride (PVC) pipe, and mesocosm net pens were manufactured using 0.62-cm^2 mesh (20-kg) nylon and corner-to-corner sleeves held the PVC frames. All vertical sides of net pens were wrapped in 2.54-cm^2 poultry wire to prevent mammalian predation. Bird netting with 2.5-cm^2 mesh hung across the top of mesocosms to prevent avian predation. Buoyant docks (1–2 m wide) surrounded the net pen on all sides and kept mesocosms anchored in place.

In each mesocosm, three vertically stacked antennae (1.2 × 0.6 m) detected fish movements near the surface, at mid-water column, and on the benthos. The surface antenna at Fish Banks was placed near the water surface such that as lake elevations declined throughout the season, the surface antenna was removed, and the middle antenna became the surface antenna. Surface antennas at deep sites (Mid North and Rattlesnake Point) were placed about 0.5 m below the water surface at the beginning of the season and continued to detect suckers near the surface as lake elevations declined throughout the season. To track horizontal benthic movement and to increase probability of detection, two smaller (0.3 × 0.3 m) antennas were placed in opposite bottom corners in each mesocosm. Biomark® MTS systems (master controller and IS1001™ nodes) remotely monitored fish movements within mesocosms. To prevent overloading internal memory of master controllers, a 10-min detection delay was enabled for each antenna. This delay resulted in the more frequent detection of fish that moved rapidly among antennas.

Wild adult Lost River suckers captured from spawning grounds in Upper Klamath Lake were used to propagate suckers for this study. Eggs and milt were collected during spring 2015 and suckers were raised by the Coleman National Fish Hatchery (U.S. Fish and Wildlife Service, Anderson, California), then kept as juveniles at the Klamath Tribes Fish Research Facility in Chiloquin, Oregon. A total of 450 age-1 juvenile suckers were sedated with tricaine mesylate (MS-222) and PIT-tagged using Biomark® MK25 implant guns and 12-mm, 134.2-kHz, full duplex PIT tags in preloaded needles. All tags were implanted from the anterior end towards the posterior end in the body cavity between the pectoral fins to keep the needle and tag away from sensitive organs such as the heart (Burdick, 2011). Fish were held in research tanks for at least 5 weeks post-tagging to allow the tag site to heal. All tag sheds and tag-related mortalities occurred within 1 week. Before being transported to the mesocosms, all fish were scanned for a PIT tag, weighed, and measured to standard length (SL). Fish ranged in SL from 83 to 124 mm and in weight from 7.8 to 24.6 g (table 2). Suckers were transported in coolers equipped with aerators to each site as quickly as possible on July 11, 2016. Lake and road conditions were smooth, cool, and calm, and no mortality occurred during transport. At each site, lake water was slowly added to the transport water every 10–15 min for 45-60 min to allow fish to acclimate to local conditions. A total of 102 (Fish Banks), 102 (Mid North), and 104 (Rattlesnake Point) juvenile suckers were introduced to each mesocosm. Stocking density was based on results of a pilot study in which suckers stocked at 100 suckers per mesococosom survived and grew (Hereford, Burdick, and others, 2016). Mortalities observed within the first week (N=6 at Fish Banks, N=2 at Mid North, N=2 at Rattlesnake Point) were considered associated with transport or acclimatization stress and were removed from further analyses.

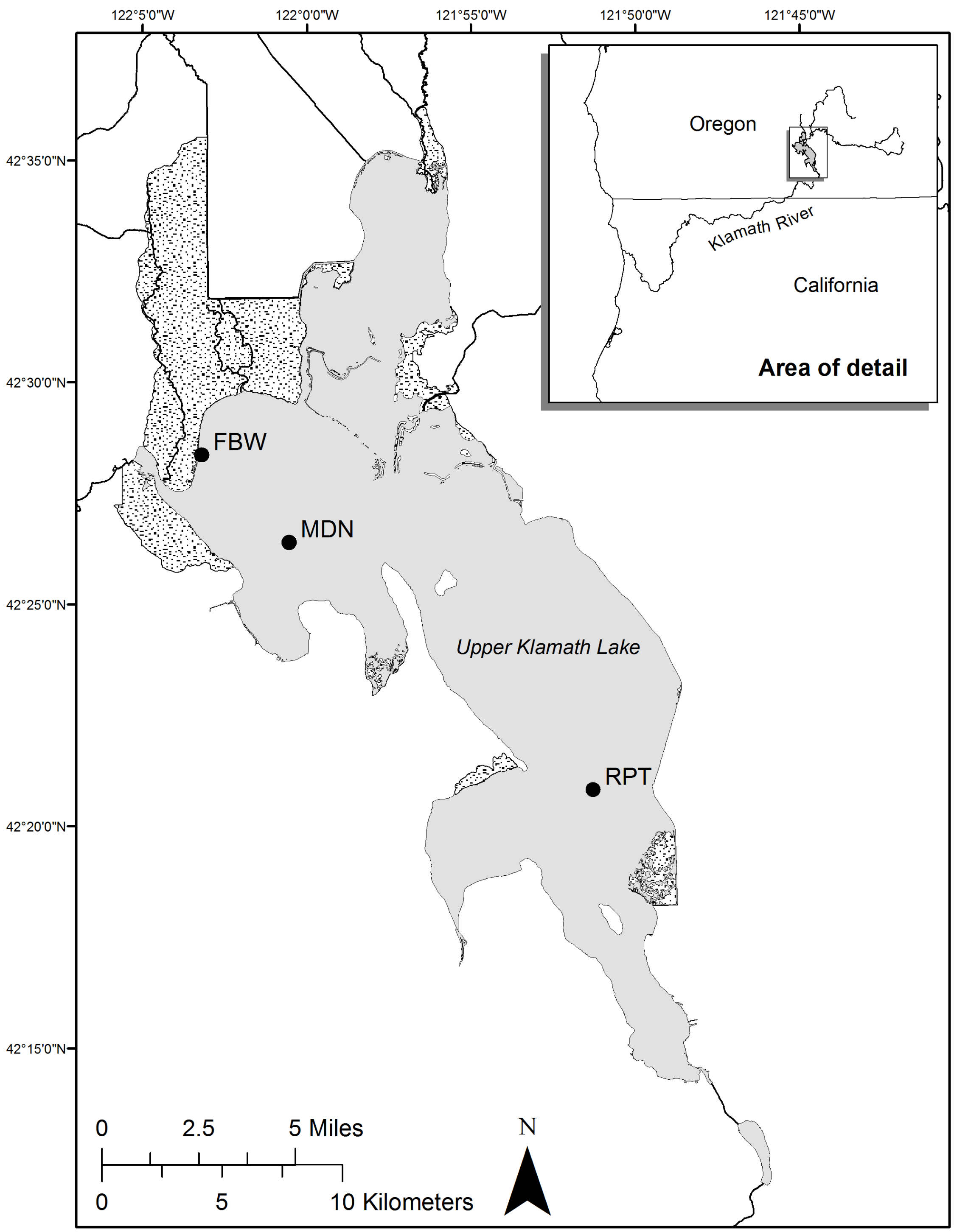

Figure 1. Map showing locations of mesocosms at Fish Banks West (FBW), Mid North (MDN), and Rattlesnake Point (RPT) sites, Upper Klamath Lake, south-central Oregon, 2016.

Table 2. Initial size information for 308 Lost River suckers, mortalities that occurred throughout the study (before the end of October), and fish that survived the entire duration of the study, Upper Klamath Lake, south-central Oregon, July–November 2016.

[Measurements were taken prior to the introduction of suckers to mesocosms in Upper Klamath Lake. All indicates suckers introduced on July 11, 2016, Mortalities indicates suckers that died throughout the study, and Survivors indicates suckers that survived the entire duration of the study. Fish Banks, July 11–October 28; Mid North, July 11–October 31; Rattlesnake Point, July 11–November 1. ±, plus or minus]

Parameter	Group	Fish Banks	Mid North	Rattlesnake Point
Sample size	All	102	102	104
	Mortalities	60	29	13
	Survivors	42	73	91
Standard length[1]				
	All[2]	102.6 ± 7.1	102.4 ± 6.8	102.5 ± 7.5
	Mortalities[2]	103.1 ± 7.4	102.1 ± 7.5	101.7 ± 5.3
	Survivors[2]	102 ± 6.6	102.5 ± 6.6	102.6 ± 7.8
	All[3]	87–124	91–117	83–120
	Mortalities[3]	87–124	91–116	91–111
	Survivors[3]	90–118	92–117	83–120
Weight[4]				
	All[2]	14.8 ± 3.2	14.6 ± 3.1	14.9 ± 3.4
	Mortalities[2]	14.9 ± 3.2	14.4 ± 3.6	14.6 ± 2.2
	Survivors[2]	14.5 ± 3.1	14.7 ± 2.9	14.9 ± 3.5
	All[3]	8.7–23.1	8.7–22.7	7.8–24.6
	Mortalities[3]	9.1–22.4	8.7–22.7	10–18.8
	Survivors[3]	8.7–23.1	9.6–21.5	7.8–24.6
Body condition[5]				
	All[2]	1.35 ± 0.11	1.35 ± 0.08	1.36 ± 0.08
	Mortalities[2]	1.35 ± 0.12	1.33 ± 0.10	1.38 ± 0.07
	Survivors[2]	1.35 ± 0.08	1.35 ± 0.08	1.36 ± 0.08
	All[3]	0.83–1.59	1.15–1.53	1.16–1.52
	Mortalities[3]	0.83–1.59	1.15–1.53	1.28–1.52
	Survivors[3]	1.13–1.54	1.16–1.49	1.16–1.51

[1]Standard length, in millimeters.

[2]Mean ± standard deviation.

[3]Range (minimum–maximum).

[4]Weight measured in grams.

[5]Body condition (K)=(weight/standard length^3)×10^5.

Mesocosms were visited several times each week in July, August, and September and once each week in October. Any suckers found dead or moribund were removed from mesocosms. Fish found dead were scanned for a PIT tag and measured to SL when possible. An external health assessment and a modified Goede index (internal organ assessment) were completed on all moribund fish (Goede and Barton, 1990). When dead or moribund fish were removed from a mesocosm, they were replaced as soon as feasibly possible (usually within 1-8 d) to keep the number of live fish consistent among sites (table 3).

Table 3. Number of hatchery-raised, passive integrated transponder-tagged age-1 Lost River suckers introduced to mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016.

[Locations of mesocosms are shown in figure 1]

Date	Fish Banks	Mid North	Rattlesnake Point
July 11	102	102	104
July 18	2	0	0
July 22	3	6	3
August 5	17	2	0
August 18	11	6	1
August 25	11	0	8
September 1	25	6	1
September 15	7	0	1
Total	178	122	118

Water Quality

Hourly water temperature, DO concentration, pH, conductivity, and depth measurements were recorded by two YSI® 6920-V2-1 sondes at Fish Banks, two EXO2 sondes at Mid North, and one EXO2 sonde at Rattlesnake Point to assess sucker response relative to changing water quality. Water-quality measurements at Mid North and Rattlesnake Point were taken as part of the U.S. Geological Survey (USGS) long term water-quality monitoring program. Measurements at Mid North were taken 1 m below the water surface and 1 m above the sediments (Eldridge, Eldridge, and others, 2012). At Rattlesnake Point, measurements were taken in the middle of the water column (Eldridge, Eldridge, and others, 2012). Water-quality measurements at Fish Banks were collected specifically for this project and were taken about 30 cm below the water surface and 30 cm above the sediments. As lake elevation and mesocosm depths declined throughout the season, sonde placements were adjusted during weekly maintenance. Field sondes were retrieved, cleaned, and (or) replaced regularly with a laboratory-calibrated replacement sonde according to USGS protocol each week.

All water-quality data collected by sondes were processed, corrected when necessary, reviewed, and released as final on the publicly available USGS National Water Information System (NWIS) website (https://waterdata.usgs.gov/nwis/qw). Collection of water-quality data presented in this report began on July 11, the day suckers were placed in mesocosms, and ended on September 20 for Fish Banks and October 4 for Mid North and Rattlesnake Point. In-text summary statistics for seasonal water-quality conditions included all measurements from July 18 to September 20, 2016, for all sites.

We opportunistically collected water-column profiles at all sites from July 11 to September 20. A laboratory-calibrated YSI® 6920-V2-1 sonde was lowered into the water column 0.25 m at a time. Sondes were held steady until all parameters had stabilized. We took a final measurement as close to the bottom as possible, regardless of depth, without taking measurements in the sediments.

The Oregon Water Science Center (OWSC) collected weekly total ammonia water samples from the middle of the water column at Mid North and Rattlesnake Point. Concentrations of toxic un-ionized ammonia were derived from total ammonia by use of pH and temperature measurements taken at each site when the sample was collected using methods of Emerson and others (1975). To better understand diurnal variation in un-ionized ammonia concentrations and to augment the weekly un-ionized ammonia sampling, additional un-ionized ammonia samples were collected using automated Teledyne ISCO™ 6712 portable samplers. Automated ammonia samples were collected about 0.5 m from the benthos every 2 h for four 24-h intervals at each site. Weekly samples were collected at mid-water column using a hose and peristaltic pump. Pumped water was filtered through a 0.45-µm capsule filter attached to the end of the hose. Ammonia samples collected by ISCO™ samplers were kept cool by dry ice and ice packed into the sampler until samples were transferred to the laboratory. Teledyne ISCO™ samples were filtered within 24 h of collection, and then sent to the Sprague River Water Quality Laboratory where they were analyzed for total nitrogen. Weekly ammonia samples were analyzed by the National Water Quality Laboratory and stored in the NWIS.

Water samples for microcystin cyanotoxin analysis were taken weekly for assessment of sucker health and survival relative to large (≥63 µm) and small (<63 µm) microcystin particles present in the water column. We separated particles by size owing to a difference in how the toxin is absorbed. Uptake of toxin from the large particle fraction is attributable to dietary consumption, whereas dissolved microcystins may be transported directly across the gills. Previous research indicated that toxin concentrations were similar between samples containing single cells and those dissolved in water (Eldridge, Eldridge, and others, 2012); therefore, small fraction includes single-cell and dissolved microcystins. Depth-integrated samples were collected from each site and analyzed according to USGS OWSC protocol, which uses a freeze-thaw method to release toxins from cells (Eldridge, Wood, and Echols, 2012).

Movement

Individual fish movement patterns among antennas were analyzed to identify the date of mortality for each sucker that died during the study period. The date of mortality was assigned as the date that movements among antennas ceased. Moribund fish were assigned a date of mortality as the day that they were removed from the mesocosm. Detections on antennas that occurred for fish post-mortem were removed from further movement analysis. If we recovered the fish, we referred to it as "found dead," whereas if no body was recovered, we referred to it as a "remote death."

Vertical movements for each living sucker within each hour were assigned to one antenna (top, middle, or bottom), or combination of antennas (top and middle; middle and bottom; or all three antenna depths, "entire water column") throughout the study. For example, if a sucker was detected on the bottom and middle antennas (but not the top antenna) between 8:00 and 8:59 a.m., it would be assigned to the "middle and bottom" antenna group for that hour. Hourly movement patterns for all live suckers then were summarized by quantifying the total percentage of individual tags detected at each antenna or combination of antennas (hereinafter, "vertical location") during each 1-h interval throughout the study. For example, if 70 percent of the live tags were detected by one or more bottom antenna and by the middle antenna between 11:00 and 11:59 a.m., then the "middle and bottom" antenna group would be 0.7, and the remaining 30 percent would be dispersed across the other antennas or combination of antenna groups such that each tag detected in that 1-h interval was only represented in one group. For each antenna and group of antennas, we averaged these percentages within each day to derive a daily water column use average. Daily averages were assessed to identify seasonal changes in water-column use.

Mortality

Daily mortality relative to daily water-quality conditions was estimated using known fate models for all suckers that were introduced at the beginning of the study period and that survived at least 7 d (N= 298, Kaplan and Meier, 1958). Live-dead encounter histories were created for 65 d (July 18–September 20) using remote detection patterns among antennas. Water-quality condition models were built using data from July 18 to September 20 because we had water-quality data for all sites for these dates. All data were used from both top and bottom sondes (when available; see section, "Methods: Water Quality," for more information) to calculate input parameters for each day. For example, minimum values were the lowest value at either sonde during the day, and means were the average for both sondes during a day. The known fate models use logistic regression to estimate effects of continuous covariates on a binary outcome (live or dead), while allowing the sample size to change through time as fish die or are censored from the sample population. Fish in our study were censored when they were sacrificed mid-season for histology. Collinearity between covariates used in the same model is not allowed. We assumed a linear relation between the dependent and independent variables on the logit scale. All parameters were scaled to balance data variability among parameters by subtracting the data mean from each data point, and then dividing by the standard deviation of the data.

We developed a modeling strategy that combined conservative methods advocated by Burnham and Anderson (2002) and more comprehensive methods suggested by Doherty and others (2012). First, we developed a model set of biologically meaningful, *a priori* hypotheses about how sucker mortality may vary with daily water-quality conditions (model names in *italics* throughout section, "Methods," table 4). These hypotheses were developed in collaboration with regional water-quality and sucker experts by assessing conditions measured during the 2016 field season, reviewing Lost River sucker thresholds in the literature, and identifying how tolerance may vary relative to body size. Single-parameter and interactive daily-condition models were ranked in Program MARK using Akaike's information criterion adjusted for small sample sizes (AICc) using a c-hat of 1.0. We then combined non-correlated parameters that had model weight of at least 2 percent and that predicted mortality (in directionality) as hypothesized to create new additive and interactive models. We compared water-quality models with general time (*time*), site (*site*), and constant (*dot*) models to assess the relative performance of water-quality models (table 4). We derived daily mortality estimates for the range of standardized water-quality conditions observed using the logit link function and beta parameter estimates from the top model. Confidence intervals around predicted survival were generated in program R using the variance covariate matrix and 30 representative values across the range of water-quality data from the most parsimonious model. We assessed the goodness-of-fit of the top-ranked model by plotting (1) the predicted and observed mortality, (2) the residuals, and (3) the daily water-quality data against the number of mortalities that occurred each day.

In place of temperatures comparable to those reported to cause mortality in laboratory studies, and considering that larger bodied fish (such as those in our study) are more sensitive to warm temperatures (Roze and others, 2013; Eliason and others, 2011), regional experts hypothesized that temperatures cooler than median lethal levels (table 1 and 4) and (or) large fluctuations in daily temperature would be stressful for suckers in mesocosms and may contribute to juvenile mortality. Experts were unable to hypothesize specific temperature thresholds, and thresholds of 23 and 25 °C were selected based on the distribution of temperature data. Continuous models were tested using the percentage of measurements within one 24-h interval that were greater than 23 (*p23.temp*, table 4) and 25 °C (*p25.temp*); mean daily temperature (*mean.temp*); maximum daily temperature (*max.temp*); and range of daily temperatures (*range.temp*, table 4). Binary models also were tested; days where mean water temperature reached or did not reach 23 °C (*mean.temp > 22.9°C*), and days where maximum water temperature reached or did not reach 25 °C (*max.temp > 24.9°C*).

Models to describe the relation between DO concentrations and mortality considered laboratory trials, empirical observations of the effects of low DO on survival, and the range of observed conditions at mesocosms in 2016. We hypothesized that low DO concentrations may be associated with mortality in mesocosms despite laboratory trials identifying very high tolerances for prolonged hypoxia (24-h median lethal concentration [LC50] <1.21 mg/L; Meyer and Hansen, 2002) and observations of suckers gulping air during extreme low DO concentrations (Loftus and others, 2004; Foott and others, 2007) because the synergistic effects of other factors (for example, parasites) may make expectedly benign DO concentrations lethal. Continuous DO concentration models were tested using the mean daily DO concentration (*mean.DO*, table 4), minimum daily DO concentration (*min.DO*), and the percentage of hourly measurements within a day less than 2 mg/L (*p2.DO*). We also tested a binary model for days where minimum DO concentrations were or were not less than 2 mg/L (*min.DO<2*). This threshold of 2 mg/L has been hypothesized as potentially stressful for suckers by Loftus and others (2004). We also tested the hypothesis that juvenile sucker mortality is associated with large fluctuations in DO concentrations where the range in DO concentrations was continuous (*range.DO*), and by using a binary model where the range in daily values fluctuated or did not fluctuate by at least 9 mg/L (*range.DO>9*, table 4; Burdick and others, 2015). The threshold of 9 mg/L was selected based on the distribution of the data.

Regional experts hypothesized that oxygen percent saturation models may be better able to describe the observed mortality than DO alone, because DO concentration and temperature are combined in one parameter. The solubility of DO (as percent saturation) was calculated by Steward Rounds (U.S. Geological Survey, written commun., 2017) as a function of water temperature, a salinity correction derived from specific conductivity, and elevation using Benson and Krause (1980, 1984) equations (Rounds, 2011). Using the 24-h DO median lethal level and reporting laboratory target conditions (20 °C, 62 ft or 18.9 m elevation in Dixon, California) of Saiki and others (1999), we estimated lethal concentrations for oxygen percent saturation at 17–18 percent. Without guidance from the literature, we selected 50- (*p50.psat,* table 4) and 35-oxygen percent saturation (*p35.psat)* as thresholds for continuous (percent of measurements less than) and binary (measured or not) models based on the distribution of the data (*mean.psat<50*). We also tested continuous hypotheses like those for DO concentrations; mortality would be higher on days when minimum (*min.psat*), maximum (*max.psat*), or mean daily oxygen percent saturation (*mean.psat*) was low, and mortality would be higher on days when there were large fluctuations in oxygen percent saturation (*range.psat*). We also tested the binary hypothesis that there would be more mortality on days where oxygen percent saturation fluctuated by more than 140 percent (*range.psat>140*, table 4).

In place of comparable pH conditions that cause mortality for juvenile suckers in laboratory stress tests (table 1), regional water-quality experts hypothesized that large fluctuations in daily pH measurements (*range.pH*, table 4) and pH conditions greater than 9.5 and 9.75 may be stressful for suckers in Upper Klamath Lake and may be contributing to juvenile mortality. We built continuous models using the percentage of hours each day that exceeded pH 9.5 (*p.9.5pH*) and 9.75 (*p.9.75pH*), and binary models (whether thresholds were reached or not) using the daily mean pH and a pH threshold of 8.45 (*mean.pH>8.45*), the daily maximum pH and a threshold of 8.9 (*max.pH>8.9*), and the daily range of pH measurements and a threshold of 0.9 (*range.pH>0.9*). These thresholds were selected based on the distribution of the measured data. We also tested continuous daily condition models that used the daily mean pH (*mean.pH*) and daily maximum pH (*max.pH*, table 4).

Regional experts hypothesized that microcystin toxins may contribute to sucker mortality because microcystin concentrations in Upper Klamath Lake reach levels that are known to be lethal to other fish species in other systems (Pavagadhi and Balasubramanian, 2013). Microcystin toxins in the environment may affect fishes in two ways— through ingestion of large particles, or by immersion into dissolved and suspended small particles (Pavagadhi and Balasubramanian, 2013). In contrast, doses as low as 6.6 µg/g of body weight are fatal to common carp (*Cyprinus carpio*; Fisher and Dietrich, 2000). Immersion trials have not been conducted on Lost River suckers; however, increases in antioxidant enzymes have been observed in catfish (*Corydoras paleatus*), common carp, and zebrafish (*Danio rerio*) for microcystin concentrations ranging from less than 1 to 10 µg/L (Cazenave and others, 2006; Jinlin and others, 2011; Pavagadhi and others, 2012). Increased plasma cortisol levels occur in brown trout (*Salmo trutta*) within 4 h of immersion in 24–42 µg/L of lysed (small fraction) microcystin (Bury and others, 1996). We tested the hypothesis that high microcystin concentrations are directly correlated with higher mortality through immersion (particulates less than 63 µm, *small.mcystin*, table 4), or through ingestion (particles greater than or equal to 63 µm, *large.mcystin*, table 4). Continuous models were built using weekly microcystin concentrations or interpolated concentrations for small and large particles.

Interactive models were built using hypotheses generated from the literature. We hypothesized that the interactive effects of pH and temperature may cause sucker mortality (*max.temp*max.pH*). High pH may impair proper function of the gills through reduction of oxygen uptake (Das and others, 2006), and high temperature may cause increased metabolic demand and compromised cardiovascular function (Saiki and others, 1999). Typically, neither of these parameters alone is high enough or sustained for long enough to be the direct cause of mortality for suckers in Upper Klamath Lake (Hoilman and others, 2008; Lindenberg and others, 2009; Kannarr and others, 2010; Eldridge, Eldridge, and others, 2012), but we hypothesized that the combined, or interactive effects may cause mortality.

We further hypothesized that the interaction of high temperatures and low DO concentrations may be stressful for suckers (*max.temp*min.DO*). Typically, temperature and DO concentrations in Upper Klamath Lake increase together throughout the day as AFA photosynthesizes. Whereas high temperature results in increased metabolic rate and oxygen demand in fish (Pörtner and Knust, 2007; Pörtner and Farrell, 2008), concurrent elevated DO concentrations during AFA photosynthesis may lessen effects of temperature stress. However, there are isolated instances where AFA dies off (typically when weather conditions are very calm and hot) and DO concentrations are low while temperature is high. We hypothesized that the interaction of low DO concentrations and high temperatures may be causing mortality of juvenile suckers. We used the daily maximum temperature and daily minimum DO concentration as parameters in this interactive model because these two models were the most competitive stand-alone models for these parameters.

Regional experts hypothesized that high un-ionized ammonia concentrations would be associated with increased mortality of juvenile suckers. Because un-ionized ammonia can change weekly and we did not have weekly samples at Fish Banks and only had weekly samples at other sites, we were unable to model the effects of un-ionized ammonia concentrations on survival. Furthermore, we had hoped to estimate un-ionized ammonia from weekly total concentrations and diel changes in pH and temperature, but 24-h ISCO™ samples indicated substantial diel variation in total ammonia. Therefore, we resorted to a qualitative approach to examining the relation between patterns in un-ionized ammonia and mortality events.

To better understand potential causes of mortality and to possibly formulate new hypotheses about how water quality may be contributing to juvenile sucker mortality in mesocosms, we described and summarized water-quality conditions 10 d prior to mortality events as well as conditions during mortality events. Mortality events, characterized by an average of 1 or more for at least 4 days, are highlighted gray in water-quality figures to improve readability and to speculate about potential time delays or cumulative effects.

Known-fate models typically are used to assess the survival (or mortality) of wild, free-ranging animals implanted with radio tags. When assumptions are violated, survival estimates can be biased high or low, so understanding infractions puts estimates in context. Many of the *assumptions* (denoted in this paragraph with *italics*) associated with known fate models of tagged animals are not pertinent to this study because animals were contained in mesocosms and constantly monitored. *Tags were not lost* because tag wounds healed before fish were introduced to mesocosms and fish were checked for tags prior to being introduced to mesocosms. *Tag failure did not occur* because tags were assessed during tagging, double-checked for detectability before fish were released (minimizing malfunction associated with cracked tags), were frequently detected when fish were alive, were detected in most cases for several days after fish died, and were checked again upon fish retrieval (found dead, moribund, or healthy) from the mesocosm. *The tagged population was representative of the total population* because it was the total population in the mesocosm. Although we inferred that the population of mesocosm-held fish used in this study represented wild fish in Upper Klamath Lake, we did not need to explicitly make that assumption for the estimates derived in this study. *Detection probability is 1.0* because living suckers were detected many times (usually every 10 min) each day.

We could *identify the status (live or dead) for each individual during each sampling occasion* (daily from July 18 to September 20) by assessing daily movement patterns, and because of our constant detections, *time intervals were similar among occasions*—1 d. The assumption, *individual animals have independent survivals*, seemed to have been met based on distribution of fates and observations of individual behavior, and movement patterns; namely, fish in mesocosms did not show schooling behavior. Our ability to identify the timing of mortality was limited to within 1 day, so it is unclear whether mortality seemed to occur during a specific time of day (for example); however, 1 d is a short time period for this type of analysis and we did not violate the assumption that *survival is constant over the defined interval*. We did not violate the assumption that *censorship of individuals is random, and not related to fate* by only assessing daily mortality during July 18–September 20. This assumption removed all fish that died within the first week whose mortality may have been associated with transportation stress or acclimation (including one fish whose fate could not be determined).

Table 4. Description of *a priori* variables tested to describe juvenile Lost River sucker mortality within mesocosms in Upper Klamath Lake, south-central Oregon, July 18–September 20, 2016.

[Temperature (temp) measured in degrees Celsius, dissolved-oxygen (DO) concentration measured in milligram per liter (mg/L), and oxygen percent saturation denoted as psat. Mean, mean of all hourly measurements each day at site; max, maximum of all hourly measurements each day at site; min, minimum of all hourly measurements each day at site. All parameters were standardized to ensure equal variance. **Variable:** Water-quality parameters that performed well independently and were not correlated were combined in additive and interactive models. **Abbreviations:** °C, degrees Celsius; <, less than; >, greater than]

Variable	Explanation	Format
time[1]	Variation is date specific	65 unique
site[1]	Variation is site specific	3 unique
dot[1]	No variation, null model	Constant
p23.temp	Percentage of hours greater than 23 °C per day	Continuous
p25.temp	Percentage of hours greater than 25 °C per day	Continuous
mean.temp	Mean daily temperature	Continuous
max.temp	Maximum daily temperature	Continuous
range.temp	Range of daily temperatures	Continuous
mean.temp>22.9°C	Mean daily temperature greater than 22.9 °C	Binary
max.temp>24.9°C	Maximum temperature greater than 24.9 °C	Binary
mean.DO	Mean daily dissolved-oxygen concentration	Continuous
min.DO	Minimum daily dissolved-oxygen concentration	Continuous
p2.DO	Percentage of hours less than 2 mg/L DO concentration	Continuous
min.DO<2	Minimum dissolved-oxygen concentration less than 2 mg/L	Binary
range.DO	Range of daily dissolved-oxygen concentration	Continuous
range.DO>9	Range of DO concentration greater than 9 mg/L	Binary
p50.psat	Percentage of hours less than 50-oxygen percent saturation	Continuous
p35.psat	Percentage of hours less than 35-oxygen percent saturation	Continuous
mean.psat<50	Mean oxygen percent saturation less than 50	Binary
min.psat	Minimum daily oxygen percent saturation	Continuous
max.psat	Maximum daily oxygen percent saturation	Continuous
mean.psat	Mean daily oxygen percent saturation	Continuous
range.psat	Range in daily oxygen percent saturation	Continuous
range.psat>140	Range of oxygen percent saturation greater than 140	Binary
range.pH	Daily range in pH	Continuous
p9.5.pH	Percentage of hours greater than pH 9.5 per day	Continuous
p9.75.pH	Percentage of hours greater than pH 9.75 per day	Continuous
mean.pH>8.45	Mean pH greater than 8.45	Binary
max.pH>8.9	Max pH greater than 8.9	Binary
range.pH>0.9	Range in pH greater than 0.9	Binary
mean.pH	Mean daily pH	Continuous
max.pH	Maximum daily pH	Continuous
small.mcystin	Measured (or interpolated) microcystin less than 63 µm	Continuous
large.mcystin	Measured (or interpolated) microcystin greater than or equal to 63 µm	Continuous

[1]Time, site, and null models included to assess fit relative to water-quality models.

Growth and Condition

To examine growth and changes in conditions in each mesocosm, suckers introduced at the beginning of this study were weighed (to the nearest 10th of a gram) and measured to standard length (SL, nearest millimeter) 5 d prior to being introduced to mesocosms; suckers introduced throughout the study were weighed and measured the day they were introduced to the mesocosms. All moribund suckers and suckers removed from the mesocosms at the end of the study period were measured to standard length and weighed. The Fulton body condition was calculated using $K=[\text{weight (wt)}/SL^3]\times10^5$ (Ricker, 1975). Total change in standard length, weight, and body condition was assessed among sites for all suckers introduced at the beginning of the study and sacrificed at the end of the study. Initial body size (standard length, weight, and body condition) of individuals that survived the entire study period and those that died during this study period also was compared. Growth and condition were compared among sites using statistical graphical methods described by Chambers and others (1983).

Sucker Health and Investigation of Causes of Morbidity

To examine changes in health and causes of mortality, an overdose of MS-222 anesthetic was used to euthanize all pre-season baseline suckers, moribund and apparently healthy suckers captured during the study, and suckers sacrificed at the end of the study period. An external visual assessment identified afflictions including damage to fins or body, atypical pigmentation, and the presence and abundance of parasites or bacterial infections on all sacrificed fish. Internal macroscopic assessments were conducted on all moribund fish (N=13 for Fish Banks, N=2 for Mid North, and N=1 for Rattlesnake Point), one healthy fish sacrificed from Rattlesnake Point in the middle of the season, a subset of randomly selected fish that survived the entire study duration (N=5 for Fish Banks, N=9 for Mid North, and N=10 for Rattlesnake Point), and one sucker introduced to Mid North on July 22 and sacrificed at the end of the study. Internal macroscopic assessments identified the appearance and color of the gills, the color and the texture of the liver and spleen, the color and distention of the gall bladder, and the relative amount of visceral fat (Goede and Barton, 1990). External and internal assessments were quickly done and all samples for histological analysis were preserved in Carson's modified Millonig phosphate-buffered formalin (Carson and others, 1973) within 5 min of sacrifice. A gill sample from all mesocosm fish sacrificed for histological analysis was collected and stored in 95-percent ethanol for detection and quantification of *Ichthyobodo* sp. protozoan parasites by use of a real-time quantitative Polymerase Chain Reaction (qPCR) assay. Fish samples for histological examination were stored in formalin for 3–5 d, and then transferred to 70-percent ethanol. Preserved fish were weighed in the laboratory to the nearest 0.1g.

Tissue Preparation for Histology

To microscopically assess health and learn about causes of mortality, histopathological evaluations were done on 18 suckers from Fish Banks, 12 suckers from Mid North, and 12 suckers from Rattlesnake Point, and were compared with 5 suckers sacrificed at the beginning of the study from the Klamath Tribes Fish Research Facility (table 5). Comparisons between healthy and moribund fish were made to determine potential causes of death in mesocosms. Most of histopathological analyses were done on suckers sacrificed at the end of the study period, although a few healthy and moribund suckers were collected when available.

Table 5. Sample dates, sample types, and number of suckers collected for histopathological assessments prior to mesocosm study (baseline) from the Klamath Tribes Fish Research Facility and throughout the study from mesocosms in Upper Klamath Lake, south-central Oregon, 2016.

[– indicates that no fish were collected in a particular week]

Group	Baseline	Fish Banks	Mid North	Rattlesnake Point
Sample dates	July 6	Aug 16–18	Aug 17	–
Sample type	Pre-season assessment	Healthy	Moribund	–
Count	5	3	1	–
Sample dates	–	Aug 22–26	Aug 25	Aug 31
Sample type	–	Moribund	Moribund	Moribund[1]
Count	–	5	1	1
Sample dates	–	Sept 9–28	–	Sept 9
Sample type	–	Moribund	–	Healthy
Count	–	5	–	1
Sample date	–	Oct 28	Oct 31	Nov 1
Sample type	–	End of season	End of season	End of season
Count	–	5	10	10
Total	5	18	12	12

[1]Gross field assessments of this sucker indicated that it appeared healthy; however, a histological assessment indicated that its health was compromised.

We collected samples of gill, liver, spleen, pancreatic tissue, gastrointestinal tract, heart, anterior kidney, and posterior kidney from formalin-preserved suckers for histopathological analysis. Samples of skin and skeletal muscle also were collected from fish with external lesions or parasites. Samples were prepared using methods described by Hereford, Burdick, and others (2016) and examined by light microscopy. The degree of host response, including distribution and severity of inflammation, fibrosis and cell necrosis per 200× microscope field was scored using a four-point scale. Host response distribution was ranked as none (0), focal (1), multifocal (2), or diffuse (3), and severity was scored as none (0), minimal to mild (1), moderate (2), or severe (3). Parasites were identified and the degree of host response was assessed. The amount of liver energy storage (as hepatocyte glycogen) was used as an index of relative nutritional status and was assessed by the presence and appearance of vacuoles in hepatocyte cytoplasm, and the staining characteristics of the cytoplasm. Periodic acid-Schiff (PAS) and PAS-diastase (D-PAS; Carson, 1997) were used to stain liver tissue and estimates of the amount of glycogen stored in the hepatocyte cytoplasm were rated as none (0), focal (low levels = 1), or multifocal to diffuse (high levels = 2). We compared the estimates of hepatocyte glycogen to estimates of fat abundance as assessed during internal macroscopic Goede Index exams. Bacteria were stained with May-Grünwald giemsa (Carson, 1997) and Lillie-Twort, West modification Gram (Culling, 1974) stains.

Ichthyobodo Evaluation

To test for the presence of *Ichthyobodo* sp. gill parasites, gill samples from 20 control specimens at the Klamath Tribes Fish Research Facility were collected on April 12, 2016, and were genetically assayed using qPCR for *Ichthybodo* sp. before the beginning of the study. Gill samples also were collected throughout the study from all moribund suckers and a subsample from end-of-season sacrifices at each mesocosm (Fish Banks N=7, Mid North N=29, Rattlesnake Point N= 20). Deoxyribonucleic acid (DNA) extraction was completed using Qiagen DNeasy® Blood and Tissue Kits following the manufacturer protocol, with the following modifications: 360 µL of Buffer ATL and 40 µL of Proteinase-K were used for membrane lysis, and the volume of 100-percent ethanol and Buffer AL was increased to 400 µL. DNA was stored at -20 °C prior to analysis. A subsample of extracted DNA was assayed for the gill parasite *Ichthyobodo* sp. using qPCR methods and cycles described by Isaksen and others (2012) and done using the ViiA™ 7 Real-Time PCR System (Thermo Fisher Scientific). The reactions contained 6 µL of real-time PCR master mix (TaqMan® Gene Expression Master Mix; Life Technologies), 900 nanomolar (nM) of each primer, 200 nM of the probe, and 5 µL of DNA template in a total reaction volume of 12 µL. Quantification of target DNA was achieved using a standard curve generated from a plasmid-based artificial positive control. The artificial positive control encodes the qPCR target amplicon plus an artificial tag sequence (Integrated DNA Technologies). Estimated numbers of *Ichthyobodo* cells per sample were based on threshold cycle values (C_T) according to Isaksen and others, 2012.

Results

Seasonal Variation in Depth, Temperature, Dissolved Oxygen, and pH

Water temperatures increased as total depth decreased in July, after which depth and temperature were uncorrelated (figs. 2 and 3). Water temperatures at all three sites generally increased through July, decreased slightly in the beginning of August, gradually increased again and remained high until August 22 (Fish Banks and Rattlesnake Point) or August 23 (Mid North) when temperatures primarily decreased for the rest of the season (fig. 3). Over the course of the season (July 18–September 20), temperatures had the greatest range at Fish Banks, the lowest range at Mid North, and an intermediate range at Rattlesnake Point (table 6). Maximum daily temperatures were greatest and temperatures had the greatest diel range at Fish Banks (tables 6 and 7). Seasonal mean daily temperature ranges were similar at Mid North and Rattlesnake Point (table 6). Temperatures typically were stratified from late morning (10:00 or 11:00 a.m.) to around midnight (11:00 p.m., 12:00 a.m., or 1:00 a.m.) at Fish Banks and Mid North. Hourly temperature measurements exceeded 25 °C at least once on 20 d at Fish Banks, but only on 2 d each at Mid North and Rattlesnake Point.

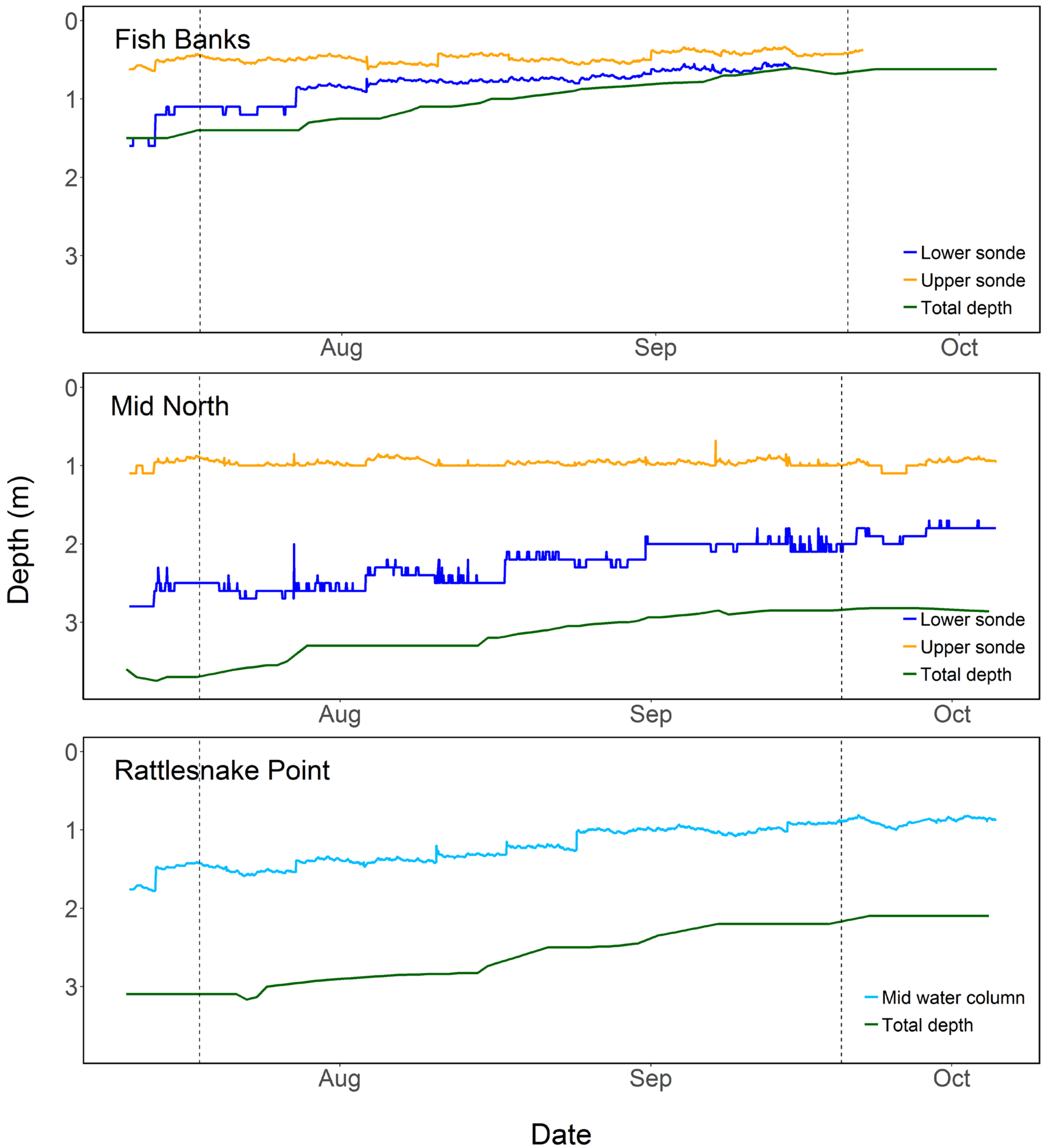

Figure 2. Graphs showing total water depth and depth of water-quality measurements near mesocosms (in meters below water surface [m]), Upper Klamath Lake, south-central Oregon, 2016. Water-quality measurements were taken during July 11–September 20, 2016 at Fish Banks. Black dashed vertical lines indicate beginning and end of season for analysis.

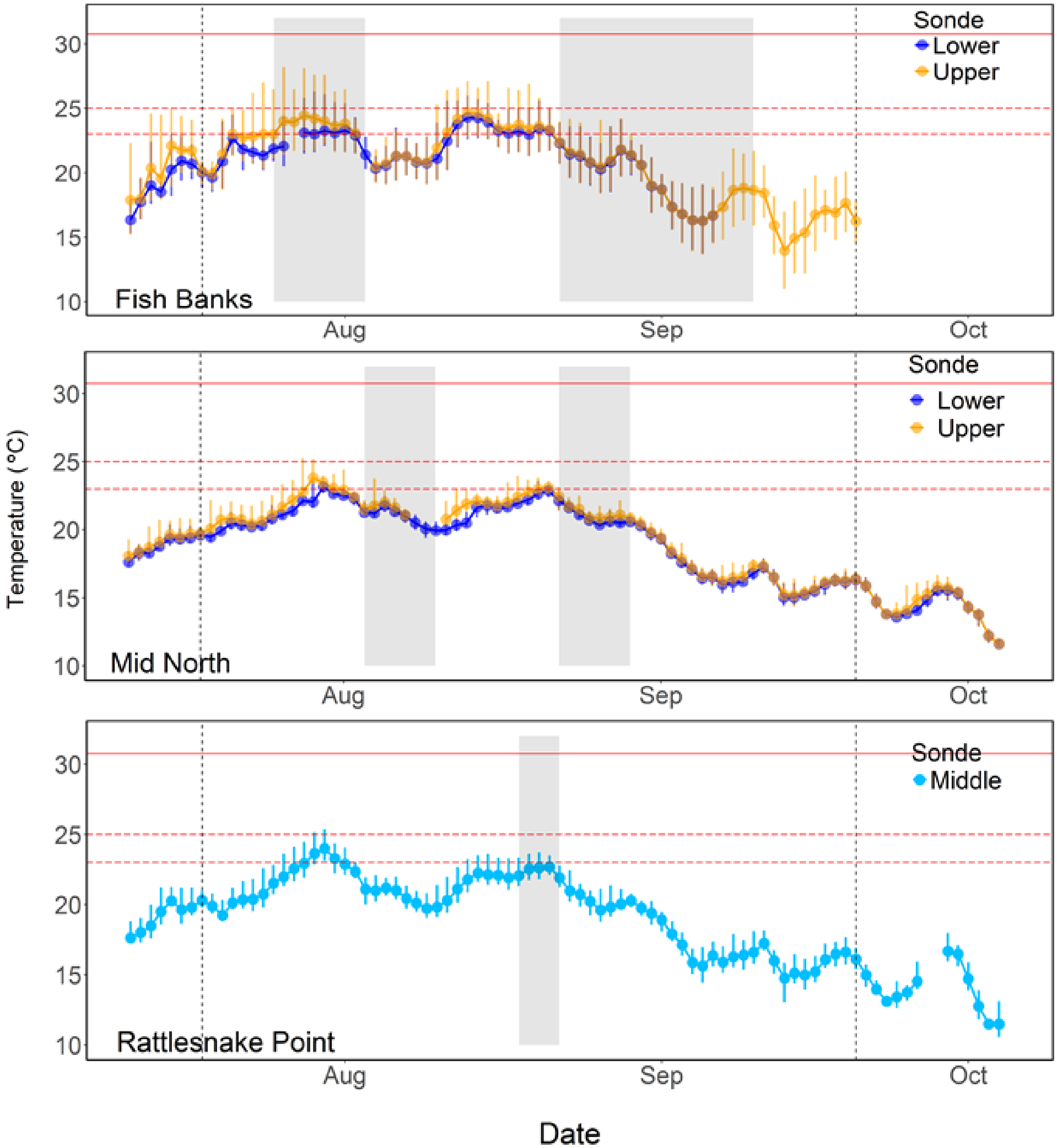

Figure 3. Graphs showing mean (circles), minimum (bottom of vertical lines) and maximum (top of vertical lines) of daily water temperature measurements near mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016. Solid horizontal lines at 30.76 degrees Celsius (°C) represent 24-hour median lethal temperature LC50 for juvenile Lost River suckers identified by Saiki and others (1999). Dashed horizontal lines represent 23 and 25 °C, the temperature thresholds selected to build some models for this study based on conditions measured in 2016. Black dashed vertical lines indicate beginning (July 18) and end (September 20) of season for mortality analysis. Gray regions highlight sucker mortality events.

Table 6. Summary of seasonal water-quality conditions measured at Fish Banks, Mid North, and Rattlesnake Point sites in Upper Klamath Lake, south-central Oregon, 2016.

[Seasonal summary are statistics of all hourly data measured, July 18–September 20, 2016. Small fraction microcystins were less than 63µm, whereas large fraction were greater than or equal to 63 µm. **Abbreviations:** °C, degrees Celsius; DO, dissolved oxygen; pH, potential hydrogen; sd, standard deviation; m, meter; µg/L, microgram per liter; mg/L, milligram per liter; ±, plus or minus]

Statistic	Site		
	Fish Banks	Mid North	Rattlesnake Point
Number of sondes	2	2	1
Location of sonde(s)	0.3 m from surface/benthos	1 m from surface/benthos	Mid-water column
Seasonal summary			
Temperature (°C)			
Mean ± sd	21.0 ± 2.9	19.9 ± 2.5	19.7 ± 2.6
Minimum (date)	11.0 (September 13)	14.4 (September 13, 14)	13.0 (September 13)
Maximum (date)	28.2 (July 26)	25.3 (July 28)	25.4 (July 30)
DO concentration (mg/L)			
Mean ± sd	6.5 ± 2.8	6.9 ± 2.3	8.3± 1.5
Minimum (date)	0.6 (Aug 30)	0 (July 29, August 13)	3.3 (July 29)
Maximum (date)	16.1 (September 11)	15.4 (August 4)	13.0 (July 23)
Oxygen percent saturation			
Mean ± sd	84.8 ± 37.7	87.3 ± 29.6	105.0 ± 19.1
Minimum (date)	8 (August 30)	0 (July 29, August 13)	46 (July 29)
Maximum (date)	220 (July 29)	211 (August 4)	172 (July 23)
pH			
Mean ± sd	8.7 ± 0.5	9.0 ± 0.5	9.3 ± 0.4
Minimum (date)	7.2 (August 20)	7.3 (September 19)	7.9 (September 13)
Maximum (date)	9.6 (July 20, 22-26, 29)	10 (July 26)	10.3 (July 22)
Un-ionized ammonia (µg/L)			
Mean ± sd	24.1 ± 13.7	137.5 ± 69.1	96.5 ± 104.1
Minimum (date)	5.6 (July 19)	1.2 (September 13)	1.8 (September 13)
Maximum (date)	72.2 (August 15)	251.0 (August 15)	384.3 (August 17)
Microcystin (small fraction)			
mean ± sd	0.18 ± 0.07	0.16 ± 0.02	0.16 ± 0.02
minimum (date)	0.15 (many dates)	0.15 (August 2-September	0.15 (many dates)
maximum (date)	0.37 (August 16)	0.21 (July 26)	0.22 (August 16)
Microcystin (large fraction)			
Mean ± sd	0.36 ± 0.26	0.09 ± 0.07	0.17 ± 0.22
Minimum (date)	0.06 (July 19)	0.02 (July 19)	0.01 (September 20)
Maximum (date)	0.84 (September 6)	0.23 (September 13)	0.64 (August 23)

Table 7. Summary of diel water-quality conditions measured at Fish Banks, Mid North, and Rattlesnake Point sites in Upper Klamath Lake, south-central Oregon, July 18–September 20, 2016.

[Diel summary statistics were derived from daily statistics (hourly data summarized by day). For example, the maximum diel mean is the day that had highest mean, which for temperature at Fish Banks occurred on August 13 and was 24.5 °C. **Abbreviations:** °C, degrees Celsius; DO, dissolved oxygen; pH, potential hydrogen; sd, standard deviation; m, meter; mg/L, milligram per liter; ±, plus or minus]

Statistic	Site		
	Fish Banks	Mid North	Rattlesnake Point
Number of sondes	2	2	1
Location of sonde(s)	0.3 m from surface/benthos	1 m from surface/benthos	Mid-water column
Diel summary			
Temperature (°C)			
Diel mean ± sd	20.6 ± 2.8	19.9 ± 2.4	19.7 ± 2.6
Maximum diel mean (date)	24.5 (August 13)	23.3 (July 30)	24.0 (July 30)
Mean diel range ± sd	4.6 ± 1.2	1.7 ± 0.7	1.9 ± 0.4
Maximum diel range (date)	7.7 (July 26)	3.6 (July 29)	2.8 (July 24, September 13)
DO concentration (mg/L)			
Diel mean ± sd	6.7 ± 1.9	6.8 ±1.5	8.3 ± 0.9
Minimum daily mean (date)	2.9 (August 16)	2.9 (August 16)	5.8 (August 15)
Mean diel range ± sd	7.1 ± 2.5	6.5 ± 2.3	3.7 ± 1.4
Maximum range (date)	13.3 (July 29)	12.2 (July 28)	7.4 (July 29)
Oxygen percent saturation			
Diel mean ± sd	86.7 ± 21.8	86.9 ± 18.5	105.0 ± 10.3
Minimum diel mean (date)	40.1 (August 16)	39.1 (August 16)	77.2 (August 15)
Maximum diel mean (date)	125.3 (September 11)	116.4 (August 26)	125.8 (July 23)
Mean diel range ± sd	100.4 ± 36.4	86.1 ± 33.0	51.1 ± 19.8
Maximum range (date)	199 (July 29)	164 (July 28)	105 (July 29)
pH			
Diel mean ± sd	8.7 ± 0.4	9.0 ± 0.5	9.3 ± 0.4
Maximum diel mean (date)	9.3 (July 21)	9.8 (July 18)	10.0 (July 18)
Mean diel range ± sd	1.1 ± 0.4	0.6 ± 0.2	0.4 ± 0.2
Maximum diel range (date)	2.1 (July 29)	1.2 (September 17)	1.1 (September 13)

Dissolved-oxygen concentrations varied diurnally, seasonally, vertically throughout the water column, and among sites (tables 6 and 7). Diurnal DO concentrations typically were lowest from 7:00 to 8:00 a.m. at both Fish Banks sondes, Mid North upper sonde, and Rattlesnake Point. In contrast, DO concentrations on the Mid North lower sonde typically were lowest at 3 p.m. There were three general decreases in DO concentrations (bloom-crashes) at Fish Banks, and two each at Mid North and Rattlesnake Point (fig. 4). The daily mean DO concentration and seasonal range in daily mean DO concentrations were lower at Fish Banks and Mid North than at Rattlesnake Point (tables 6 and 7). Dissolved-oxygen concentrations usually were greater near the surface than near the benthos at Fish Banks and Mid North where measurements were taken at two depths (fig. 4). The most extreme low DO concentrations (<1 mg/L) occurred near the bottom sonde at Mid North for 17 consecutive hours on July 29, 9 non-consecutive hours August 12, and 17 non-consecutive hours on August 13. DO concentrations typically were divergent (stratified) from late morning (9 or 10 a.m.) to around midnight at Fish Banks and Mid North. Prolonged (that is, more than the typical 14–15 hours) stratification of DO concentrations occurred three periods at Mid North—July 26–29, August 12–14, and August 18–19. Diurnal DO concentrations typically were greatest from 4 to 6 p.m. at both Fish Banks sondes, and from 5 to 8 p.m. at Mid North upper sonde and Rattlesnake Point.

Temporal and spatial variation in oxygen percent saturation followed the same general patterns as DO concentrations but identified more continuous periods of potentially stressful conditions (fig. 5; tables 6 and 7). At Fish Banks, oxygen percent saturation was 18 percent or less during 9 d (1–7 hours each time) in the lower water column and 6 d throughout the entire water column. At Mid North, oxygen percent saturation was less than 18 percent on 12 d near the benthos; most noteworthy were 18 consecutive hours on July 29 and 22 consecutive hours during August 12–13. However, oxygen saturation was always greater than 18 percent near the surface sonde at Mid North and at the mid-water column at Rattlesnake Point.

Throughout the season, pH fluctuated substantially at Fish Banks and did not have an apparent seasonal trend (fig. 6). In contrast, pH at Mid North and Rattlesnake Point was highest at the beginning of the season and generally declined as the season progressed (fig. 6). Diurnal fluctuations in pH were on average similar among sites (table 7) but were nearly two times greater at Fish Banks than at the other two sites several times throughout the season (fig. 6).

At Fish Banks and Mid North, stratification of pH commonly occurred from about 9:00 a.m. until 1:00 a.m., and pH typically was higher near the surface. Maximum diurnal pH typically occurred from 3 to 6 p.m. at Fish Banks (upper and lower sondes), Mid North upper sonde, and Rattlesnake Point (mid-water column sonde). Minimum diurnal pH typically occurred at 7 or 8 a.m. at Fish Banks upper sonde, Mid North upper sonde, and Rattlesnake Point. Minimum diurnal pH typically occurred at 11:00 a.m. at Fish Banks lower sonde. Diurnal pH at Mid North lower sonde was on average highest at 11 p.m. and lowest at 2 p.m.

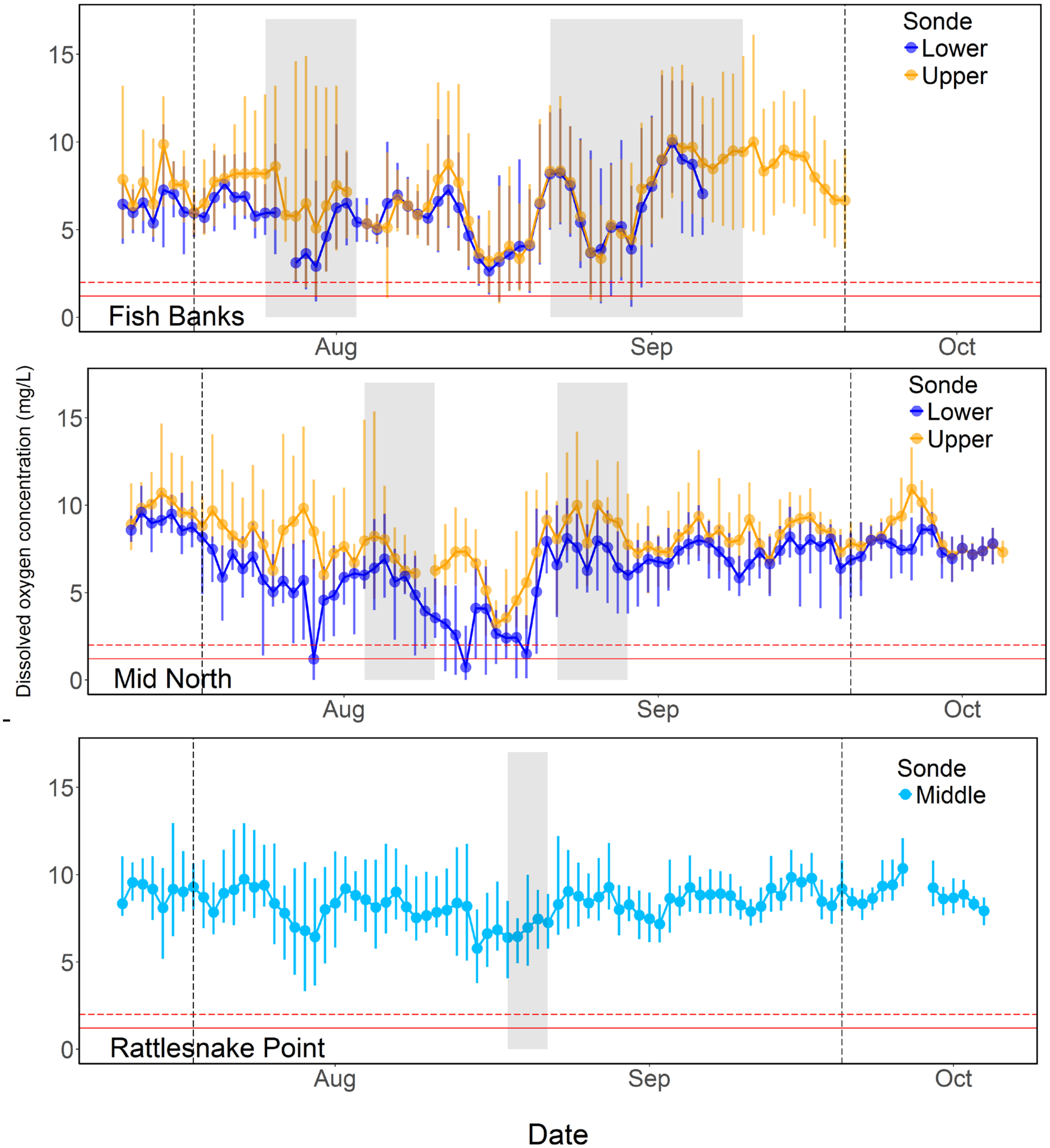

Figure 4. Graphs showing mean (circles), minimum (bottom of vertical lines) and maximum (top of vertical lines) of daily dissolved-oxygen (DO) concentration measurements near mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016. Solid horizontal line at 1.21 milligrams per liter (mg/L) DO concentration represents the lowest 24-hour (h) median lethal concentration (LC50) tested for juvenile Lost River suckers by Meyer and Hansen (2002). Meyer and Hansen reported that actual DO LC50 was less than 1.21 mg/L, and also less than 1.16 mg/L, the lowest 48-h DO concentration in which more than 50 percent of juvenile Lost River suckers survived their lethal trials. Dashed horizontal lines represent 2 mg/L—DO concentration thresholds used to build some models for this study based on conditions measured in 2016. Black dashed vertical lines indicate beginning (July 18) and end (September 20) of season for mortality analysis. Gray regions highlight sucker mortality events.

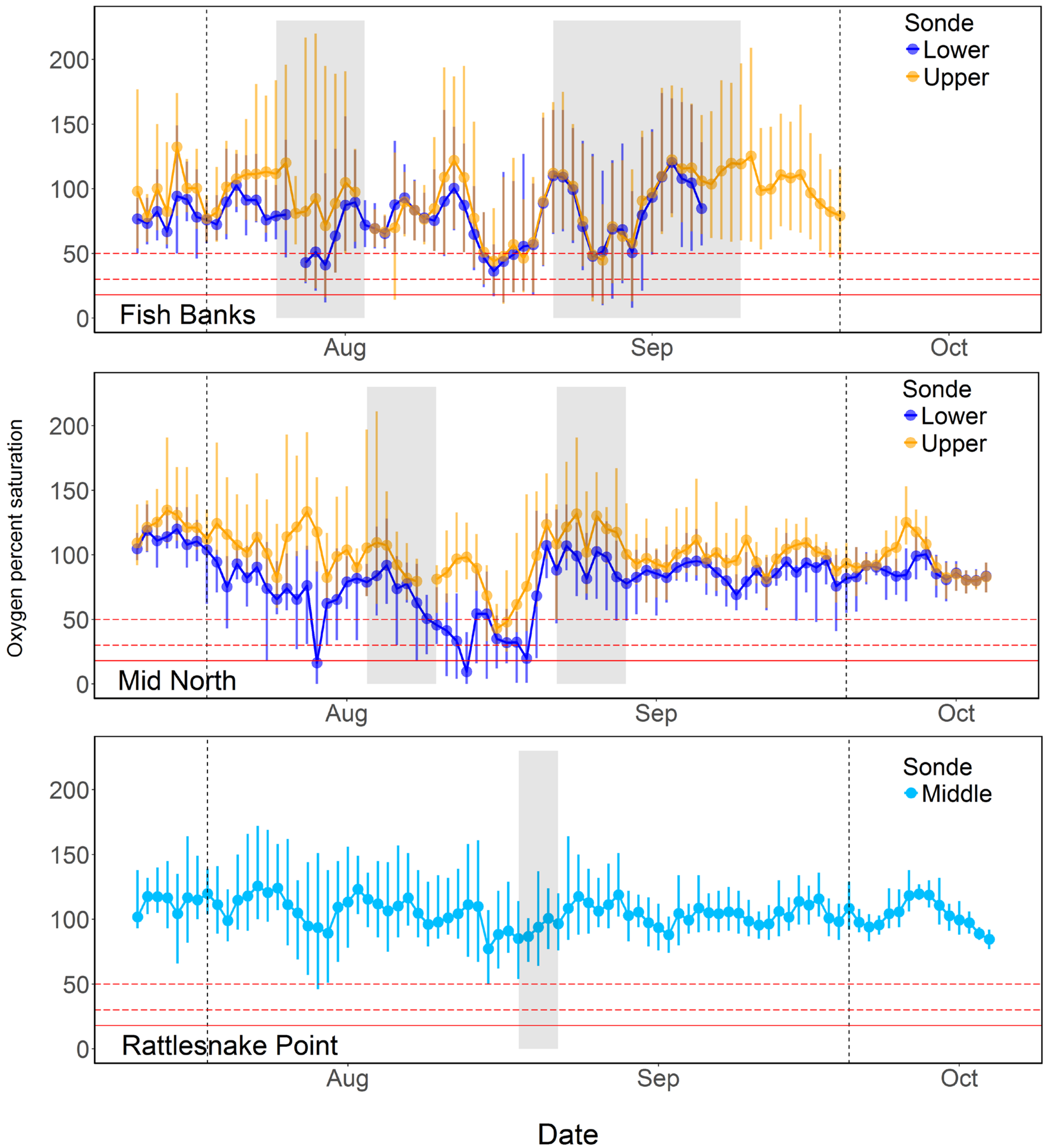

Figure 5. Graphs showing mean (circles), minimum (bottom of vertical lines) and maximum (top of vertical lines) of daily oxygen percent saturation measurements near mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016. Measurements were taken in middle water column at Rattlesnake Point. Horizontal dashed lines represent 30- and 50- percent oxygen saturation—thresholds selected to build some models for this study based on conditions measured in 2016. Solid horizontal lines represent estimated percent saturation LC50 (median lethal concentration; 18 percent) derived from dissolved oxygen LC50, and laboratory elevation and temperature in Meyer and Hansen (2002). Black dashed vertical lines indicate beginning and end of season for mortality analysis. Gray regions highlight sucker mortality events.

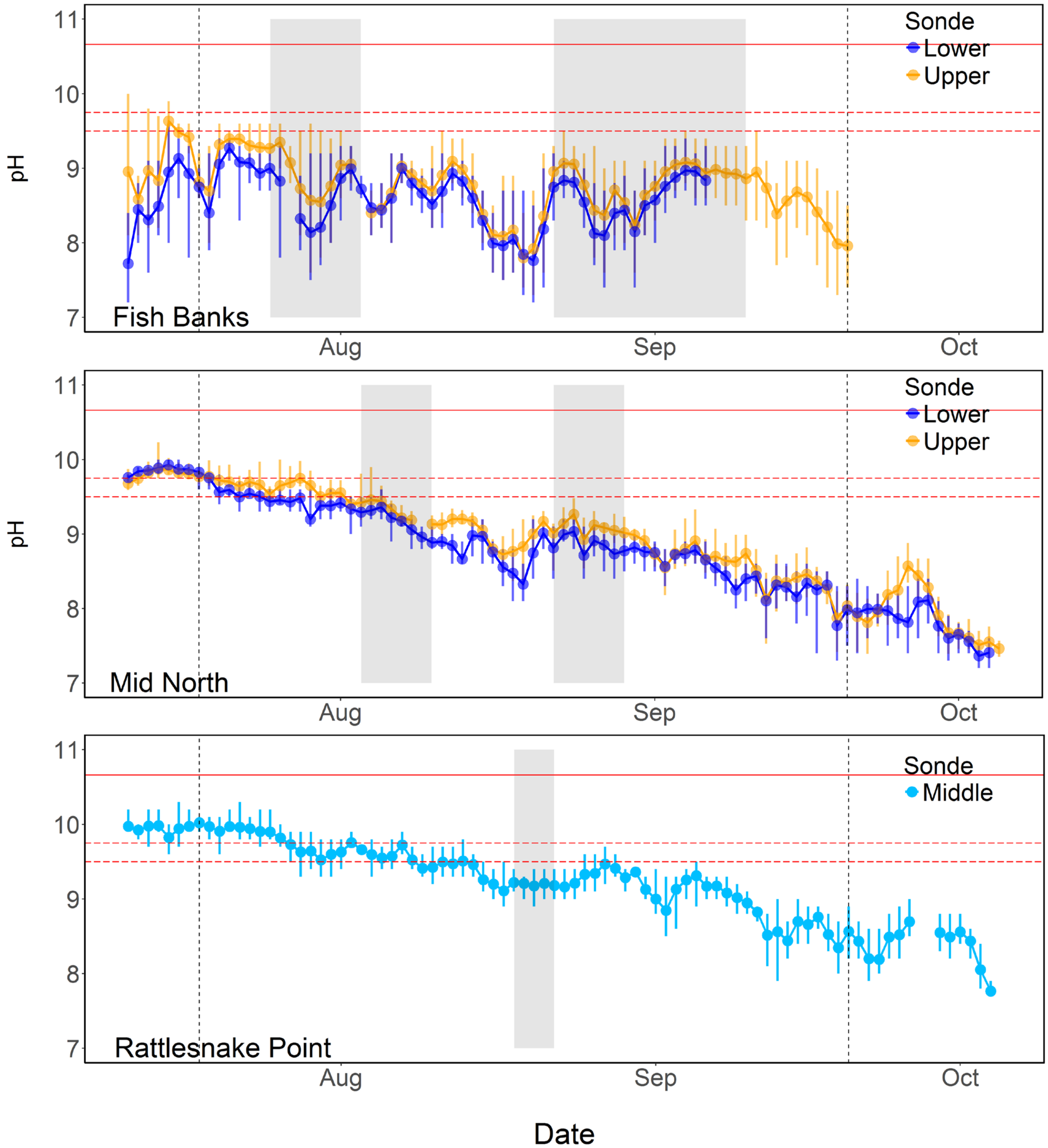

Figure 6. Graphs showing mean (circles), minimum (bottom of vertical lines) and maximum (top of vertical lines) of daily pH measurements near mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016. Solid horizontal lines at pH 10.66 represent 24-hour LC50 (median lethal concentration) for juvenile Lost River suckers identified by Saiki and others (1999). Dashed horizontal lines represent 9.5 and 9.75—pH thresholds selected to build some models for this study based on conditions measured in 2016. Black dashed vertical lines indicate beginning and end of season for mortality analysis. Gray regions highlight sucker mortality events.

Water-Column Stratification

At Fish Banks, DO concentrations were consistent throughout the water column except for very near the benthos where DO concentrations were much lower than the rest of the water column (fig. 7). A few exceptions include July 14, when DO concentrations were about 3.5 mg/L in the lowest meter but about 10 mg/L in the top 0.25 m. Several stratification events occurred at Mid North in July and August. DO concentrations reached high and extremely high levels on July 11 and July 28, respectively, indicative of massive AFA blooms in the upper 1 m of the water column (fig. 8). Water-column stratification occurred most often in August at Rattlesnake Point. Stratification typically occurred about 1 m below the surface (fig. 9).

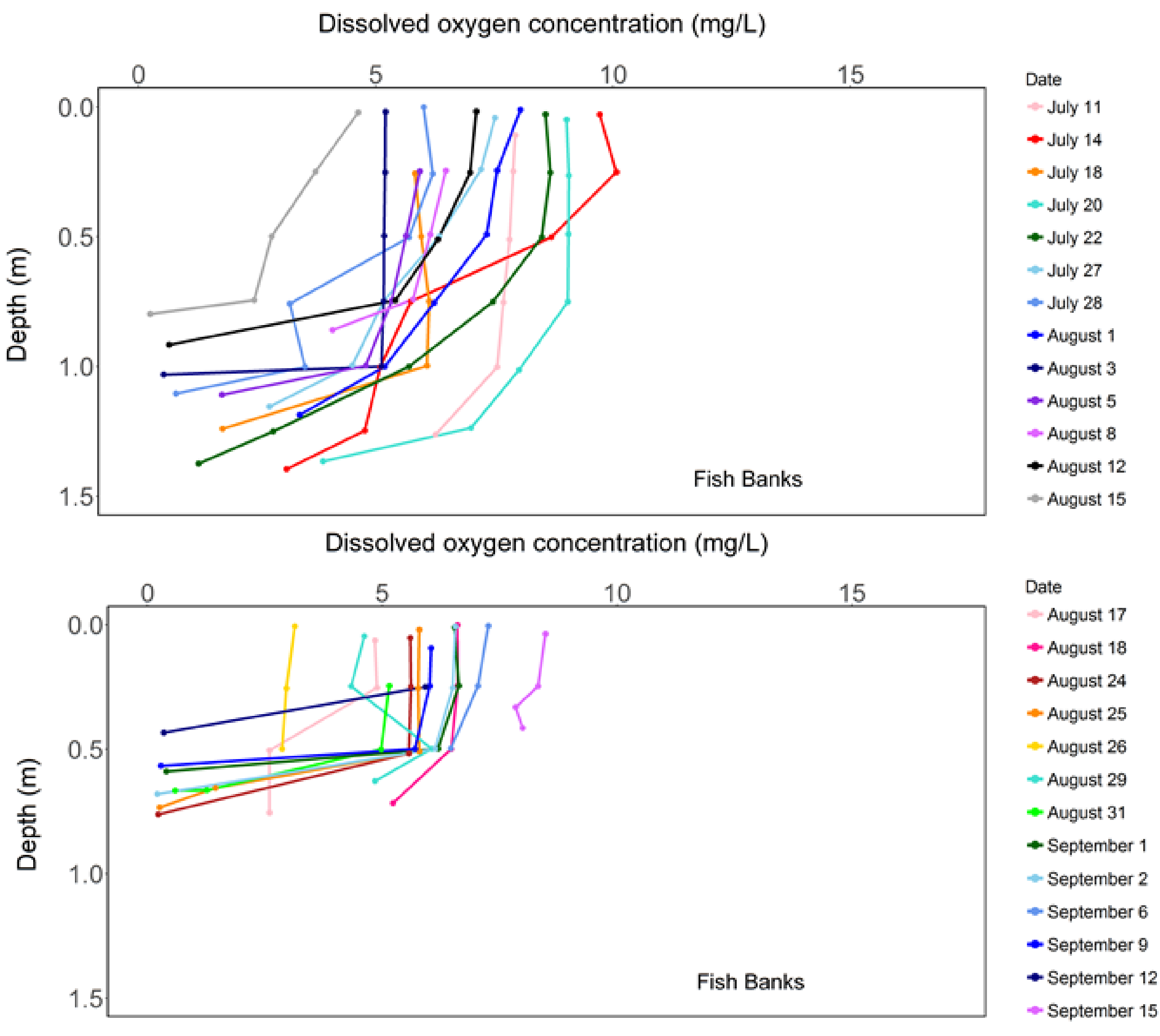

Figure 7. Graphs showing dissolved-oxygen concentration profiles (in milligrams per liter [mg/L]) taken about every 0.25 meters (m) during site visits at Fish Banks mesocosm in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016.

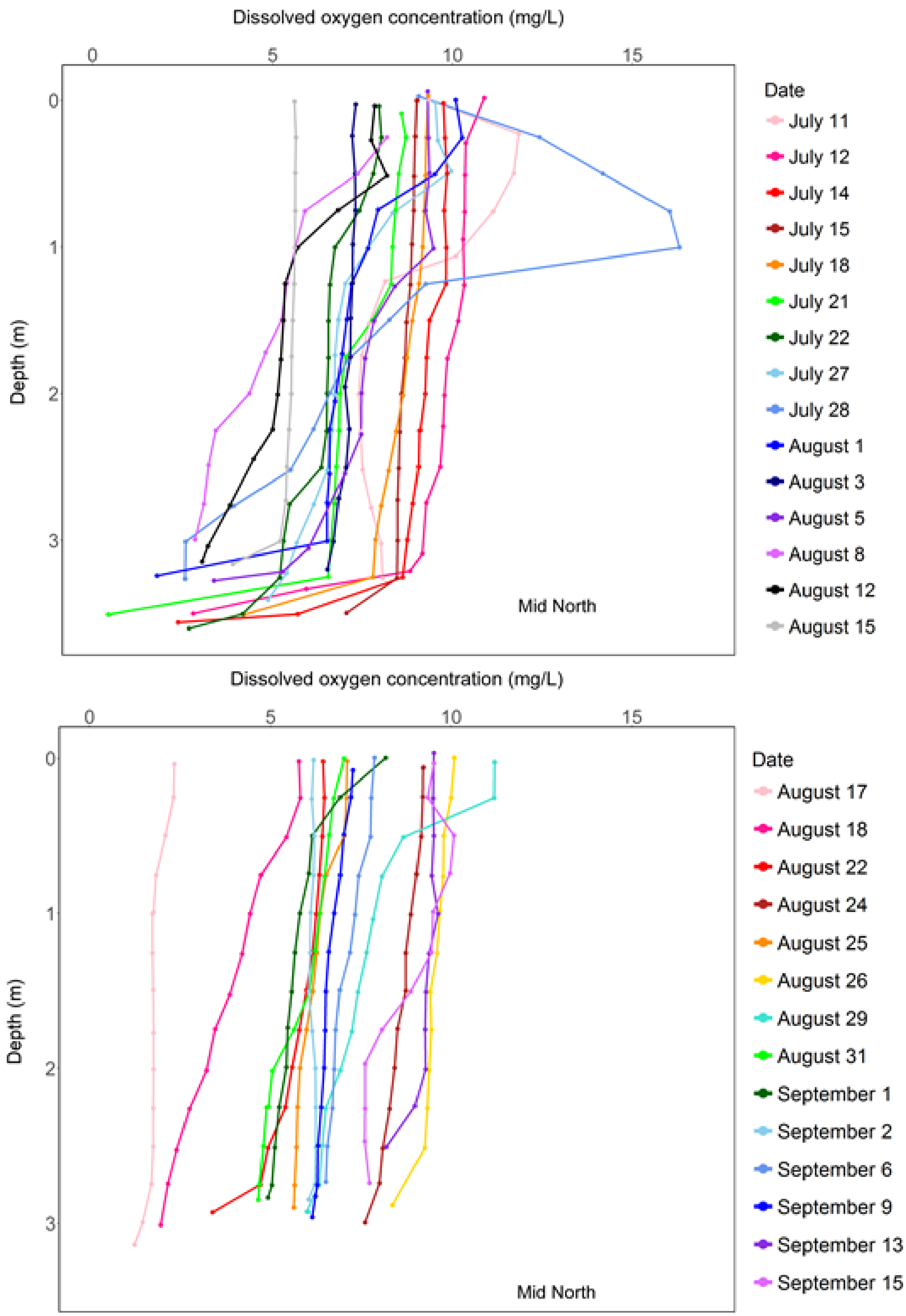

Figure 8. Graphs showing dissolved-oxygen concentration profiles (in milligrams per liter [mg/L]) taken about every 0.25 meters (m) during site visits at Mid North mesocosm in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016.

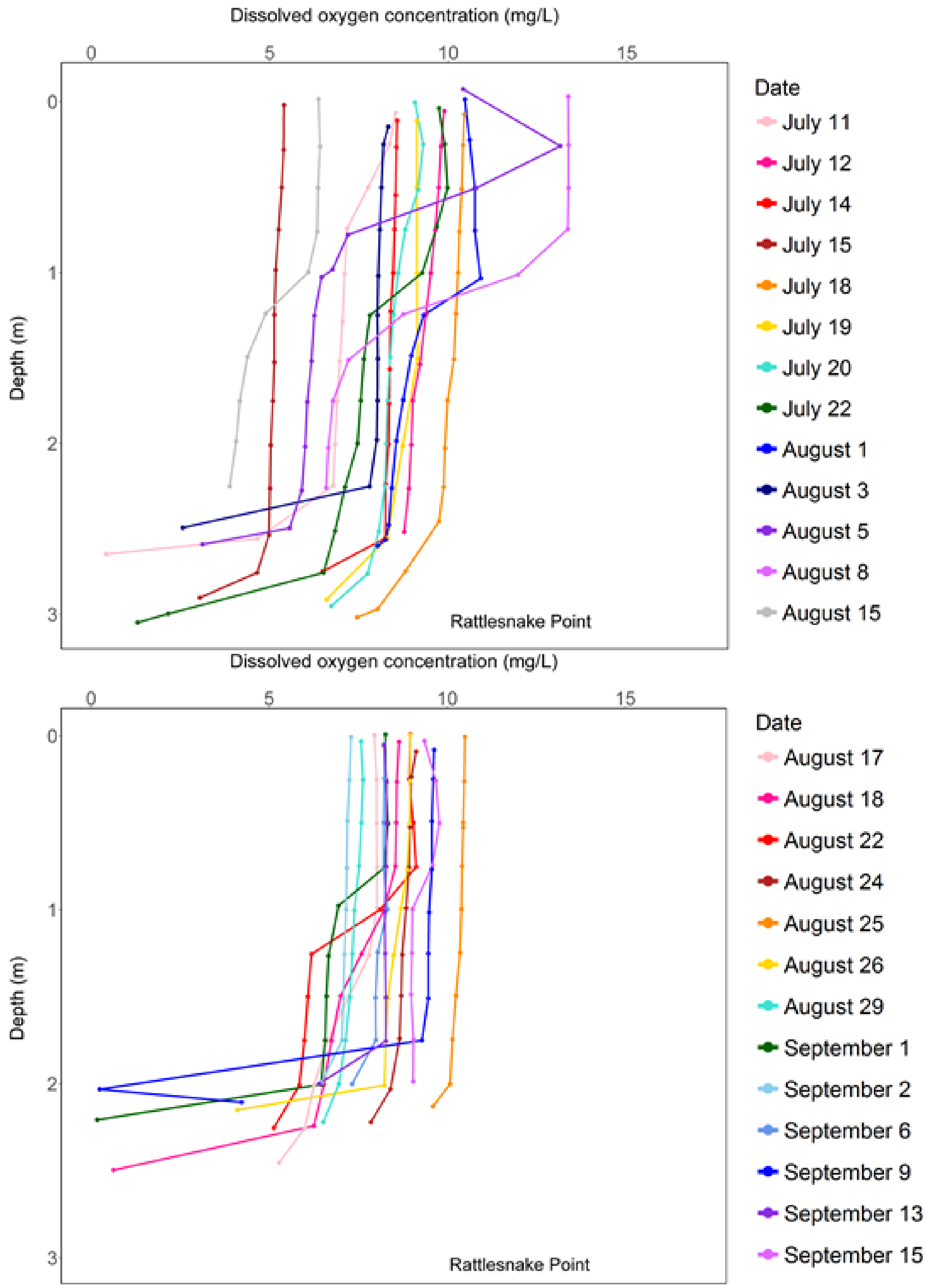

Figure 9. Graphs showing dissolved-oxygen concentration profiles (in milligrams per liter [mg/L]) taken about every 0.25 meters (m) during site visits at Rattlesnake Point mesocosm in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016.

Microcystin

Concentrations of large fraction (≥63 µm) microcystins were less than 0.85 µg/L at all sites during all sampling occasions in 2016. Concentrations of large fraction microcystins ranged from 0.06 to 0.84 µg/L at Fish Banks, 0.02 to 0.23 µg/L at Mid North, and 0.01 to 0.64 µg/L at Rattlesnake Point. Large fraction microcystins were highest at Fish Banks in August and September, relatively constant at Mid North throughout the entire season, and highest at Rattlesnake Point in August (fig. 10).

Concentrations of small fraction (<63 µm) microcystins were relatively constant and less than 0.23 µg/L at all sites during all sampling occasions in 2016 except at Fish Banks on August 16 when the small fraction increased to 0.37 µg/L. Concentrations of small fraction microcystins ranged from 0.15 to 0.37 µg/L at Fish Banks, 0.15 to 0.21 µg/L at Mid North, and 0.15 to 0.22 µg/L at Rattlesnake Point (fig. 10).

Un-ionized Ammonia

Measured concentrations of un-ionized ammonia were relatively low throughout the season but were highest in August at all sites (fig. 11, table 6). Measurements of un-ionized ammonia ranged from 5.6 to 72.2 µg/L at Fish Banks, 1.2 to 251.0 µg/L at Mid North, and from 1.8 to 384.3 µg/L at Rattlesnake Point. The highest concentrations of un-ionized ammonia were all collected by ISCO™ samplers in the evening and occurred at Fish Banks on August 15 at 5 p.m. (72.2 µg/L), Mid North on August 15 at 8 p.m. (251.0 µg/L), and Rattlesnake Point on August 17 at 7 p.m. (384.3 µg/L; fig. 11). At Rattlesnake Point, un-ionized ammonia was greater than 200 µg/L for 10 hours with only one hourly measurement exceeding 370 µg/L, the threshold at which gill damage was observed in laboratory suckers after 30 h exposures (Lease and others, 2003). At Mid North, un-ionized ammonia was greater than 200 µg/L for 2 h on August 15.

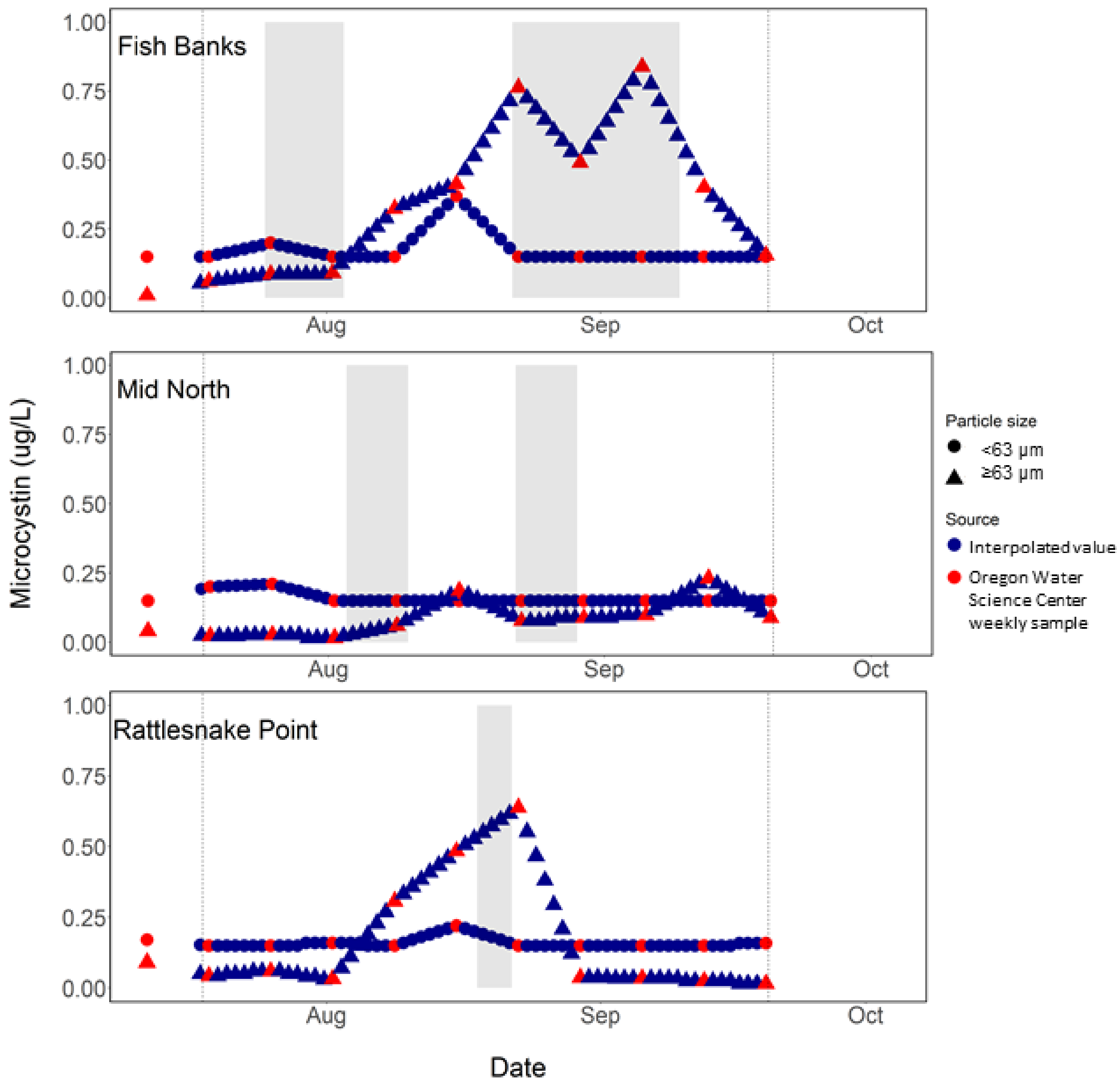

Figure 10. Graphs showing concentrations of small (less than 63 micrometer [µm]) and large (63 µm or larger) fraction microcystins (in micrograms per liter [µg/L]) near mesocosm sites in Upper Klamath Lake, south-central Oregon, July 12–September 20, 2016. Black dashed vertical lines indicate beginning and end of season for mortality analysis. Gray regions highlight sucker mortality events.

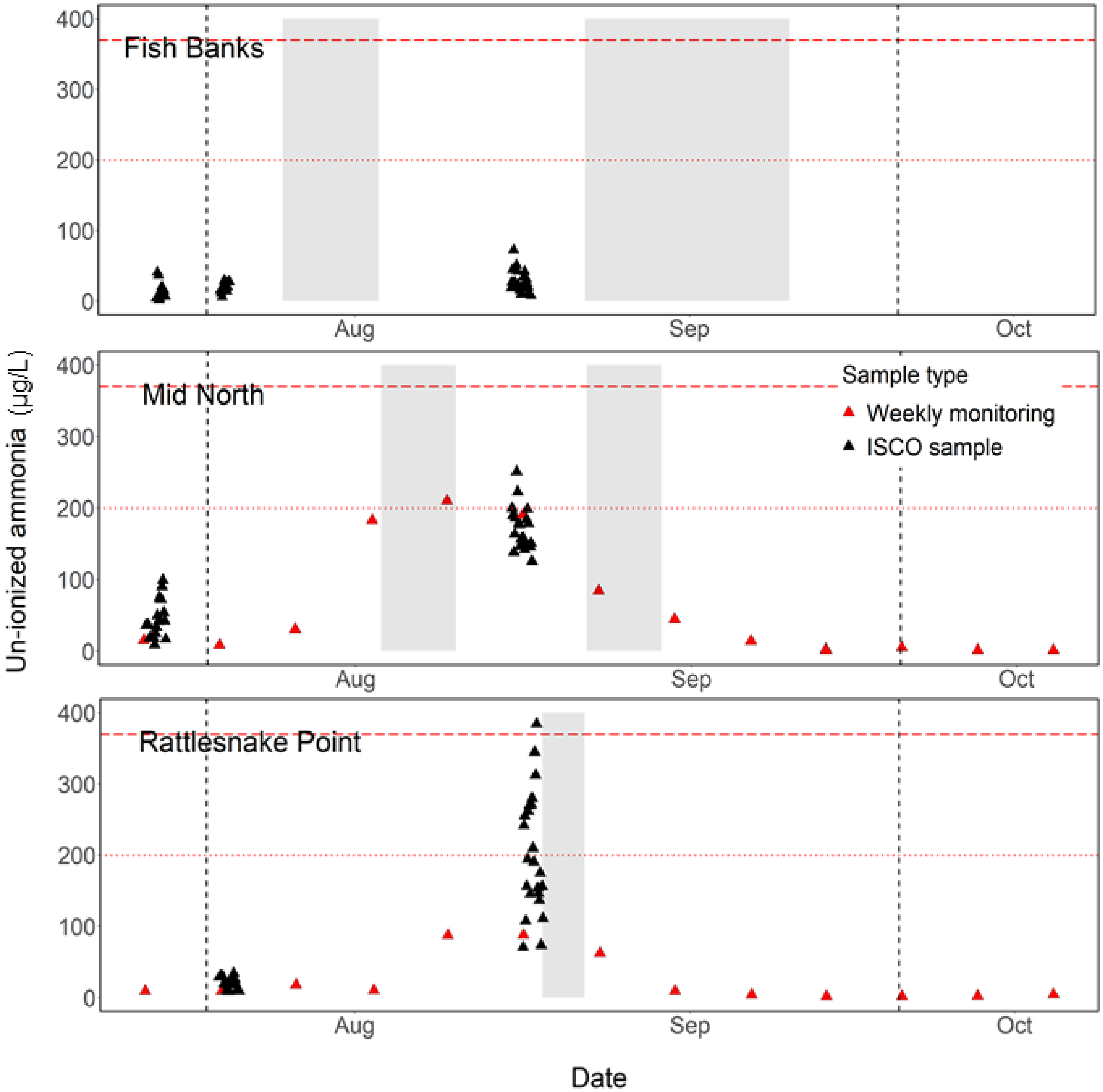

Figure 11. Graphs showing un-ionized ammonia concentrations near mesocosm sites in Upper Klamath Lake, south-central Oregon, July 12–October 4, 2016. Weekly samples were not collected at Fish Banks. Weekly un-ionized ammonia samples were collected at mid-water column and ISCO™ samples were collected about 0.5 meters from benthos. Dashed horizontal lines at un-ionized ammonia concentrations of 370 micrograms per liter (µg/L) cause sublethal effects to gills of juvenile Lost River suckers after 30 days of exposure (Lease and others, 2003). Dotted horizontal lines at 200 µg/L un-ionized ammonia concentrations were associated with gill thickening after 30 hours of exposure (Lease and others, 2003). Black dashed vertical lines indicate beginning and end-of-season for mortality analysis. Gray regions highlight sucker mortality events.

Movement

Vertical movement of suckers in mesocosms varied diurnally, seasonally, and among mesocosms. Movement patterns among mesocosms did not have consistent patterns, although a few noteworthy patterns were detected. Suckers at Fish Banks, the shallowest site, generally used the entire water column during dark hours, and primarily the benthos during light hours throughout the entire season, although they used the upper water column less frequently as the season progressed (fig. 12). During a relatively low DO event at Fish Banks that affected the entire water column on August 27, the diurnal pattern in vertical position in the water column continued despite low DO that persisted well into daylight hours (fig. 13).

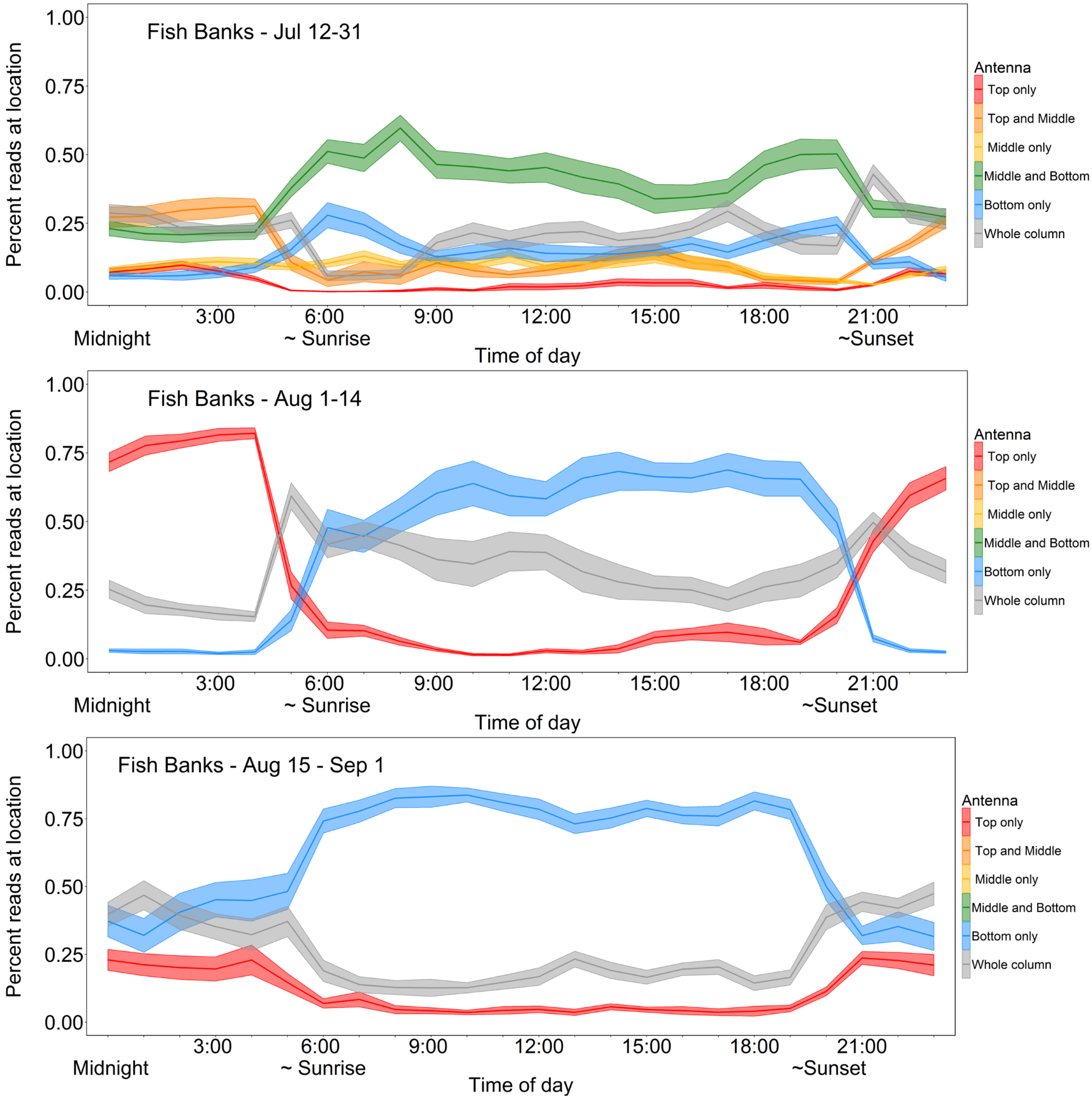

Figure 12. Vertical locations of passive integrated transponder-tagged age-1 Lost River suckers in mesocosms located at Fish Banks in Upper Klamath Lake, south-central Oregon, July 12–September 1, 2016. Locations are shown as the proportion of fish detected on each antenna or combination of antennas by dates in which fish had similar movement patterns. Lines represent average percent of reads detected during each hour interval; ribbons represent one standard error.

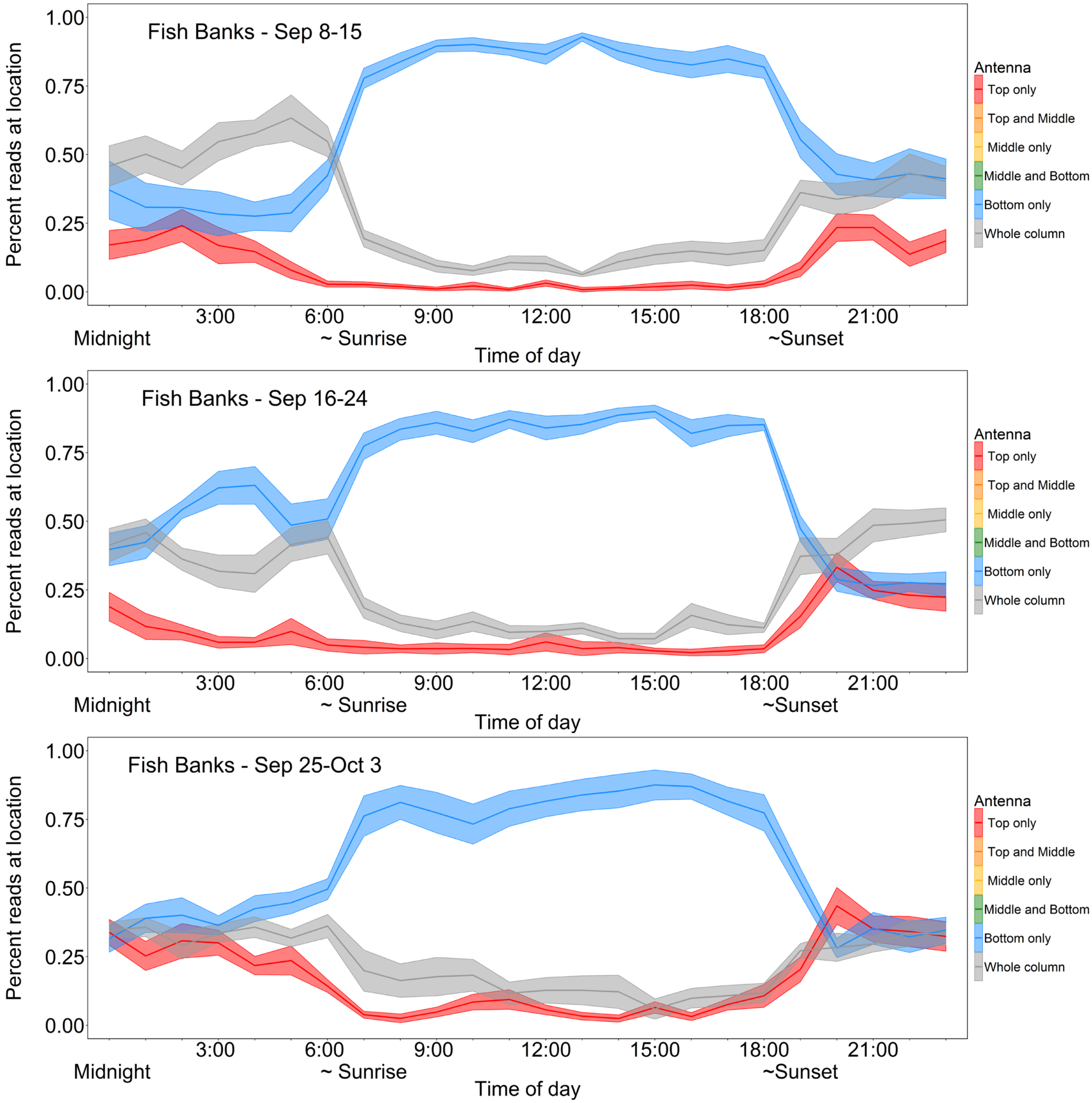

Figure 12. –Continued

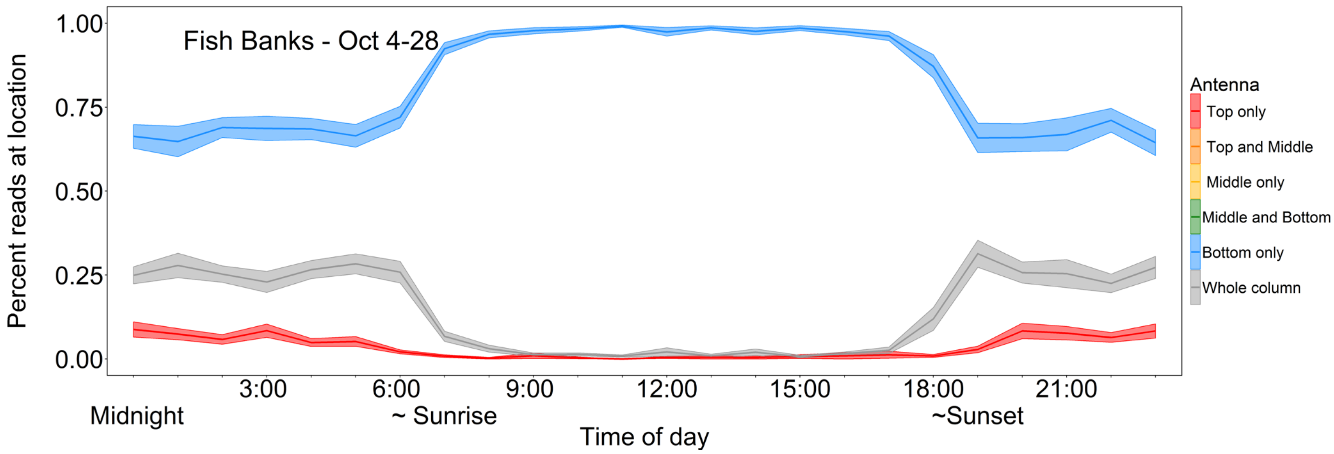

Figure 12. –Continued

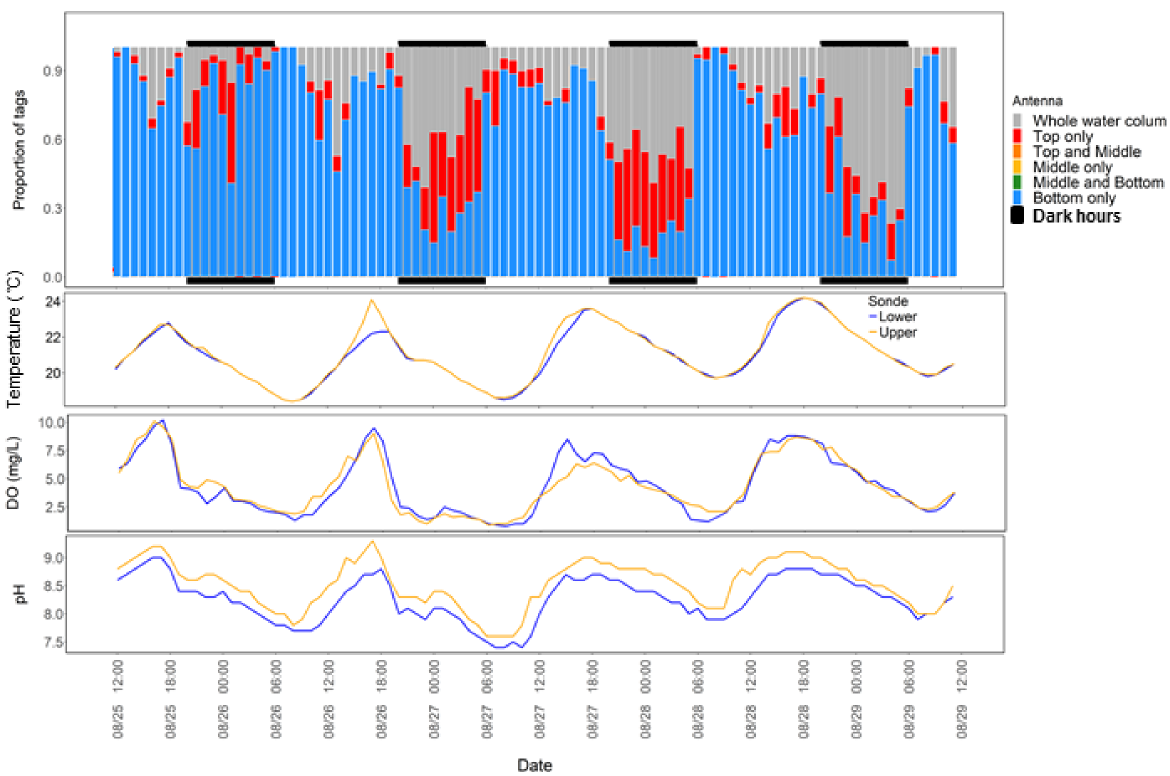

Figure 13. Graphs showing hourly vertical locations for passive integrated transponder-tagged Lost River suckers in mesocosms at Fish Banks in Upper Klamath Lake, south-central Oregon, August 25–29, 2016. Dates were selected to include the first few days of a mortality event that occurred at Fish Banks from August 22 to September 9. During this event, a total of 19 suckers died, 3 of them on August 25. The proportion of suckers (tags) detected at a single antenna or combination of antennas is shown for each hour of each day. Antennas were located near the surface (top), mid-water column (middle), and near the benthos (bottom). Hours of darkness are indicated with black horizontal bars in the top graph. Water temperature (in degrees Celsius [°C]), dissolved oxygen (DO) concentration (in milligrams per liter [mg/L]), and pH are measured 1 meter above the benthos (Lower) and below the surface (Upper) and are given in the bottom three graphs.

When first introduced, Mid North suckers almost exclusively used the middle and surface regions of the water column 24 h a day, and many Mid North suckers were only detected near the surface, even in the middle of the day (fig. 14). At the end of July and in early August, Mid North suckers seemed to have diurnal movement patterns; during dark hours, commonly using the surface and mid-water column, and, during light hours, retreating to the middle water column and sometimes the bottom (fig. 14). On July 29, the water column stratified at Mid North and it was essentially anoxic near the benthos. During this period, suckers continued to avoid the benthos after the sun rose, apparently avoiding the bottom and taking advantage of greater oxygen availability near the top of the water column (fig. 15). In contrast, on August 12, a similar stratification event occurred, but suckers continued their diel use of the bottom despite near anoxic conditions near the benthos (fig. 16). By mid-August, Mid North suckers continued to use the middle water column, began using the benthos more frequently, and rarely used the surface. Apparent diurnal movements were not observed at Mid North after the end of August for the remainder of the season. By the end of the season, Mid North suckers began using the surface again, most often during dark hours. Overall, Mid North suckers were less likely to use the surface during light hours than at other sites (fig. 14).

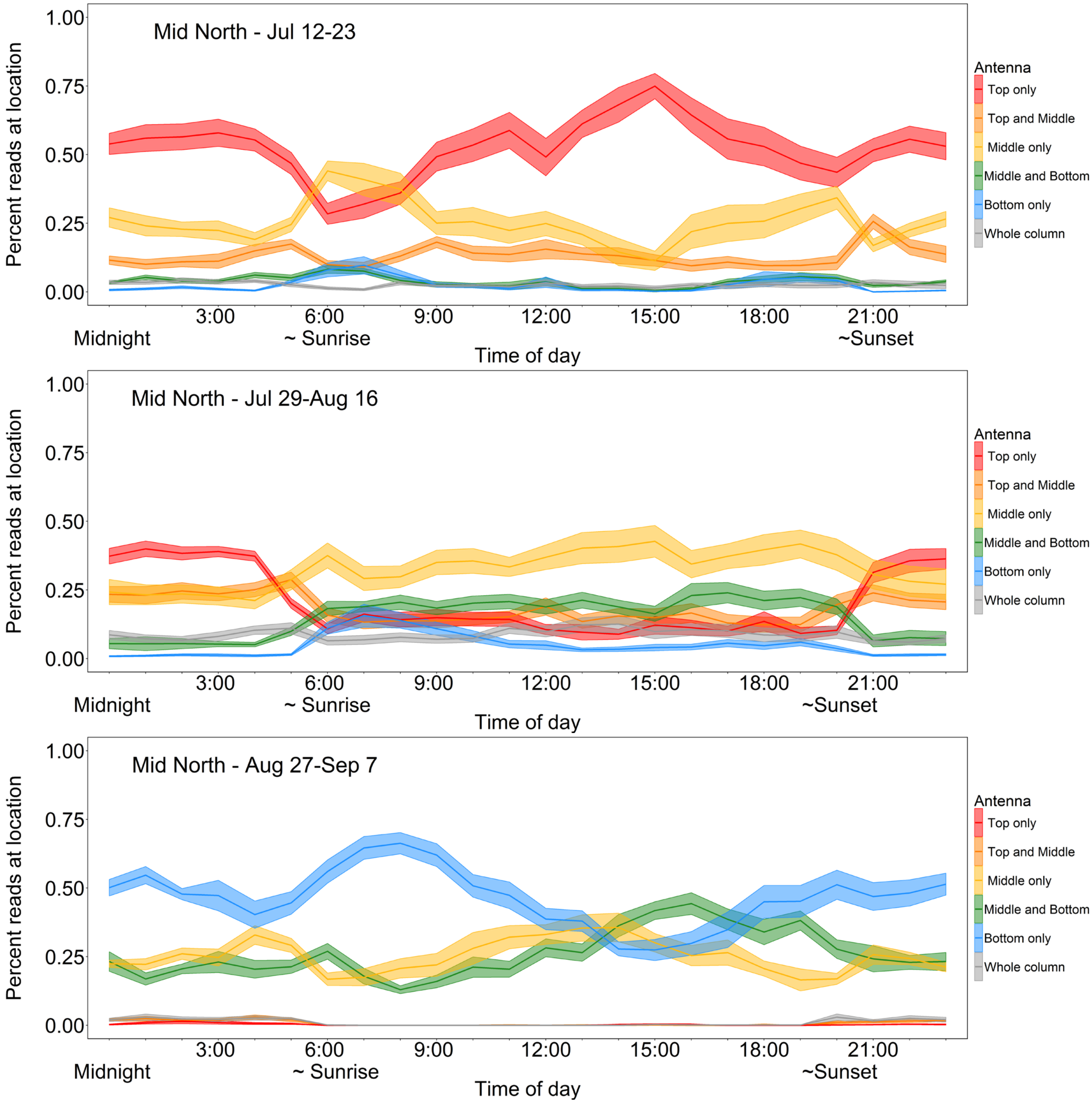

Figure 14. Vertical locations of passive integrated transponder-tagged age-1 Lost River suckers in mesocosms located at Mid North in Upper Klamath Lake, south-central Oregon, July 12–October 24, 2016. Locations are shown as the proportion of fish detected on each antenna or combination of antennas by dates in which fish had similar movement patterns. Lines represent average percent of reads detected during each hour interval; ribbons represent one standard error.

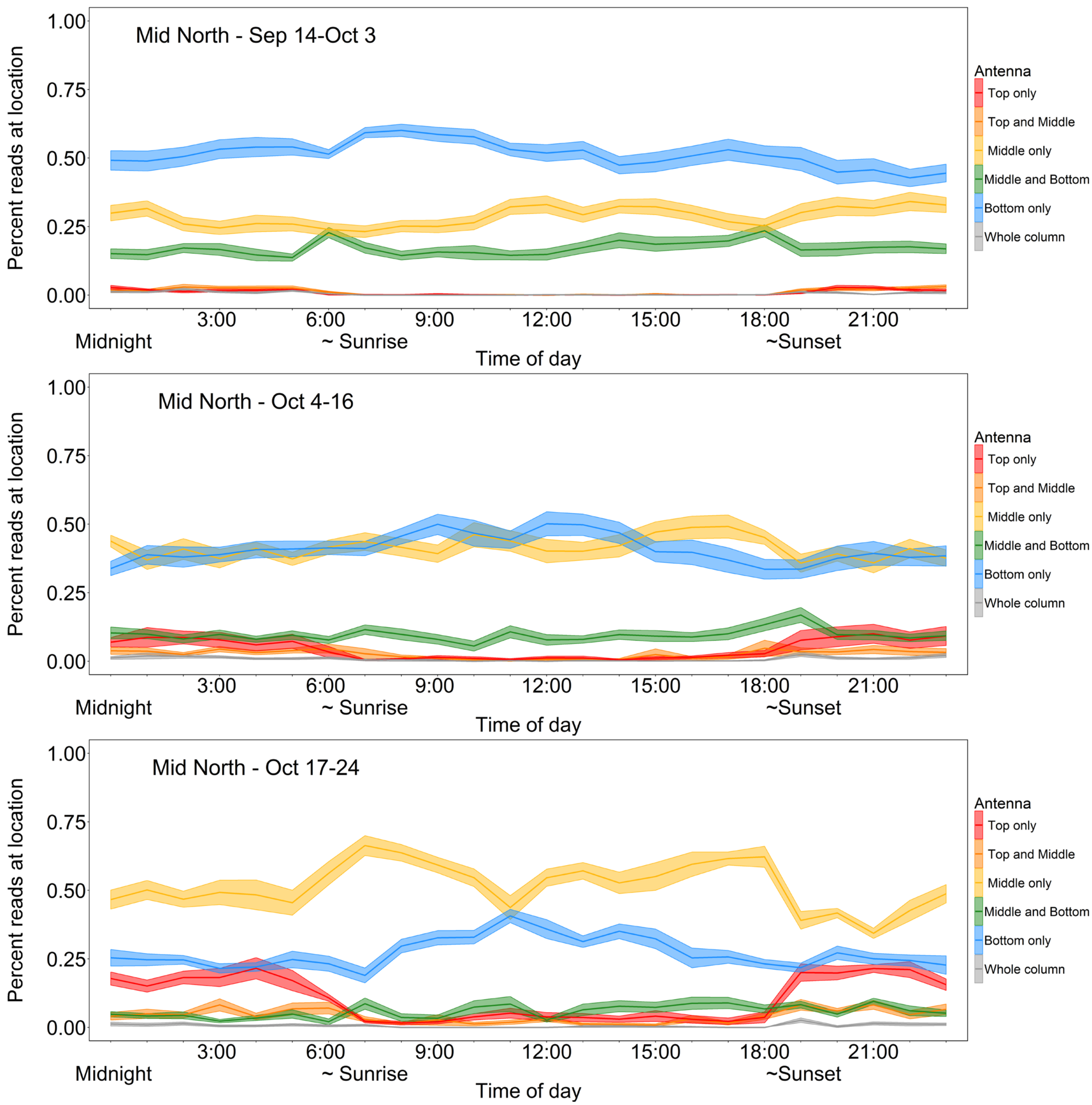

Figure 14. –Continued

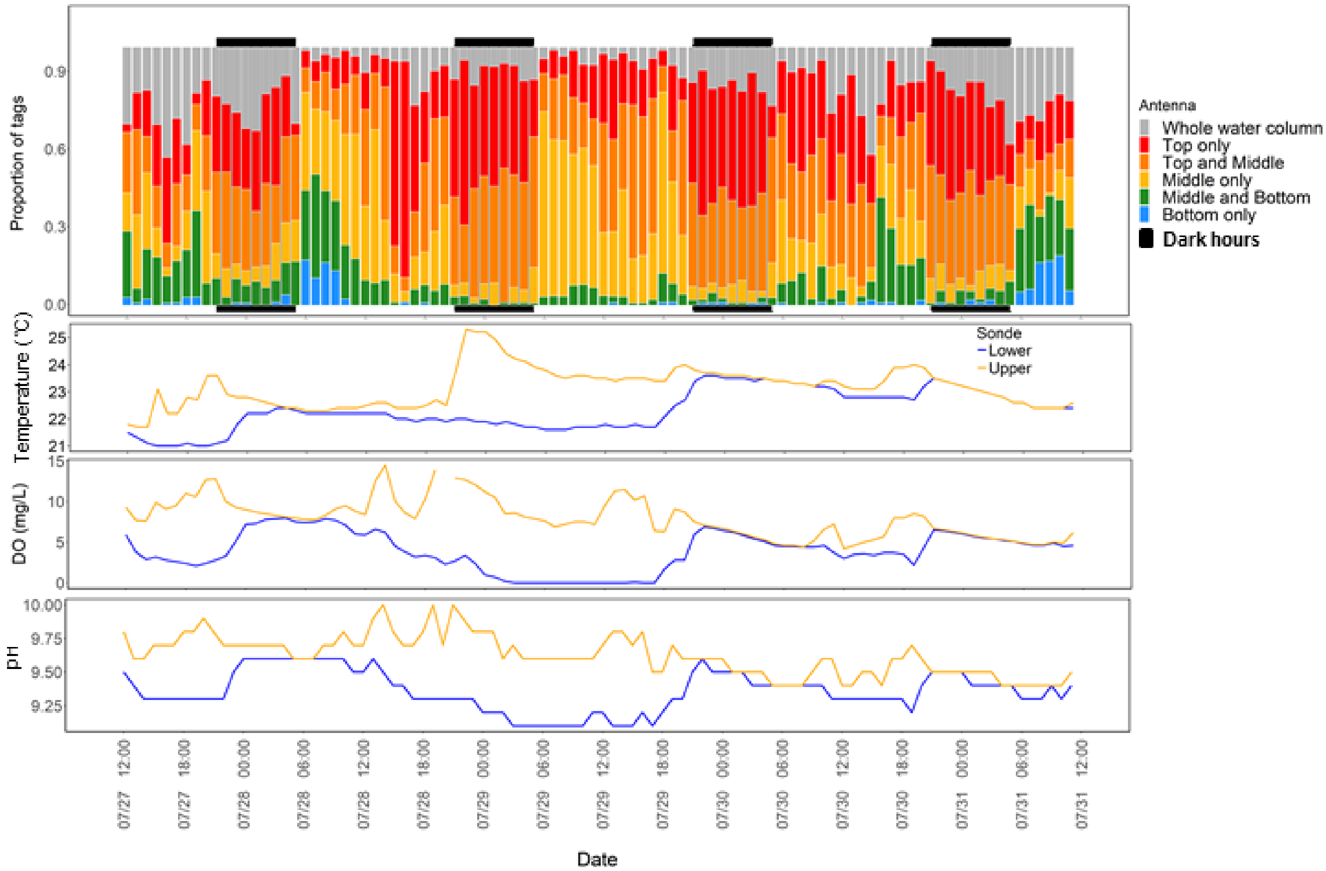

Figure 15. Graphs showing hourly vertical locations for passive integrated transponder-tagged Lost River suckers in mesocosms in at Mid North in Upper Klamath Lake, south-central Oregon, July 27–31, 2016. Dates were selected to include July 27 when the water column stratified and dissolved oxygen (DO) near the benthos was very low. The proportion of tagged suckers detected at a single antenna or combination of antennas is shown for each hour of each day. Antennas were located near the surface (top), mid-water column (middle), and near the benthos (bottom). Hours of darkness are indicated with black horizontal bars in the top graph. Water temperature, DO concentration, and pH measured 1 meter above the benthos (Lower) and below the surface (Upper) and are given in the bottom three graphs.

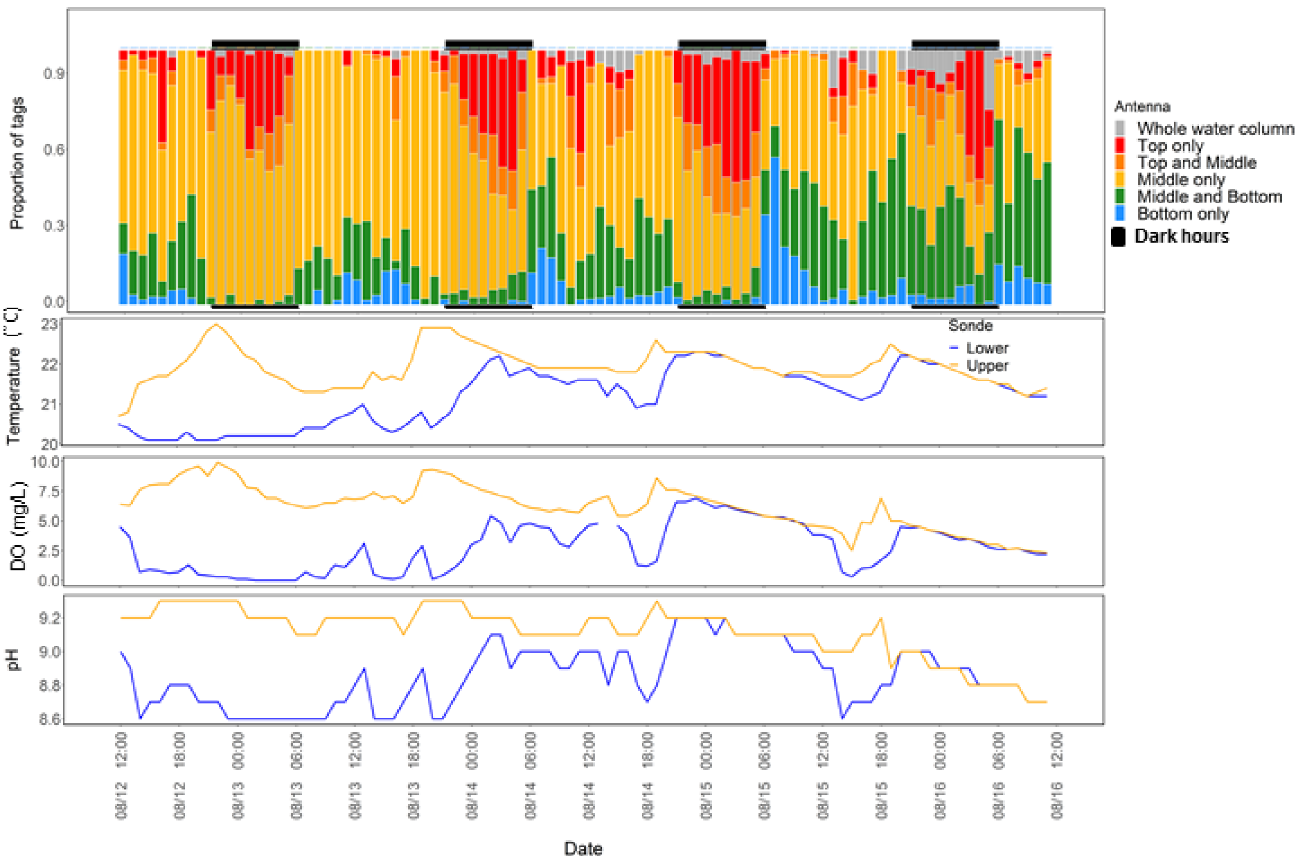

Figure 16. Graphs showing hourly vertical locations for passive integrated transponder-tagged Lost River suckers in mesocosms in at Mid North in Upper Klamath Lake, south-central Oregon, August 12–16, 2016. Dates were selected to include August 12 when the water column stratified and dissolved oxygen (DO) near the benthos was very low. The proportion of tagged suckers detected at a single antenna or combination of antennas is shown for each hour of each day. Antennas were located near the surface (top), mid-water column (middle), and near the benthos (bottom). Hours of darkness are indicated with black horizontal bars in the top graph. Water temperature, DO concentration, and pH measured 1 meter above the benthos (Lower) and below the surface (Upper) and are given in the bottom three graphs.

When first introduced, Rattlesnake Point suckers spent the most time near the surface, and rarely used the benthos (fig. 17). Seasonally summarized diurnal movements of Rattlesnake Point suckers seem to have no pattern. However, when separated by month, some patterns arise. In July, a diurnal pattern of using the surface during daylight hours, and the entire water column (including the surface) during dark hours was apparent (fig. 17). Movements of suckers at Rattlesnake Point had no diurnal movement patterns in August and suckers used all antennas almost equally throughout the day, although suckers used the surface more often than other areas in the water column. In September, suckers were in the middle of the water column most of the time, but during daylight hours they spent more time near the benthos. In October, Rattlesnake Point suckers had diurnal movement patterns that resembled behavior observed at Fish Banks; suckers used the entire water column during dark hours, and primarily the benthos or mid-water column during light hours (fig. 17).

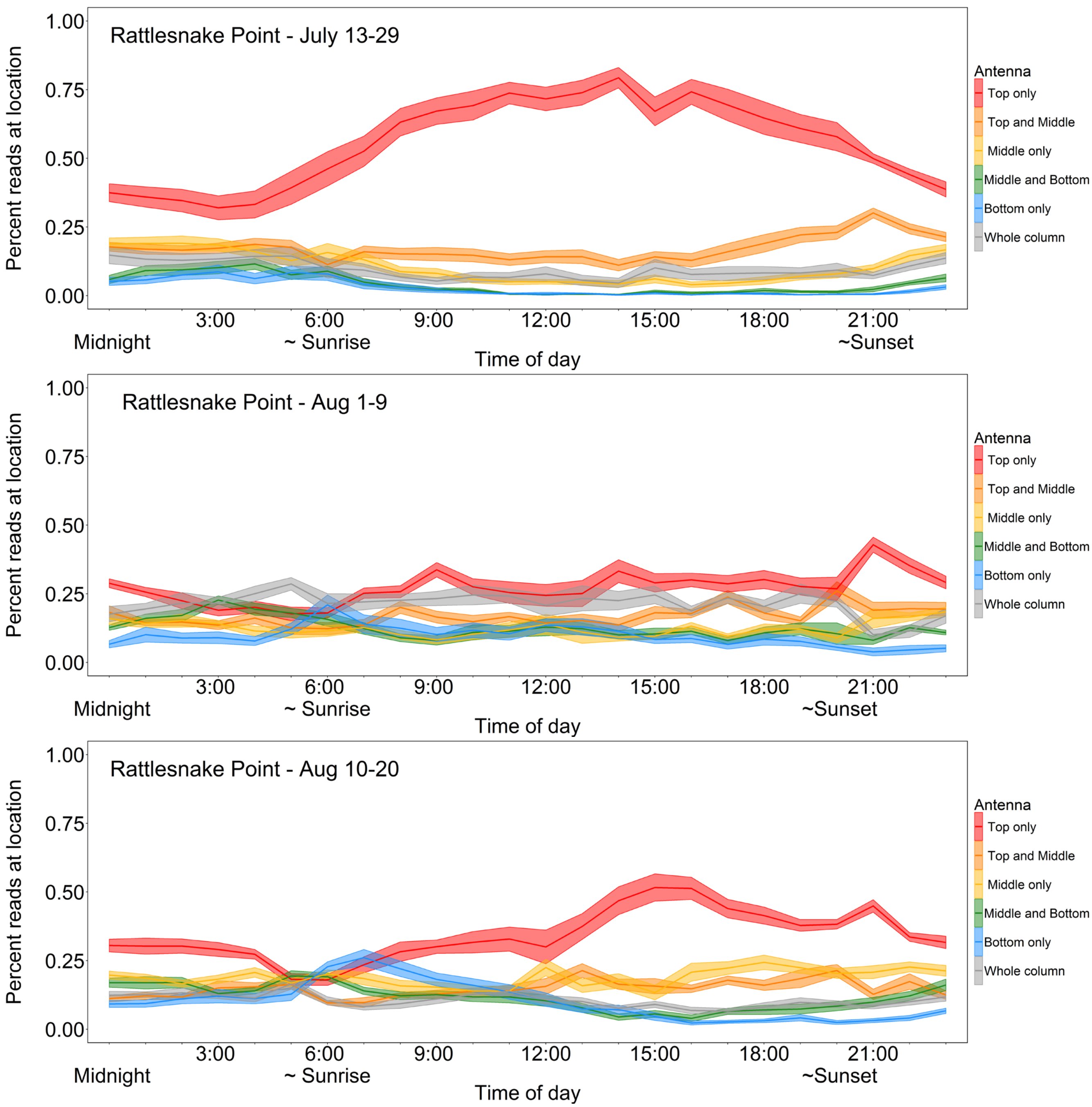

Figure 17. Vertical locations of passive integrated transponder-tagged age-1 Lost River suckers in mesocosms located at Rattlesnake Point in Upper Klamath Lake, south-central Oregon, July 13–September 16, 2016. Locations are shown as the proportion of fish detected on each antenna or combination of antennas by dates in which fish had similar movement patterns. Lines represent average percent of reads detected during each hour interval; ribbons represent one standard error.

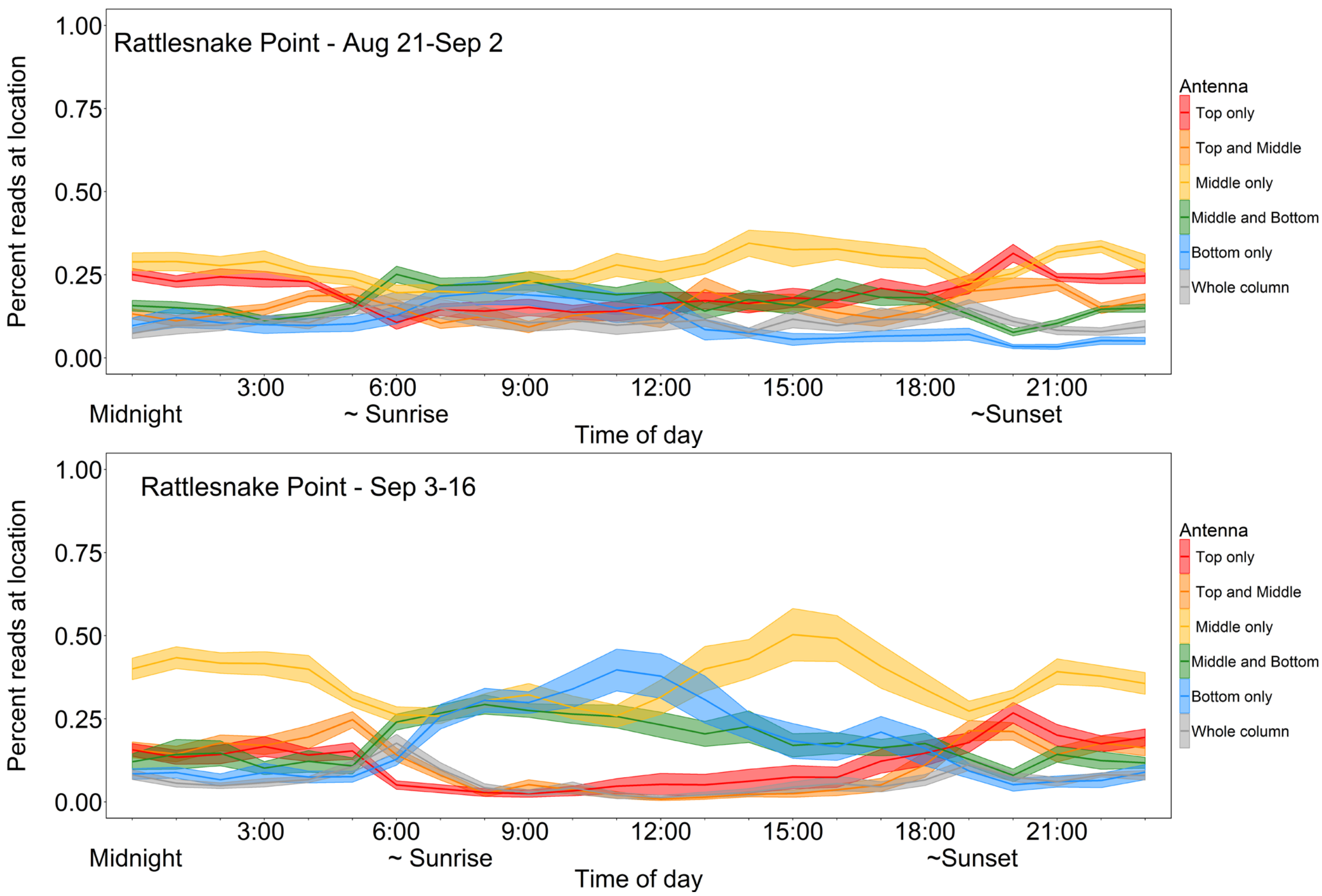

Figure 17. –Continued

When some of the highest water temperatures were measured at Fish Banks at the end of July and beginning of August, Fish Banks suckers seemed to have movement patterns relatively similar to their patterns during days when temperatures were not as extreme (fig. 13). One of the lowest DO events occurred on July 29 at Mid North and, qualitatively, suckers seemed to spend less time near benthos antennas on this day relative to the days preceding and following the low DO event, especially during daylight hours (fig. 15). Similarly, Mid North suckers seemed to avoid the benthos and spend less time near the benthos than on other days during two other low DO events on August 13 and August 18, respectively (fig. 16). When pH was exceptionally high at Rattlesnake Point, suckers used predominantly the upper water column (data not presented). Water column-profiles for Rattlesnake Point had essentially uniform pH conditions (except in the lowest 0.5 m near the sediments where pH was substantially lower) during July when pH was highest (data not presented).

Mortality

Analysis of remote detection movement patterns enabled the date of mortality to be identified for 307 of 308 (99.7 percent) suckers introduced at the beginning of the study, and 109 of 110 (99.1 percent) suckers introduced throughout the study. We were unable to account for one fish introduced at the beginning of the study after 6 d of active detections. It is expected that this fish died, floated on the surface undetected by our antenna, and was removed by an avian scavenger as the bird netting at this site was near the water surface during this time, although it also is possible that this fish swam out of the mesocosm when a particularly large swell caused substantial water displacement in the mesocosm. This fish was censored out of the mortality analysis. A second fish that was introduced to the study in the middle of the field season seems to have been accidently released during clean-up as active detections were recorded until the antennas were removed. Living fish were active within mesocosms and daily status (live or dead) was apparent for all tagged suckers. Other fish that were removed (9 individuals) from the survival analysis died within the first week of the study. These suckers were removed because mortality occurred during the first week and may have been associated with transportation stress or acclimatization.

Mortality was highest at Fish Banks, intermediate at Mid North, and low at Rattlesnake Point. For fish introduced at the beginning of the study, 58.8 percent (60 of 102) died at Fish Banks, 27.4 percent (28 of 102) died at Mid North, and 11.5 percent (12 of 104) died at Rattlesnake Point before the end of the study (fig. 18). Many suckers introduced at the beginning of the study were found dead (72) or had a remote death (21), and we captured 7 moribund suckers for histopathological analysis (fig. 19).

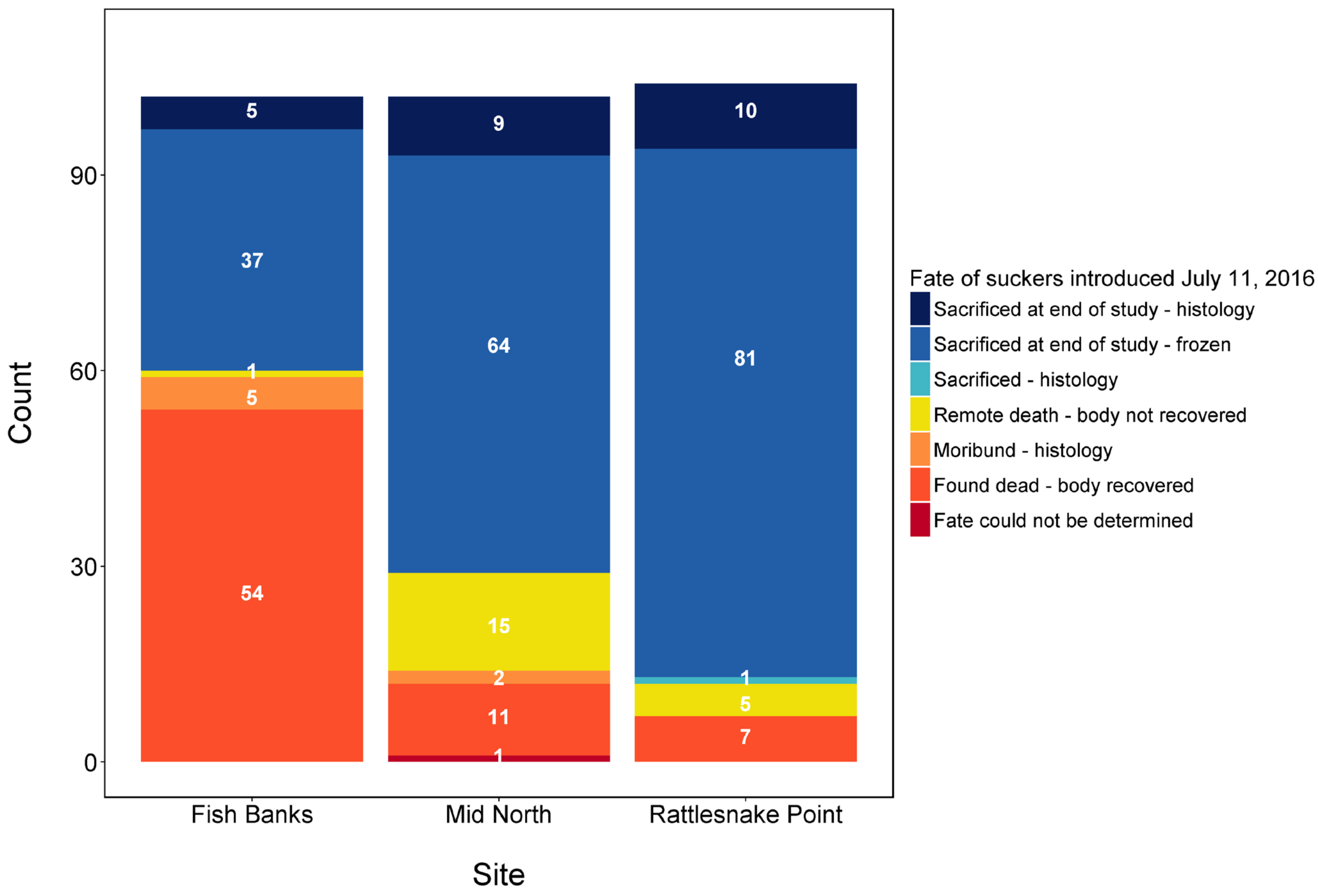

Figure 18. Graph showing summary of fates for all suckers introduced to mesocosms at the beginning of the study, Upper Klamath Lake, south-central Oregon, July 11, 2016. Total numbers of suckers introduced to each mesocosm were 102 each at Fish Banks and Mid North, and 104 at Rattlesnake Point.

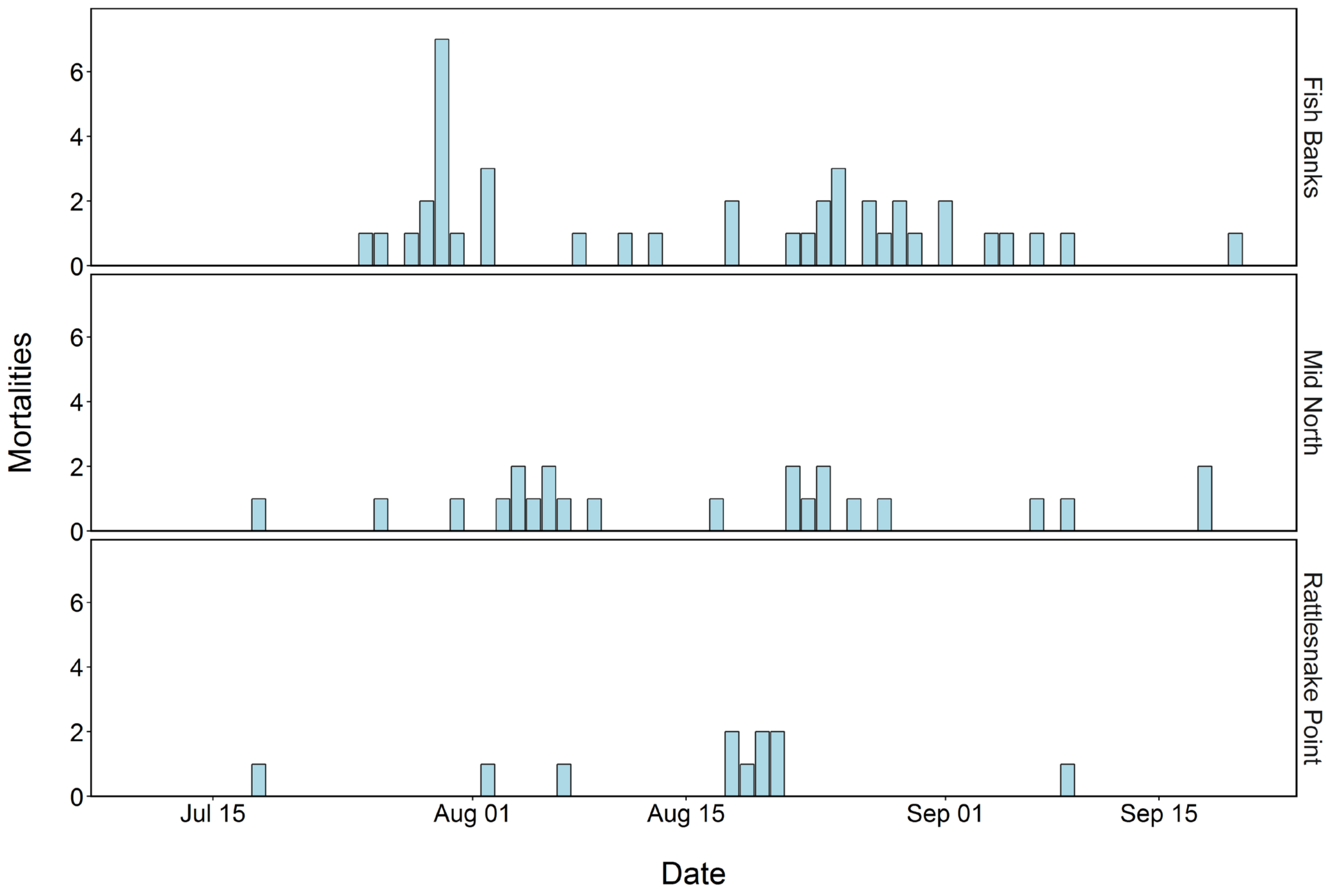

Figure 19. Graphs showing number of natural mortalities (sacrifices of healthy suckers excluded) on each day for all suckers introduced at the beginning of the study at Fish Banks, Mid North, and Rattlesnake Point mesocosm sites, Upper Klamath Lake, south-central Oregon, July 11, 2016. Mortalities that occurred before July 18 (N_{FBW} = 6, N_{MDN} = 1, N_{RPT} = 2), and after September 20 (N_{FBW} = 13, N_{MDN} = 4, N_{RPT} = 0) are not included, and healthy suckers sacrificed for histology (N_{FBW} = 3, N_{MDN} = 0, N_{RPT} = 1) are not included. Total numbers of suckers introduced to each mesocosm were 102 each at Fish Banks and Mid North, and 104 at Rattlesnake Point.

Fish Banks Mortality Event 1

The first mortality event at Fish Banks occurred during July 25–August 2 (fig. 19). Over the course of 9 d, 16 mortalities occurred, of which 7 occurred on July 30. In the 10 d (July 15–July 24) prior to the first mortality event, temperature was increasing and ranged from 18.2 to 27.0 °C (mean ±sd = 21.4 ±1.7). DO concentrations varied by 2.7–8.6 mg/L and oxygen saturation varied by 36.6–124.1 percent. In the 10 d prior to the mortality event, DO concentrations ranged from 3.6 to 12.6 mg/L and oxygen saturation ranged from 45.7 to 181.0 percent. Mean (±sd) pH was high relative to other days at Fish Banks (but low compared to pH at other sites; 9.1 ±0.39, range=7.8–9.9), and pH fluctuations on any given day were greater than 1 on 4 (of 10) days prior to the first Fish Banks mortality event. Microcystin and un-ionized ammonia concentrations were low prior to the mortality event.

During the first Fish Banks mortality event, temperature throughout the water column was greater than 20.4 °C, and daily maximum surface temperatures were at least 26.3 °C or greater every day except on August 2 when maximum water temperature was 24.2 °C and occurred throughout the entire water column. On July 26 and 28, surface temperatures reached seasonal highs of 28.2 and 28.1 °C, respectively. Dissolved-oxygen concentrations fluctuated by more than 10 mg/L during July 28–

July 31. Minimum DO concentrations were very low (<1.7 mg/L) on July 29 (fig. 15, July 28–31). On July 29, DO concentrations were less than 2.9 mg/L 1 m above the benthos from midnight to 8 p.m. Oxygen percent saturation reached a daily low of 12 oxygen percent saturation and was less than 17 percent throughout the entire sampled water column (both sondes) for 3 h (7–9 a.m.) on July 30 when 7 suckers died at Fish Banks. During the first Fish Banks mortality event, mean pH was 8.8 ±0.5 (mean ±sd). Substantial fluctuations in pH were observed on July 26, 29, 30, and 31, and August 1, and mortalities were observed on July 26, 29, and 30, and August 2.

Fish Banks Mortality Event 2

The second mortality event at Fish Banks occurred during August 22–September 9 (fig. 19). Over the course of 19 d, 19 mortalities occurred, of which 3 occurred on August 25. In the 10 d (August 12–21) prior to the second mortality event, temperatures ranged from 21.3 to 27.1 °C and the mean (±sd) temperature was 23.7 ±1.3 °C. Mean (±sd) DO concentrations were 4.8 ±2.7 mg/L and mean (±sd) oxygen saturation was 66.6 ±38.3 percent (fig. 5). Mean (±sd) pH at Fish Banks was moderate (8.3 ±0.5; fig. 6) and pH fluctuated daily by 0.7–1.8 pH units. Prior to the second Fish Banks mortality event, microcystin concentrations in the large (≥63 µm) and small (<63 µm) fractions were increasing. Un-ionized ammonia concentrations were low prior to the mortality event.

During the second Fish Banks mortality event, mean (±sd) temperature was 19.4 ±2.5 °C and ranged from 13.7 to 24.2°C. Mean (±sd) DO concentrations were relatively moderate (7.1 ±3.1 mg/L) although some measurements were low towards the end of August (fig. 4). For example, the lowest DO concentration at Fish Banks (0.6 mg/L) was recorded on August 30; one mortality occurred on that day. Dissolved oxygen concentrations remained ≤ 2.6 mg/L throughout the water columns for 15 hours during the night of August 26 and 27 (fig. 13). Mean pH generally was moderate, although fluctuations of at least 1 pH unit occurred most days during the mortality event. Microcystins in the large fraction generally increased and reached their seasonal high (0.85 µg/L) during the second Fish Banks mortality event, whereas small fraction microcystins were low (fig. 10).

Mid North Mortality Event 1

The first mortality event at Mid North occurred during August 3–9 (fig. 19). Over the course of these 7 d, 8 mortalities occurred. In the 10 d (July 24–August 2) prior to the first Mid North mortality event, temperatures reached seasonal highs (mean ±sd = 22.1 ±1.1 °C; range =19.9–25.3 °C) throughout the water column. Mean (±sd) DO concentrations (6.3 ±2.5 mg/L) and mean (±sd) oxygen saturation (85.1 ±33.8 percent) were moderate but the lake was stratified and DO concentrations were very low near the bottom, especially on July 29 prior to the mortality event (figs. 4 and 5). Mean (±sd) pH was 9.5 ±0.2 and pH ranged from 9.0 to 10.0 prior to the mortality event. Microcystins and un-ionized ammonia concentrations were low prior to the first Mid North mortality event.

During the first Mid North mortality event, mean (±sd) temperature was slightly lower than average (21.3 ±0.65 °C) and ranged from 17.4–23.8 °C. Mean (±sd) DO concentrations (6.4 ±2.0 mg/L) and percent oxygen saturation (84.4 ±27.0 percent) were on average slightly higher than the seasonal average but ranged from high at the beginning of the mortality event, to low at the end of the mortality event (fig. 4). Mean (±sd) pH was 9.3 ±0.2 and pH ranged from 8.8 to 9.9 during the mortality event (fig. 6). Microcystins and un-ionized ammonia concentrations were low during the mortality event (figs. 10 and 11).

Mid North Mortality Event 2

The second mortality event at Mid North occurred during August 22–28 (fig. 19). Over the course of 7 d, 7 mortalities occurred. In the 10 d (August 12–21) prior to the second Mid North mortality event, mean (±sd) temperature exceeded 23 °C a few times and was high relative to other seasonal measurements (22.0 ±0.8 °C, range =19.9–24.0 °C; fig. 3). Mean (±sd) pH was seasonally low (8.9 ±0.3, range = 8.1–9.3; fig. 6). Mean (±sd) DO concentrations (4.7 ±2.7 mg/L, range = 0–11.87 mg/L) and mean (±sd) oxygen saturation (62.6 ±36.8 percent, range = 0–163) also were low (figs. 4 and 5). The lake was stratified when lake profiles were measured on August 12, 15, and 18 (fig. 8). DO concentrations and oxygen saturation were very low near the bottom sonde during August 11–13 and 18–19, prior to the mortality event. Minimum DO concentrations were ≤ 1.21 mg/L for 9 consecutive days during this same period (fig. 4). Microcystins were low prior to the mortality event (fig. 10). Measured un-ionized ammonia concentrations exceeded 200 µg/L during one weekly and two hourly measurements prior to the mortality event (fig. 11).

During the second Mid North morality event, mean (±sd) temperature was 21.2 ±0.7 °C (range = 20.2–23.2), mean (±sd) pH was 9.0 ±0.2 (range = 8.4–9.5), and pH greater than or equal to 9 often occurred throughout the entire water column (figs. 3 and 6). Mean (±sd) DO concentrations were relatively high (8.1 ±1.9 mg/L, range = 3.6–14.2 mg/L), often greater than 5 mg/L (fig. 4). Mean (±sd) oxygen saturation was 106.5 ±26.1 percent (range = 47.4–191.0) during the second Mid North mortality event (fig. 5). Microcystin concentrations were low during the mortality event (fig. 10).

Rattlesnake Point Mortality Event

The only relatively large mortality event at Rattlesnake Point occurred during August 18–21 (fig. 19). Over the course of 4 d, 7 mortalities occurred. There were only 11 natural mortalities between July 18 and the end of the season at Rattlesnake Point. In the 10 d (August 8–17) prior to the Rattlesnake Point mortality event, mean (±sd) temperature was 21.2 ±1.2 °C (range = 19.1–23.6 °C; fig. 3). Mean (±sd) pH was low relative to measurements taken earlier in season at Rattlesnake Point, but relatively high compared to other sites (9.4 ±0.2, range = 8.9–9.8; fig. 6). In the 10 d prior to the Rattlesnake Point mortality event, mean (±sd) DO concentrations (7.5 ±1.5 mg/L, range = 3.8–11.8 mg/L) and mean (±sd) oxygen saturation (98.2 ±20.5 percent, range = 49.9–161.0) were about average for this site. Large fraction microcystins, although low, were increasing prior to the mortality event (fig. 10). Measured un-ionized ammonia concentrations exceeded 200 µg/L for as many as 18 hours, with one of these measurements exceeding 370 µg/L prior to the mortality event (fig. 11).

During the Rattlesnake Point mortality event, mean (±sd) temperature was 22.5 ±0.6 °C (range = 21.3–23.7 °C) and mean (±sd) pH was 9.2 ±0.1 (range = 8.9–9.4; figs. 3 and 6). Mean (±sd) DO concentrations were 6.8 ±1.3 mg/L (range = 4.1-10.0 mg/L) and mean (±sd) oxygen saturation was 91.7 ±18.2 percent (range = 54.4–137.0) during the Rattlesnake Point mortality event (figs. 4 and 5). Microcystins were very low throughout the season at Rattlesnake Point but large fraction microcystins reached seasonal highs during (and following) the mortality event at Rattlesnake Point (fig. 11).

Estimated Effects of Water Quality on Mortality

When daily mortality was modeled relative to daily water-quality measurements (hereinafter "daily conditions"), mortality was higher on days when there were large fluctuations in oxygen percent saturation (figs. 5 and 20). The top model, range.psat, had an AICc weight of 0.53 (table 8). This model outcompeted all other single or multiple parameter models; however, the second ranked model (range.DO) included similar data, the daily range of DO concentrations. The second-ranked model (range.DO) carried 29 percent of the AICc weight and was somewhat confounded in the top model, so it was not combined with the top model (range.psat) to create a new model. The third-ranked model included the daily range of DO concentrations, the maximum temperature each day, and an interaction of these parameters. The third-ranked model carried 16 percent of the weight and included data similar to data in the top two models (table 8). All other single-parameter models failed to carry substantial weight (<2 percent) and, therefore, were not combined with the daily range in oxygen percent saturation, or other top models to create new models (table 8).

The goodness-of-fit for the top-ranked model was poor. The predicted compared to the observed mortality were far removed from the isometric line and were not equally distributed. Predicted mortality residuals were not normally distributed around 0 (fig. 21). The top model overestimated mortality when mortality was 0, and underestimated mortality when mortality was greater than 1 percent. The general relation between the number of mortalities compared to the range in oxygen percent saturation data was relatively weak. However, mortalities occurred on all 3 d when oxygen percent saturation fluctuated by at least 182 percent and mortality did not occur on 13 d when oxygen percent saturation fluctuations were measured at less than 32 percent (fig. 20).

Table 8. Model selection results for *a priori* daily condition known fate models fit to estimate daily survival relative to water-quality conditions measured near mesocosms in Upper Klamath Lake, south-central Oregon, July 11–September 20, 2016.

[Variables used in models are listed and explained in table 4. AIC, Akaike's information criterion; AICc, Akaike's information criterion for small sample size; ΔAICc, the difference in AICc between a given model and the best model]

Model	AICc	ΔAICc	AIC weights	Number of parameters
range.psat	919.1	0.0	0.53	2
range.DO	920.3	1.2	0.29	2
range.DO * max.temp	921.4	2.3	0.16	4
site	926.5	7.4	0.01	3
range.pH	927.9	8.8	0.01	2
max.temp * min.DO	930.1	11.1	0	4
max.temp*max.pH	931.5	12.4	0	4
max.temp	932.2	13.1	0	2
min.DO	934.0	14.9	0	2
min.psat	935.9	16.9	0	2
mean.temp	937.4	18.3	0	2
max.psat	938.0	18.9	0	2
range.psat > 140	939.0	19.9	0	2
large.mcystin	939.8	20.7	0	2
range.pH > 0.9	940.6	21.5	0	2
range.temp	940.8	21.7	0	2
p35.psat	941.3	22.2	0	2
mean.DO	941.6	22.5	0	2
p50.psat	942.4	23.3	0	2
range.do > 9	943.3	24.3	0	2
p2.DO	943.4	24.3	0	2
p9.5pH	944.2	25.1	0	2
mean.psat < 50	945.6	26.5	0	2
mean.psat	945.6	26.5	0	2
mean.pH	946.0	26.9	0	2
mean.DO < 5	946.1	27.0	0	2
p23.temp	947.0	27.9	0	2
mean.temp > 23C	947.2	28.1	0	2
mean.pH > 8.45	947.8	28.7	0	2
p25.temp > 25	948.9	29.8	0	2
max.temp > 25C	949.3	30.2	0	2
min.DO < 2	949.7	30.6	0	2
max.pH > 8.9	949.8	30.7	0	2
p9.75pH	950.8	31.7	0	2
dot	952.2	33.1	0	1
max.pH	954.0	34.9	0	2
small.mcystin	954.2	35.1	0	2
time[1]	1,476.1	557.0	0	65

[1]One or more parameters are inestimable.

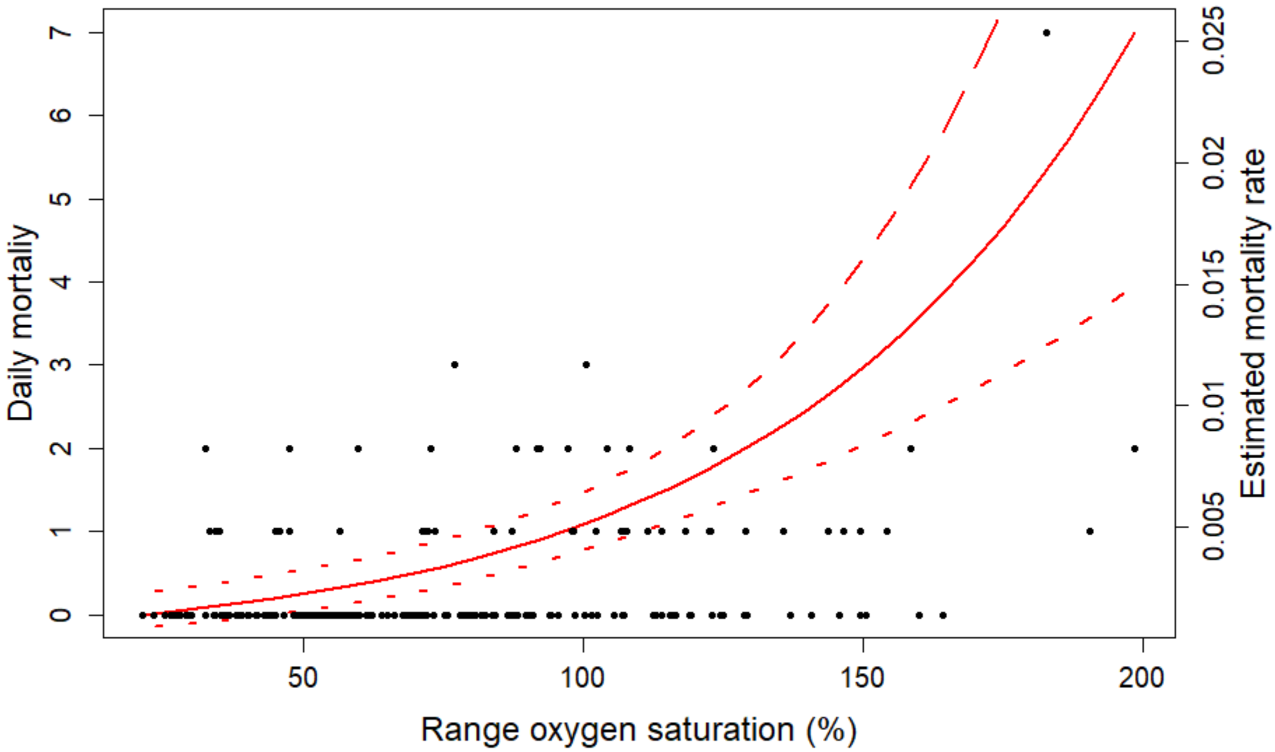

Figure 20. Graph showing daily mortality estimates derived from beta estimates (solid line), 95-percent confidence intervals (dotted lines), and actual daily mortality data (dots) relative to the daily range of oxygen percent (%) saturation at mesocosm sites in Upper Klamath Lake, south-central Oregon, July 18–September 20, 2016.

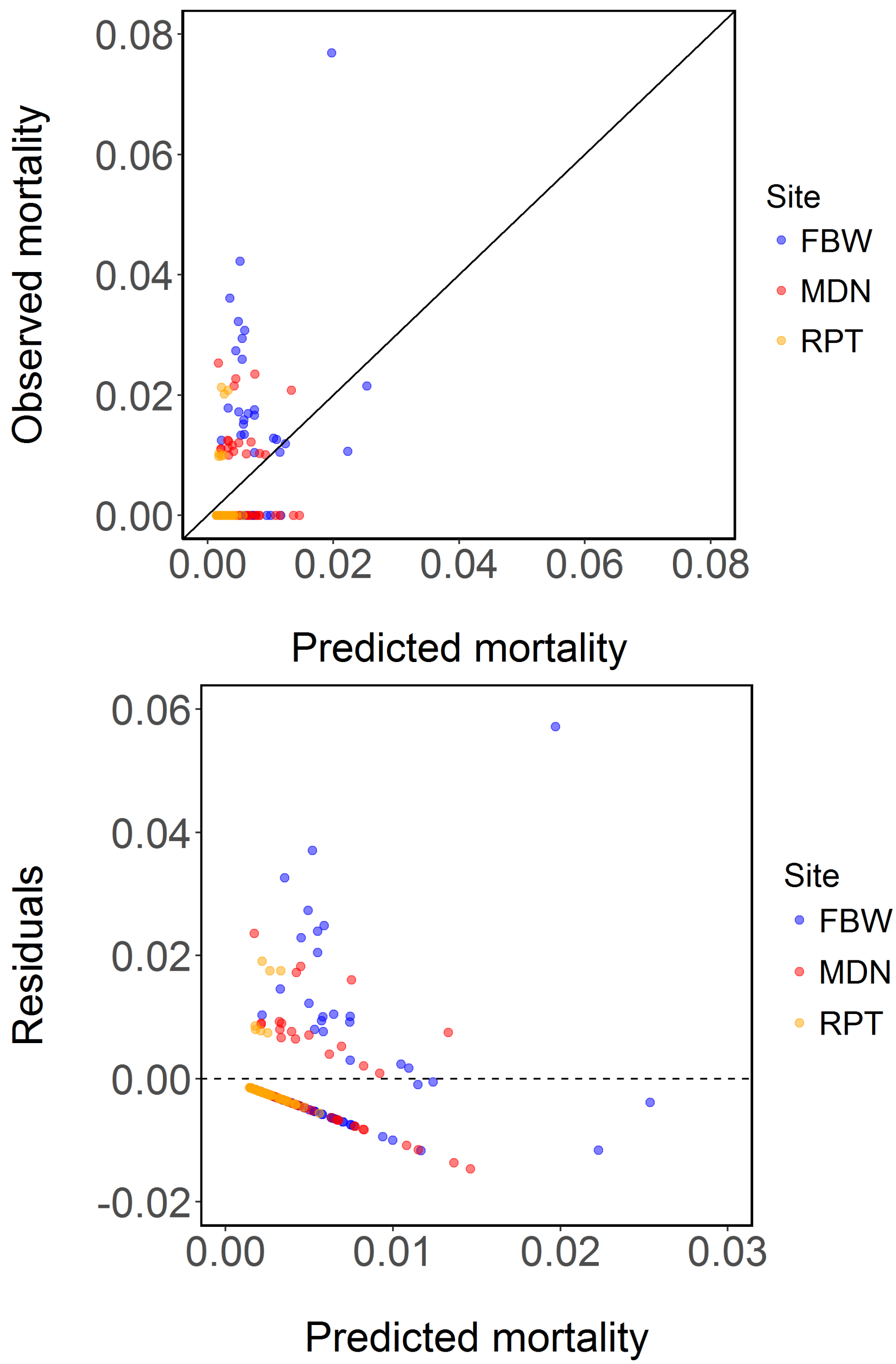

Figure 21. Graphs showing daily mortality estimated by top-ranked daily condition water-quality model (daily range of oxygen percent saturation) relative to observed mortality at each site and residuals (observed-predicted) relative to predicted mortality at Fish Banks (FBW), Mid North (MDN), and Rattlesnake Point (RPT) mesocosms, Upper Klamath Lake, south-central Oregon, July 18–September 20, 2016.

At least one mortality occurred every day (N=4) that temperature exceeded 26.5 °C at Fish Banks. One mortality occurred on August 30 when the lowest seasonal DO concentration was measured at Fish Banks. However, mortalities did not occur at Mid North or Rattlesnake Point when DO concentrations were lowest. Additionally, no mortalities occurred on days when the low DO concentrations persisted near the benthos—less than 1 mg/L for 17 hours on August 13 and essentially 0 mg/L for 15 hours on July 29 at Mid North.

Growth and Condition

There was no difference in initial SL, weight, or body condition between suckers that survived the entire duration of the study and those that did not, although initial range among individuals was small (table 2). Seasonal changes in SL and weight were lowest at Fish Banks, moderate at Mid North, greatest at Rattlesnake Point, and significantly different among sites (figs. 22 and 23; table 9). Changes in body condition were similar between Fish Banks and Mid North, but changes in body condition at these sites were significantly different compared to Rattlesnake Point (fig. 24, table 9). Although all suckers that survived the entire duration of the study increased in standard length and weight, most suckers at Fish Banks (83.3 percent) and Mid North (72.6 percent) had lower Fulton's condition factors at the end of the study. That is, increases in length (measured in millimeters) were more than three times as great as increases in weight measured in grams. In contrast, most fish at Rattlesnake Point increased body condition (86.8 percent; fig. 24; table 9). The sucker with the largest growth was at Rattlesnake Point and increased by 99 mm SL and 134.9 g from the beginning of July to the beginning of November.

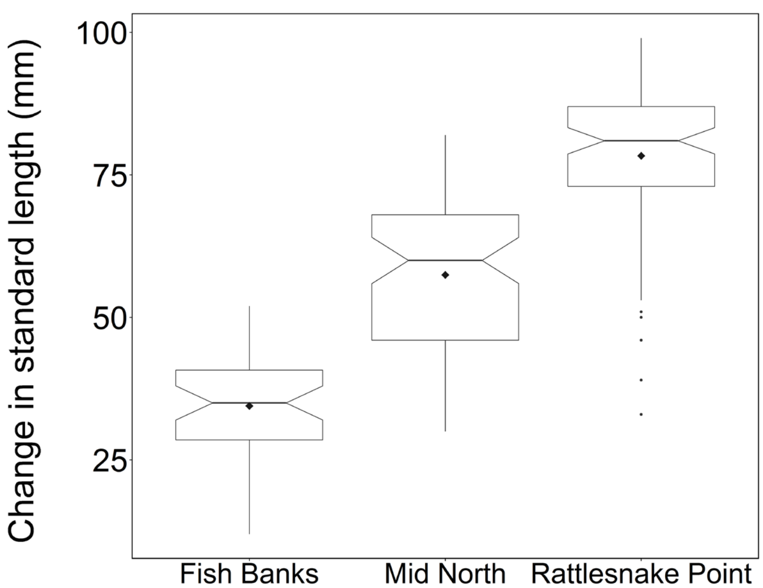

Figure 22. Boxplots showing change in standard length (in millimeters [mm]) for all suckers introduced at the beginning of the season and that survived the entire duration of the study, Upper Klamath Lake, south-central Oregon, 2016. Mean is represented by diamonds, median is center line, 95-percent confidence interval for median is notch, interquartile range is top to bottom of box, whiskers represent 1.5 times interquartile range or highest and lowest values, and outliers are represented by black dots. Non-overlapping notches are significantly different (Chambers and others, 1984). Sample sizes varied among sites; N=42 for Fish Banks, N=73 for Mid North, and N=91 for Rattlesnake Point.

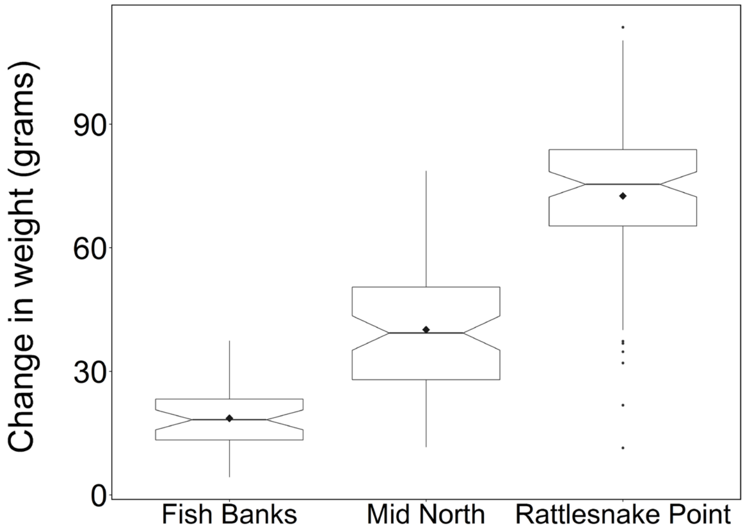

Figure 23. Boxplots showing change in weight for all suckers introduced at the beginning of the season and survived the entire duration of the study, Upper Klamath Lake, south-central Oregon, 2016. Mean is represented by diamonds, median is center line, 95-percent confidence interval for median is notch, interquartile range is top to bottom of box, whiskers represent 1.5 times interquartile range or highest and lowest values, and outliers are represented by black dots. Non-overlapping notches are significantly different (Chambers and others, 1984). Sample sizes varied among sites; N=42 for Fish Banks, N=73 for Mid North, and N=91 for Rattlesnake Point.

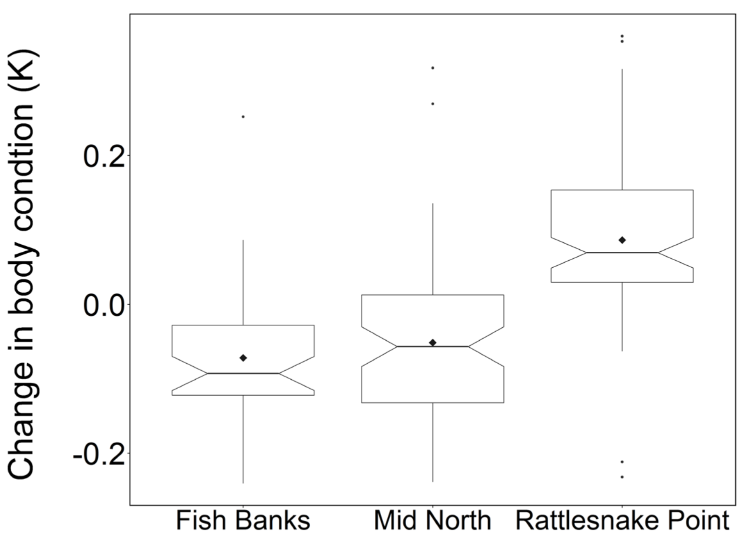

Figure 24. Boxplots showing change in body condition (K= [weight/standard length^3]×10^5) for all suckers introduced at the beginning of the season and that survived the entire duration of the study, Upper Klamath Lake, south-central Oregon, 2016. Mean is represented by diamonds, median is center line, 95-percent confidence interval for median is notch, interquartile range is top to bottom of box, whiskers represent 1.5 times interquartile range or highest and lowest values, and outliers are represented by black dots. Non-overlapping notches are significantly different (Chambers and others, 1984). Sample sizes varied among sites; N=42 for Fish Banks, N=73 for Mid North, and N=91 for Rattlesnake Point.

Table 9. End-of-season and change-in-size information for 206 Lost River suckers that were introduced at the beginning of the season and survived the entire duration of the study in mesocosms in Upper Klamath Lake, south-central Oregon, 2016.

[**Study duration:** Fish Banks, July 11–October 28; Mid North, July 11–October 31; Rattlesnake Point, July 11–November 1. ±, plus or minus]

Parameter	Fish Banks	Mid North	Rattlesnake Point
Sample size	42	73	91
Size at end of study			
SL[1,2]	136.5 ± 11.9	159.9 ± 15.3	181 ± 15.7
SL[1,3]	112–164	127–192	126–210
Wt[2,4]	33.1 ± 8.9	54.8 ± 16.5	87.4 ± 20.9
Wt[3,4]	18.2–59.1	23.9–96.5	22.2–134.9
K[2,5]	1.28 ± 0.07	1.3 ± 0.09	1.44 ± 0.08
K[3,5]	1.11–1.45	1.12–1.5	1.11–1.68
Change in size throughout season			
SL[1,2]	34.0 ± 0.0	57.5 ± 3.6	78.4 ± 13.0
SL[1,3]	12–52	30–82	33–99
Wt[2,4]	33.1 ± 0.9	54.8 ± 16.5	87.4 ± 20.9
Wt[3,4]	18.2–59.1	23.9–96.5	22.2–134.9
K[2,5]	-0.07 ± 0.09	-0.05 ± 0.1	0.09 ± 0.1
K[3,5]	-0.24–0.25	-0.24–0.32	-0.23–0.36
Mean change in size per day			
SL[1,2]	0.32 ± 0.09	0.51 ± 0.12	0.69 ± 0.11
SL[1,3]	0.11–0.48	0.27–0.73	0.29–0.88
Wt[2,4]	0.30 ± 0.10	0.49 ± 0.15	0.7 ± 0.18
Wt[3,4]	0.17–0.54	0.21–0.86	0.20–1.19
K[2,5]	-0.001 ± 0.001	0 ± 0.001	0.001 ± 0.001
K[3,5]	-0.002–0.002	-0.002–0.003	-0.002–0.003

[1]Standard length, in millimeters.

[2]Mean ± standard deviation.

[3]Range (minimum–maximum).

[4]Weight measured in grams.

[5]Body condition $K=(\text{Weight}/\text{standard length}^3)\times10^5$.

Ichthyobodo Evaluation

Pre-season gill samples from the Klamath Tribes Fish Research Facility tested negative for *Ichthyobodo* sp. parasites by qPCR (table 10). However, *Ichthyobodo* sp. was detected using qPCR in all moribund and apparently healthy suckers sacrificed throughout the season, and in most end-of-season sacrifices tested from mesocosm sites (tables 10 and 11). Quantity estimates of *Ichthyobodo* sp. DNA were higher in moribund suckers than end-of-season healthy sacrificed fish. Among moribund suckers examined, histopathological assessments identified more severe *Ichthyobodo* sp. infestations in fish that had been introduced to mesocosms later in the season than in fish that had been introduced at the beginning of the season. *Ichthyobodo* sp. were later detected in all gill and water samples collected from the Klamath Tribes Fish Research Facility (April 12, 2017; table 10). We suspect that *Ichthyobodo* sp. was inadvertently introduced to the Fish Research Facility in May 2016 (Barbara Martin, U.S. Geological Survey, written commun., 2017).

In all instances where *Ichthyobodo* sp. was detected on gills by histopathological examination, qPCR assays also detected parasites. However, low-level infestations (0.2–7.0 DNA copies per reaction) were only detected by qPCR and were not observed by histopathology. Infestations observed by histopathology ranged from 131 to 92,218 DNA copies per reaction.

Table 10. Prevalence of *Ichthyobodo* sp. detected by quantitative Polymerase Chain Reaction and histopathology in gill samples during pre-season screening and for Lost River suckers introduced to mesocosms in Upper Klamath Lake, south-central Oregon, July 11, 2016.

[Samples listed in table were collected in 2016 except where specified. Samples for histopathology were not collected on April 29, 2016. Samples for quantitative polymerase chain reaction (qPCR) were not collected on July 6, 2016. All end-of-season (EOS) sacrifices were healthy in appearance. **Sample source:** FBW, Fish Banks West; KTFRF, Klamath Tribes Fish Research Facility; MDN, Mid North; RPT, Rattlesnake Point]

Date	Sample source	Status	Positive/total number	
			qPCR	Histopathology
April 29	KTFRF	Healthy[1]	0/20	0/0
July 6	KTFRF	Healthy[1]	0/0	0/5
August 30–September 22	FBW	Moribund	5/5	4/5
October 28	FBW	EOS sacrifice	7/7	0/4
August 17 and 24	MDN	Moribund	2/2	1/2
October 31	MDN	EOS sacrifice	18/27	0/9
September 9	RPT	Healthy[1]	1/1	0/1
November 1	RPT	EOS sacrifice	17/20	0/10
April 12, 2017	KTFRF	Healthy[1]	20/20	0/0

[1]Healthy designation is based on macroscopic observations of appearance and behavior.

Table 11. Prevalence of *Ichthyobodo* sp. detected by quantitative Polymerase Chain Reaction and histopathology in gill samples from Lost River suckers added to mesocosms in Upper Klamath Lake, south-central Oregon after July 11, 2016.

[End-of-season (EOS) sacrifice was healthy in appearance. **Sample source:** FBW, Fish Banks West; MDN, Mid North; RPT, Rattlesnake Point. **Status:** Designation is based on macroscopic observations of appearance and behavior]

Date added	Date sampled	Sample source	Status	Positive/total number	
				qPCR	Histopathology
August 5	August 16 and 18	FBW	Healthy	3/3	3/3
August 5	August 22 and 26	FBW	Moribund	2/2	2/2
August 18	August 23 and 25	FBW	Moribund	2/2	2/2
September 1	September 24	FBW	Moribund	1/1	1/1
July 22	October 31	MDN	EOS sacrifice	1/1	0/1
August 25	August 31	RPT	Healthy	1/1	1/1

Necropsies

Parasites and abnormalities were most common in Fish Banks suckers and least common in Rattlesnake Point suckers (table 12). *Lernaea* sp. copepod parasites were more common on fish from Fish Banks and Mid North, where they were observed attached to both moribund and end-of-study (EOS) fish, than on any fish at Rattlesnake Point (fig. 25; table 12). Similarly, papules were commonly observed on the skin of moribund and EOS suckers from Fish Banks, were rarely observed at Mid North, and were not observed at Rattlesnake Point. Papules were most frequently present on the caudal peduncle; they appeared as elevated, solid purple or red lumps about 2 mm in diameter and protruded through scales or were subsurface to scales (fig. 25; table 12). Some papules tested positive for carbohydrates by periodic acid-Schiff staining, suggesting that the papules may be chitinous material left over from *Lernaea* attachment anchors. Lamprey wounds were observed on some suckers from Mid North. These wounds were in various stages of healing, did not appear to be infected, and did not seem to affect behavior of affected suckers. Suckers with lamprey wounds continued to move throughout the mesocosm among antennas and did not become sedentary. The wounds may have come from a single lamprey that was recovered from the Mid North mesocosm at the end of the season. Bacterial infections were rare and were macroscopically identified as presumptive columnaris disease. Gram staining identified the bacteria as gram-negative, which indicates that the bacterium could be *Flavobacterium columnare* (fig. 25; table 12). Some instances of fin damage and scale loss also were observed.

Lower levels of visceral fat generally were observed in moribund fish necropsied throughout the season than in either baseline or EOS fish (table 13). The EOS sacrifices from Fish Banks had the least amount of visceral fat, Mid North had moderate quantities, and Rattlesnake Point had the most visceral fat. Most gall bladders were yellow, although some were light or dark green, and abnormal red or white coloration was rare (table 13). Gall bladders ranged from mostly empty to very full, indicating that fish were in various stages of feeding and digestion. Pale gills were only observed twice and both instances were moribund suckers from Fish Banks. Gill condition and overall structure appeared normal during field evaluations, although a single *Lernaea* was observed on one EOS sacrifice from Mid North. All livers were pink or dark red (table 13) and most had smooth or grainy textures (table 13). All spleens were pink or dark red except for one healthy sacrifice (August 18) and one moribund fish (September 9), both from Fish Banks (table 13).

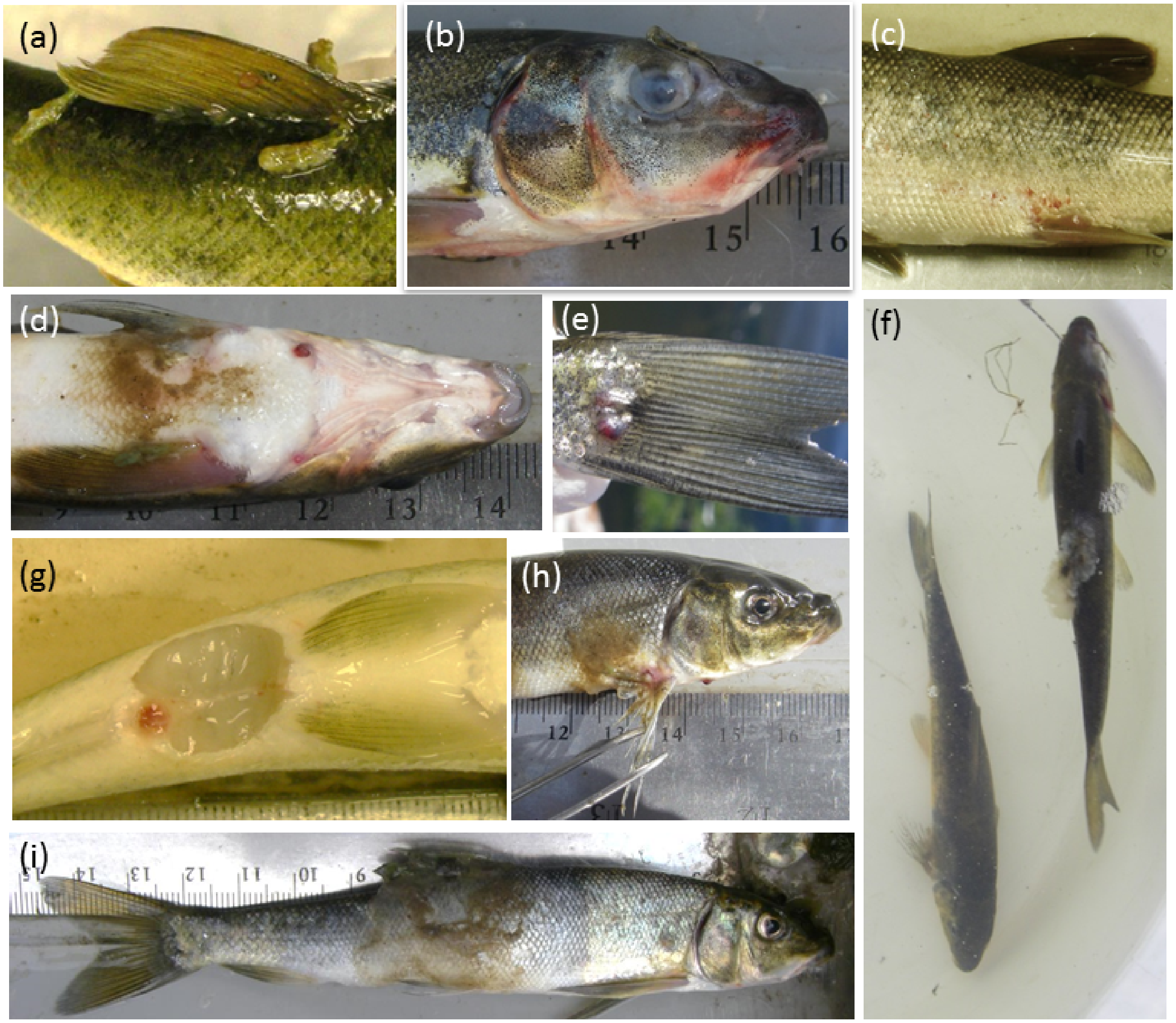

Figure 25. Photographs showing examples of abnormalities observed on Lost River suckers introduced to mesocosms in Upper Klamath Lake, south-central Oregon, 2016. (a) *Lernaea* attached near dorsal fin; (b) *Lernaea* attached to nares and petechial hemorrhaging; (c) petechial hemorrhaging; (d) skin ulcer, presumed columnaris, presumed secondary fungal infection, and papules; (e) papules in caudal peduncle; (f) skin ulcer, presumed columnaris, and presumed secondary fungal infection on moribund suckers in bucket; (g) lamprey wound; (h) damaged fin; and (i) dead tissue, skin ulcer, presumed columnaris, and presumed secondary fungal infection. Photographs by Danielle Hereford, U.S. Geological Survey, 2016.

Table 12. Prevalence of parasites (except *Ichthyobodo* sp.; see tables 10 and 11), bacterial disease, and other abnormalities for moribund suckers, healthy suckers sacrificed throughout the season (Healthy), and suckers sacrificed at the end of season (EOS) from Fish Banks, Mid North, and Rattlesnake Point mesocosms in Upper Klamath Lake, south-central Oregon, 2016.

[No healthy fish were sacrificed from Mid North during the study period. Parasites and other afflictions observed on fish found dead are not presented. – means that no fish in that category were sampled.]

Observation	Baseline	Fish Banks			Mid North		Rattlesnake Point		
		Moribund	Healthy	EOS	Moribund	EOS	Moribund	Healthy	EOS
Total fish[1]	5	10	3	78	2	77	1	1	102
Parasites									
Lernea sp.	0	4	1	23	2	17	0	0	4
Lamprey wound	0	0	0	0	0	5	0	0	0
Bacterial disease									
Presumed columnaris	0	2	0	1	1	0	0	0	0
Other abnormalities									
Fin damage	0	1	0	1	1	4	0	0	1
Papules	0	4	0	40	0	3	0	0	0
Loss of pigment	0	1	0	0	1	0	0	0	0
Petechial	0	5	3	[2]26	2	[2]7	0	0	[2,3]38
Scale loss	0	0	0	0	0	9	0	0	0
Blind	0	1	0	0	0	0	0	0	0
With 1+ affliction									
All suckers	0	8	3	50	2	39	0	0	41
FIAB and EOS[3]	–	–	–	41/42	–	36/73	–	–	36/91
No afflictions									
All suckers	5	2	0	28	–	38	1	1	61
FIAB and EOS[3]	–	–	–	1/42	–	37/73	–	–	55/91

[1]Total fish examined for afflictions. Fish found dead are not included.

[2]Petechial hemorrhaging may have occurred during sampling of fish from lifted cages at EOS or transportation of specimens to laboratory.

[3]Fish introduced at beginning of the study (FIAB) and sacrificed at the end of season (EOS).

Table 13. Condition of tissues from necropsies done in the field immediately following sacrifice for moribund suckers, apparently healthy suckers sacrificed throughout the season (Healthy), and suckers sacrificed at the end of season (EOS) from Fish Banks, Mid North, and Rattlesnake Point mesocosms in Upper Klamath Lake, south-central Oregon, 2016.

[No healthy fish were sacrificed from Mid North during the study period. Abnormalities, parasites, and disease were not observed in Baseline suckers sacrificed directly from the Klamath Tribes Fish Research Facility]

Observation	Baseline	Fish Banks			Mid North		Rattlesnake Point		
		Moribund	Healthy	EOS	Moribund	EOS	Moribund	Healthy	EOS
Total fish[1]	5	10	3	5	2	10	1	1	10
Visceral fat									
Excessive	1	0	0	0	0	0	0	0	6
Average	3	0	0	1	0	5	1	1	4
Minimal	1	5	1	2	-	2	0	0	0
None	0	5	2	2	2	3	0	0	0
Gall bladder condition and									
Full and dark red	0	1	0	0	0	0	0	0	0
Full and dark green	2	1	0	0	1	0	0	0	0
Full and light green	1	1	0	0	0	1	0	0	1
Full and yellow	1	5	1	1	1	3	0	0	5
Some fluid and yellow	1	2	2	2	0	3	1	0	1
Mostly empty and yellow	0	0	0	2	0	3	0	1	2
Mostly empty and white	0	0	0	0	0	0	0	0	1
Gill condition and color									
Normal and pink	5	7	3	5	2	10	1	1	10
Normal and pale	0	2	0	0	0	0	0	0	0
Not observed	0	1	0	0	0	0	0	0	0
Attached *Lernea* sp.	0	0	0	0	0	1	0	0	0
Not observed	0	1	0	0	0	0	0	0	0
Liver color									
Dark red	0	10	1	5	1	8	1	1	8
Pink	5	0	2	0	1	2	0	0	2
Liver texture									
Smooth	5	0	2	2	0	10	0	0	10
Grainy	0	10	1	3	1	0	1	1	0
Nodular	0	0	0	0	1	0	0	0	0
Spleen color									
Dark red	3	3	2	1	1	9	0	0	6
Pink	0	6	0	4	1	1	1	1	4
Pale	0	1	1	0	0	0	0	0	0

[1]Number of fish necropsied.

Histopathological Evaluation

Multifocal to diffuse, moderate to severe gill hyperplasia was observed on most apparently healthy and moribund suckers sacrificed throughout the study but not on baseline fish that were not introduced to mesocosms. Hyperplasia typically was mild and observed less frequently on end-of-season (EOS) suckers. *Ichthyobodo* sp. were abundant enough to be observed on most suckers collected throughout the season, but not on EOS sacrifices (table 11). Multifocal, mild gill inflammation and diffuse, severe hyperplasia were observed in moribund and healthy suckers sampled from Fish Banks and was usually (10 of 13) associated with ichthyobodiasis (fig. 26). Inflammation was not observed in gills where hyperplasia was multifocal and moderate. Focal, severe gill inflammation, and mild fibrosis and necrosis was observed in one sucker at Mid North and was associated with a *Lernaea* sp. attachment site on the gill arch (table 14). Gill inflammation was not observed from fish collected at Rattlesnake Point. Mild gill hyperplasia and epitheliocystis inclusions caused by intracellular chlamydia-like bacteria were observed at least once from each site in EOS suckers. The protozoan *Trichodina* sp. (generally considered a commensal) was observed on the gills in some moribund and EOS suckers at Fish Banks and in one moribund sucker at Mid North.

Table 14. Prevalence of inflammation, necrosis, hyperplasia, and parasites in gill tissue observed in histopathological assessment in Lost River suckers from mesocosms in Upper Klamath Lake, Oregon.

[Moribund and apparently healthy fish were collected throughout the duration of the study, end of season (EOS) sacrifices were collected October 28 at Fish Banks, October 31 at Mid North, and November 1 at Rattlesnake Point]

Observation	Baseline	Fish Banks			Mid North[1]		Rattlesnake Point		
		Moribund	Healthy	EOS	Moribund	EOS	Moribund[2]	Healthy	EOS
Total fish	5	10	3	5	2	10	1	1	10
Condition									
Inflammation	0	6	1	0	0	1	0	0	0
Fibrosis	0	0	0	0	0	1	0	0	0
Necrosis	0	0	0	0	0	1	0	0	0
Hyperplasia	0	7	3	4	1	3	1	0	1
Parasites									
Trichodina sp[3]	0	3	0	4	1	0	0	0	0
Epitheliocystis	0	0	0	2	0	1	0	0	1
Lernaea sp.	0	0	0	0	0	1	0	0	0
Apiosoma sp.	0	0	0	1	0	0	0	0	0
Ichthyobodo sp[4]	0	9	3	0	1	0	1	0	0

[1]No apparently healthy fish were sacrificed from Mid North during the study period.

[2]Suckers appeared healthy in macroscopic assessment but microscopic examination identified severely compromised health.

[3]This protozoan is usually a non-pathogenic commensal unless present in very high numbers.

[4]Positive genetic assay for *Ichthyobodo* sp. with missing histological observations not included.

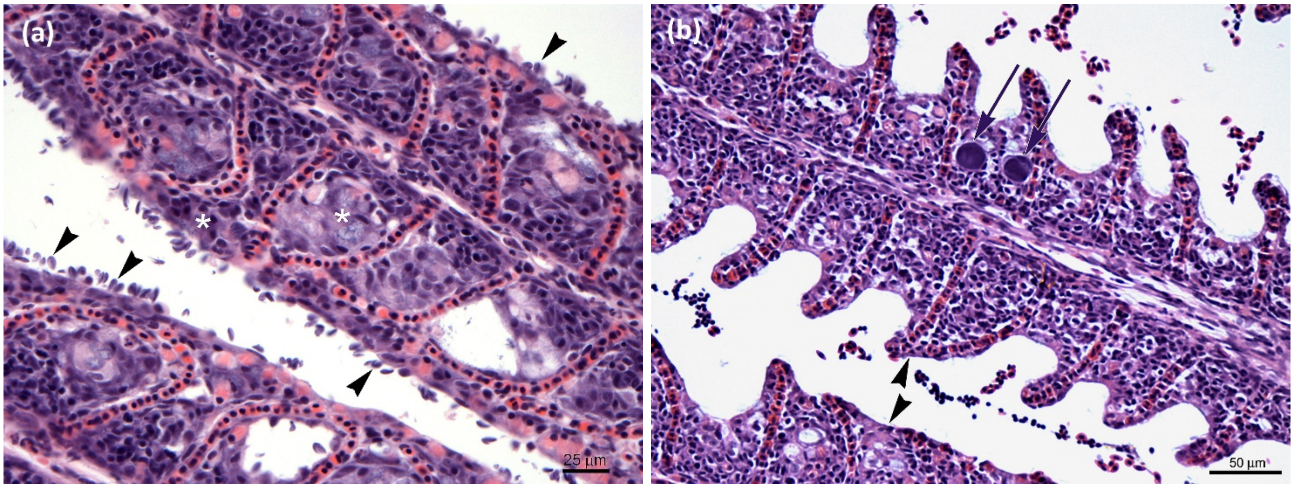

Figure 26. Microscopic images showing gill abnormalities and parasites observed in Lost River suckers collected at mesocosm sites, Upper Klamath Lake, south-central Oregon. (a) *Ichthyobdodo* sp. (arrowheads) and severe hyperplasia resulting in lamellar fusion (asterisks) in a moribund Fish Banks sucker sample taken on September 9, 2016. (b) Epitheliocystis (arrows) and mild gill hyperplasia resulting in lamellar fusion (arrowheads) observed in an end-of-season sacrificed Fish Banks sucker. Hematoxylin and eosin stain was used.

Perivascular and peribiliary cuffing and inflammation were commonly observed around the liver blood vessels and bile ducts in baseline, mid-season, and EOS fish. Livers from all moribund and mid-season healthy sacrificed fish at all sites had dense basophilic cytoplasm that lacked lipid vacuoles. In contrast, most EOS fish from Fish Banks and Mid North, and all EOS fish from Rattlesnake Point had livers, which like those of baseline fish, had flocculent cytoplasm and few apparent lipid vacuoles (table 15).

Hepatocyte glycogen storage indicated greater energy reserves for baseline fish, followed by mid-season healthy fish, and low energy storage for mid-season moribund fish and EOS fish. Glycogen storage (measured by PAS and D-PAS staining) in the liver was absent from most Fish Banks moribund fish and all Mid North moribund fish. Liver glycogen storage was diffuse in all Fish Banks, Mid North, and Rattlesnake Point EOS fish (table 15).

Table 15. Prevalence of inflammation, necrosis, hyperplasia, and parasites in tissues of Lost River suckers from mesocosms in Upper Klamath Lake, south-central Oregon, 2016.

[Moribund and healthy samples were collected throughout the duration of the study. End-of-season (EOS) sacrifices were collected on October 28 at Fish Banks, October 31 at Mid North, and November 1 at Rattlesnake Point. Unless specified, prevalence is out of total fish listed. – indicates that no fish in that category were sampled. **Hepatocyte (liver) vacuolization:** 0, dense basophilic cytoplasm; 1, flocculent cytoplasm with few apparent lipid vacuoles; 2, defined cytoplasmic presumptive lipid vacuoles. **Liver glycogen (periodic acid-Schiff [PAS] and PAS-diastase [D-PAS] staining):** 0, none; 1, some PAS-positive stain; 2, diffuse PAS-positive stain]

Observation	Baseline	Fish Banks			Mid North		Rattlesnake Point		
		Moribund	Healthy	EOS	Moribund	EOS	Moribund	Healthy	EOS
Total fish	5	10	3	5	2	10	1	1	10
Liver									
Inflammation									
Peribiliary/perivascular	1	7	1	0	1	5	0	1	5
Parenchyma	0	3	0	0	0	4	0	1	5
Vacuolization[1]	1	0	0	[2]0.6	0	[2]0.8	0	0	1
Glycogen (PAS)[3]	2	[4]0.1	[4]1	2	0	2	2	2	2
Heart									
Inflammation	0	1	1	0	0	0/9	0	–	0
Kidney									
Hyaline droplets	0	6	0	2	2	1	1	0	1
Pancreas									
Zymogen	4	7	2	4	1	10	1	1	10
Intestine									
Digenean parasite[5]	0	1	0	0	1	1	0	0	4
Skin									
Inflammation	0	4	0	4	1	7	0	0	1
Lernaea sp.	0	[6]4	0	3	1	7	0	0	1
Skeletal muscle									
Inflammation	0	5	0	4	1	6	0	0	0
Lernaea sp.	0	[6]5	0	4	1	6	0	0	0
Fibrosis	0	0	0	1	1	0	0	0	0
Necrosis	0	1	0	0	0	1	0	0	0

[1] All suckers in sample had this vacuolization score unless specified.

[2]Mean of vacuolization scores for all suckers in sample.

[3]Liver glycogen observed for all suckers in sample unless specified.

[4]Mean liver glycogen score for all suckers in sample.

[5]Number of fish with one or more adult or sub-adult parasites.

[6]Black spot parasite also observed on one individual.

Hyaline droplets were present in the epithelium of kidney tubules of 6 of 10 moribund fish examined from Fish Banks, and in all 3 total moribund fish examined from Mid North and Rattlesnake Point, but were not observed in baseline fish (table 15). Hyaline droplets were less prevalent (10–40 percent) in EOS fish at all sites. The proenzyme zymogen was observed in the exocrine pancreatic tissue of most baseline and EOS Fish Banks fish, and all EOS Mid North and Rattlesnake Point fish. Zymogen also observed in exocrine pancreatic cells of most moribund fish. Adult or sub-adult digenean parasites were observed in few moribund and EOS fish (table 15). Inflammation of the intestinal tract was not observed in any sampled suckers and focal, mild inflammation of heart tissues was rarely observed at Fish Banks (table 15).

Focal, mild-to-severe inflammation often associated with *Lernaea* sp. attachment sites was observed in the skin and (or) skeletal muscle of many suckers sampled from Fish Banks and Mid North. Multifocal, severe inflammation also was observed in the skin of one fish from Rattlesnake Point (table 15). Bacteria were observed microscopically (fig. 27) in some suckers where macroscopic assessments were noted as presumed columnaris (fig. 25). Fibrosis and necrosis of the skeletal muscle were rare (table 14). *Lernaea* sp. was the most common parasite observed in skin or in skeletal muscle and black spot was only observed on two fish, both from Mid North.

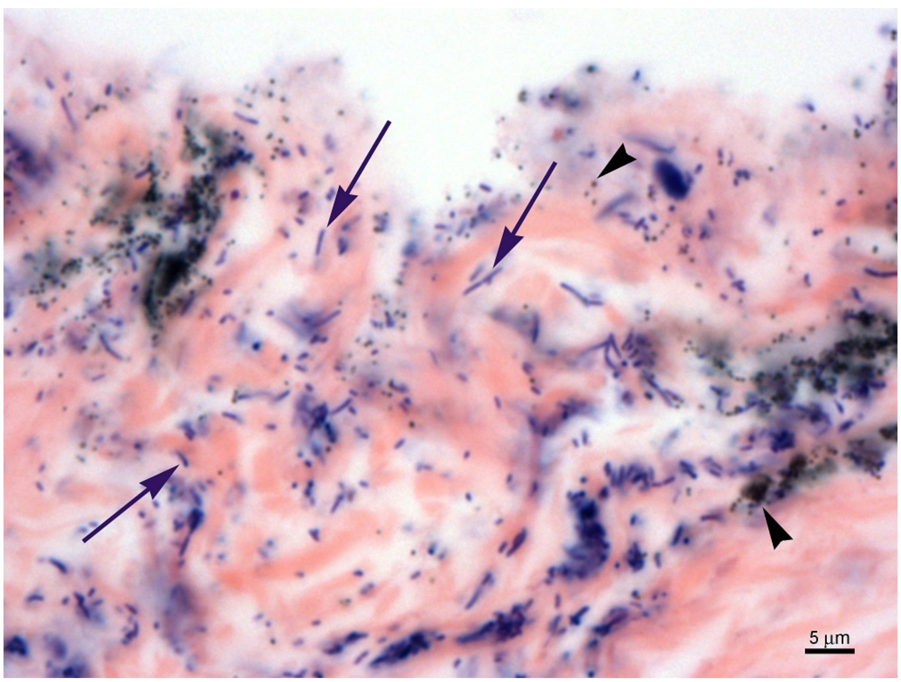

Figure 27. Histological section of the skin of a moribund Lost River sucker collected from Fish Banks mesocosm site, Upper Klamath Lake, south-central Oregon, September 21, 2016. Section was stained by the May-Grünwald giesma procedure. Notes from macroscopic observations indicated that the fish may have columnaris disease caused by the gram-negative bacterium *Flavobacterium columnare.* Long, thin, rod-shaped, blue-stained bacteria are visible in the section (arrows), and dark brown and black aggregates of melanin granules also are visible (arrowheads). Gram staining indicated that the rod-shaped bacteria were gram-negative (photograph not shown).

Discussion

Mortality Relative to Water Quality

We were unable to determine causes of mortality from known fate models. The top three models included the range in oxygen, calculated as either percent saturation or concentration and carried most of the AIC weights (0.98; table 8). Relative to any water-quality condition tested, mortality of juvenile Lost River suckers in mesocosms in Upper Klamath Lake was more likely to occur on days when there were large fluctuations in oxygen percent saturation, although the relation was relatively weak. Causes of mortality owing to factors unmeasured or unmodeled in our survival analysis (such as delayed effects of stress, immune suppression, or growth) may explain poor model fit. However, the qualitative analysis of water-quality conditions leading up to mortality also did not reveal consistent conditions. Factors unaccounted for in our models (such as parasites, disease, or availability of prey) may have caused mortality.

Although mortality, growth, health, and parasite loads summarized over the entire season all varied among sites, we were unable to conclude that water quality was the cause of these differences. The higher seasonal average DO concentration and percent saturation at Rattlesnake Point may have been related to higher survival, growth, and health at that site or may have been an artifact of the sonde location at mid-water column rather than near the surface and benthos. The lower survival, growth, and higher parasites loads at Fish Banks may have been associated with higher average diel range in temperatures at Fish Banks or may have been a sampling artifact as the top sonde was located closer to the surface than any sonde at the other two sites. Water-quality conditions prior to or during mortality events were inconsistent and did not lead to a better understanding of delayed effects on mortality. Growth is correlated with survival in early life stages of fish (Conover, 1992), and the fast growth at Rattlesnake Point may have improved survival. Therefore, differential growth among mesocosms may be related to differences in food recruitment among sites. Finally, differential among-site mortality may have been owing to differences in parasite loads attributable to differences in the number of introduced infested fish.

Water-quality stressors for suckers generally are the same as stressors for any fish species—high temperatures, high pH, high un-ionized ammonia concentrations, and low DO concentrations. However, Lost River suckers in laboratory stress tests have very high tolerances for these conditions, exceeding (either in magnitude or duration) conditions measured in Upper Klamath Lake (Castleberry and Cech, 1993; Saiki and others, 1999; Meyer and Hansen, 2002; Foott and others, 2007; Hoilman and others, 2008; Lindenberg and others, 2009). Temperatures fluctuated diurnally at all sites in Upper Klamath Lake and constant, extremely warm (≥29.99 °C for 24–96 hours) conditions resembling those in the Saiki and others (1999) median lethal trials were not observed in 2016 and do not typically occur in Upper Klamath Lake (Hoilman and others, 2008; Lindenberg and others, 2009; Eldridge, Eldridge, and others, 2012). Constant pH conditions resembling those in the Saiki and others (1999) median lethal trials (for example, median pH of 10.66 for 96 hours) were not observed at our sites in 2016 and probably do not occur in Upper Klamath Lake. Seasonal highs for pH typically are about 10 (Hoilman and others, 2008; Lindenberg and others, 2009). It is not surprising that the un-ionized ammonia model did not fit the mortality data because all measured concentrations were very low relative to the 24-hour (1,020 µg/L) and 96-hour median lethal concentrations (LC50=780 µg/L) for juvenile (0.49–0.80g) Lost River suckers (Saiki and others, 1999).

Measured minimum DO concentrations in our study were much lower than the median lethal concentrations identified by Saiki and others (1999), although low DO concentrations did not occur throughout the entire water column or did not persist. The most extreme low DO events recorded in our study were characterized by DO concentrations near the benthos of less than 1 mg/L for 14 h at MDN, but were associated with higher dissolved oxygen higher in the water column, and were not associated with direct mortality. We suspected that the large juvenile suckers in our study (range = 7.8–24.6 g) could tolerate even lower DO concentrations than the median lethal thresholds reported by Saiki and others (1999) because small juvenile suckers have a higher tolerance to low DO concentrations than larval suckers, although it is possible that the trend of increased tolerance to low DO is unfitting for larger juveniles or adult suckers. Some studies have reported that larger fish have lower tolerances for low DO concentrations than smaller fish, because the energetic costs associated with increased buccal pumping increase with body size (Robb and Abrahams, 2003). However, glycogen stores, which are used for adenosine triphosphate synthesis during hypoxia, typically increase with increasing body size (Nilsson and Östlund-Nilsson, 2008). Lethal DO concentrations for 24 h are 1.58 mg/L for juvenile and 2.01 mg/L for larval Lost River suckers (Saiki and others, 1999). When present, low DO concentrations only occurred near the benthos and fish could actively avoid these conditions by moving higher into the water column where DO concentrations were higher.

We may have failed to measure high concentrations of un-ionized ammonia because of the time or depth at which we took samples. Samples were collected weekly at Rattlesnake Point and Mid North, except during 24-hour intensive sampling periods. At Fish Banks, sampling frequency was even less for most of the season. Our 24-hour sampling events detected diel variation in total ammonia concentrations, suggesting that midday samples may not have captured daily maximums. However, the highest concentrations measured in diel sampling was only 384.3 µg/L. Concentrations in the sediment-pore-water can be extremely high (Kuwabara and others, 2016). Some regional experts have hypothesized that total ammonia (and, at times, un-ionized ammonia concentrations) may be higher at the sediment-water interface when pH is high, DO concentrations are low, and bacterial organic matter decomposition enhances ammonification (Kuwabara and others, 2016; Jake Kann, Aquatic Ecosystems Sciences LLC, written commun., 2017). However, un-ionized ammonia concentrations of samples collected throughout the water column (but not at the sediment-water interface) had nearly uniform distributions when sampled during daylight hours in Upper Klamath Lake (Loftus, 2001; Lindenberg and others, 2009). Suckers in our study showed the inclination and ability to move up in the water column to avoid adverse conditions such as low DO concentrations near the benthos. It is not clear, however, that suckers would react to high ammonia concentrations in the same way. Bortleson and Fretwell (1993) hypothesized that during wind events, sediment and thus high concentrations of ammonia in the pore-water may be temporarily suspended in the water column. The temporal frequency of our sampling was unlikely to adequately capture such events if they occurred. If such an event occurred, however, it was not associated with mass mortality because the largest number of single-day mortalities was only 7 individual fish.

Evidence that occasionally high concentrations of microcystins in Upper Klamath Lake lead to mortality of juvenile suckers is tenuous (Eldridge, Wood, and Echols, 2012). Concentrations of microcystins have substantial spatial and temporal variation and occasionally can be very high (Eldridge, Wood, and others, 2012; Hereford, Burdick, and others, 2016). Direct consumption of the microcystis cyanobacteria, secondary consumption of aquatic invertebrates that have consumed microcystins, or absorption of the suspended toxin through the gills are possible pathways for suckers to encounter microcystin toxins (Eldridge, Wood, and Echols, 2012). Consumption has been identified as the most probable way suckers would be exposed to large concentrations (Eldridge, Wood, and Echols, 2012). Concentrations of 6.6 µg/g of body weight caused mortality for carp (*Cyprinus carpio*) within 10 h and for rainbow trout (*Oncorhynchus mykiss*) within 72–96 h (Fisher and Dietrich, 2000), but studies specific to Lost River suckers have not been published. The link between water-column concentrations and oral doses of toxin also have not been established. Our study did not find an effect of microcystis concentrations on juvenile Lost River sucker survival within the range of concentrations we measured (≤ 0.85 µg/L). This finding is corroborated by a 2014 mesocosm study, in which mortality of juvenile Lost River suckers held at Fish Banks did not coincide with microcystin concentrations even when microcystin concentrations were exceptionally high (43.2 µg/L at Fish Banks, August 20, 2014; Hereford, Burdick, and others, 2016).

The results of this modeling analysis might be different if water-quality data had been consistently measured among sites. Upper Klamath Lake is shallow and polymictic; stratification and mixing both occur frequently, often daily (Hoilman and others, 2008). Two sondes at Fish Banks likely captured most of the vertical variation present at this shallow site. Similarly, two sondes at Mid North identified many stratification events, although some of the water-column profiles suggest that both sondes at Mid North were below the stratification and likely were measuring similar water-quality conditions despite different placement in the water column. Our limited number of profiles make it difficult to fully assess stratification events and how well the data represent conditions at each site. However, the single sonde at Rattlesnake Point was not able to capture all the vertical stratification that occurred throughout the water column. Our water-column profiles identified many instances of water-column stratification at Rattlesnake Point, especially in August, and water-quality conditions were more extreme throughout the entire water column than those recorded in the middle of the water column. If two sondes were continuously collecting water-quality data at two depths at Rattlesnake Point instead of one, the fit of our top model may have been reduced as two vertically stratified sondes likely would capture more variation typical of the upper and lower regions of the water column. Maximum temperatures and pH would be higher near the surface and minimum DO concentrations would be lower near the benthos, resulting in larger ranges of values. Two sondes at Rattlesnake Point may have resulted in seasonally summarized water-quality measurements, especially dissolved oxygen, more like the other two sites. The greater diel variation in temperature at Fish Banks may be an artifact of the top sonde being located only 0.3 m below the surface rather than 1 m below the surface at Mid North and mid-water column at Rattlesnake Point.

Despite differential water-quality data among sites, it seems that water-quality measurements represent reasonably well the conditions experienced by suckers in mesocosms. Movement patterns of Fish Banks and Mid North suckers were more often throughout the entire water column, whereas Rattlesnake Point suckers seems to predominately prefer the upper and middle water column during the period in which that mortality was assessed (July 18–September 20). Therefore, it is possible, that the mid-water column is representative of the conditions that suckers experienced in the Rattlesnake Point mesocosm.

Movement, Growth, and Condition

Movement patterns varied among sites. In contrast to deep sites, Fish Banks suckers did not have seasonal changes in water-column use. However, Fish Banks suckers had diel movement patterns. This behavior resembled behavior identified by Hereford, Burdick, and others (2016) during their pilot mesocosm project. Movement patterns could be the response of the suckers to the limited and artificial mesocosm environment and may not represent how wild juvenile suckers move in the water column. Furthermore, movement patterns could be associated with prey availability, predator avoidance, or some other factor such as low DO concentrations. Diel movement patterns at Mid North and Rattlesnake Point, the deeper sites, were less consistent and varied throughout the season.

Vertical diel movement behavior may be associated with avian predator avoidance. Diurnal patterns were most apparent at the shallow Fish Banks site but also occurred to a lesser extent at the other two deeper sites. Furthermore, at Rattlesnake Point and Mid North, the diurnal patterns seemed to be somewhat seasonal. American white pelicans (*Pelecanus erythrorhynchos*) and double-crested cormorants (*Phalacrocorax auritus*) are common sucker predators in Upper Klamath Lake. Pelicans have been observed actively foraging at depths as great as 2.5 m (Anderson, 1991). Double-crested cormorants are foot-propelled divers that forage for benthic and pelagic fishes as deep as 7.9 m (Ross, 1974; Enstipp and others, 2006). Suckers possibly selected deeper sites during daylight hours when they were most visible to avoid predation and ventured into the upper water column to feed at night. Cover from predation may have been provided by a depth below the surface rather than a distance above the benthos, which may explain why suckers at Fish Banks seemed to retreat to the very bottom but used the mid-water column during daylight hours at the other sites. If suckers were using deeper water to avoid predation, water clarity also may have been a factor in the depths used. We did not collect secchi depth nor other water clarity data, and secchi depth is not part of the monitoring program so we were unable to examine this hypothesis. However, seasonal changes in water clarity may help explain why the diel movement pattern was not consistent at all sites throughout the study. Alternatively, some of the observed behavior may be an artifact of fish being hatchery raised. Hatchery-raised fishes may behave differently than wild fish because of rearing conditions (Brown and Laland, 2001).

It is unclear why water-column use changed throughout the season, but possible explanations may be associated with water-quality conditions, food availability, predator avoidance, or some other factor. Although fish seemed to respond to low dissolved-oxygen concentrations near the benthos during one stratification event, they did not avoid the bottom during a second stratification event with similarly low benthic DO. We also observed one instance in which diel vertical movements did not change when dissolved oxygen was very low throughout the water column. Diurnal movements patterns, however, were not consistent throughout the season or among sites. A more extensive analysis of movement patterns than what is included in this report would be required to determine what water quality (particularly low DO) does to fish movement at different times of year among locations.

Seasonal location in the water column may be associated with changing food resources or resource availability. Lost River sucker diet studies have been very limited in scope, but benthic and pelagic invertebrates (including chironomids, crustaceans, daphnia, and copepods) have been observed in sucker digestive tracts (Markle and Clauson, 2006). Suckers analyzed by Markle and Clauson (2006) ranged in size from 15 to 70 mm and suckers seemed to shift from primarily pelagic to primarily benthic feeding when their length ranged from 20 to 30 mm. Larger juvenile suckers consume food items that are located throughout the water column and from the benthos, such as daphnia and chironomids (James Carter, U.S. Geological Survey, unpub. data, written commun., 2016). Location may be indicative of foraging behavior, and juvenile suckers at Rattlesnake Point and Mid North mesocosms likely were foraging for food resources high in the water column during the beginning of this study. Mid North suckers began to use the benthos more often in mid-August, whereas Rattlesnake Point suckers did not start using the benthos frequently until September or October. Sufficient resources, including food items, likely were present in the upper water column at these sites, especially because growth at these sites was significantly higher than growth at Fish Banks. In fact, Rattlesnake Point suckers had the highest growth rate and seemingly used the benthos the least. It is unclear whether food resources were suspended in the water column or were attached to the net pen. It also is unclear how or if food resources varied among sites. This study was not directed at understanding feeding ecology, nor did we assess growth throughout the season. Still, the remarkable growth rates of Rattlesnake Point and Mid North suckers, relative to Fish Banks suckers, suggest that ample food resources were available at these sites, and that food resources were present in the upper water column at the beginning of the study.

Causes of Mortality Identified by Histopathology

For many moribund suckers, *Ichthyobodo* sp. infestations of the gills and stresses associated with this parasite likely were the immediate cause of death, although other diseases (such as columnaris) and other stressors (such as poor water quality) may have contributed to mortality. *Ichthyobodo* sp. is an obligate ectoparasite that attaches to the gills or skin. *Ichthyobodo* sp. infestations are believed to cause mortality by destroying surface cells, impairing oxygen uptake, reducing ion-regulation, inducing anorexia, and eventually impairing the circulatory system (Lom and Dyková, 1992). Distribution of *Ichthyobodo* sp. is widespread, and the parasite has been observed on wild juvenile suckers in Upper Klamath Lake (Burdick and others, 2017). *Ichthyobodo* sp. parasites may have been acquired in Upper Klamath Lake, although our data suggests mesocosm suckers may have obtained the parasite from the Klamath Tribes Fish Research Facility.

Moribund suckers with severe *Ichthyobodo* sp. infestations typically had depleted liver glycogen stores, severe gill hyperplasia, and lamellar fusion. Depletion of liver glycogen stores likely is a result of anorexia caused by *Ichthyobodo* sp. infestations (Lom and Dyková, 1992) and increased respiratory distress. Severe lamellar epithelial hyperplasia and consequent reduction in effective respiratory epithelial surface for oxygen uptake increases the buccal pumping rate and energy expenditure during rapid respiration. Other diseases, toxins, seasonality, age, and hypoxia also can affect liver glycogen levels (Zhou and others, 2000). Liver glycogen seems to be a major energy store for suckers, and depletion of stores may identify sublethal stress. *Ichthyobodo* sp. infestations may have contributed to sucker mortality by limiting their ability to cope with changing environmental conditions.

Suckers, like anoxia-tolerant cyprinid fishes, may be able to alter (remodel) gill morphology in response to changing DO concentrations in water. During normoxic conditions, cell masses may cover gill lamellae, the primary site of oxygen uptake in fishes (Sollid and others, 2003). These cells are shed rapidly (within 24 h) when gills are remodeled during anoxic conditions to increase gill surface area and increase oxygen uptake (Sollid and others, 2003). Changes in gill morphology seem to occur within as little as 1–2 d for Lost River suckers, although changes have not been specifically studied (Scott Foott, U.S. Fish and Wildlife, oral commun., 2017). When parasites are not present, a cost associated with gill remodeling to enhance oxygen uptake is increased ion loss to the environment and eventually mitotic replacement of shed cells when normoxic conditions return. Ion regulation is metabolically expensive, ranging from 10 to 50 percent of the sucker energy budget (Bæuf and Payan, 2001; Nilsson, 2007). The rate at which suckers can remodel their gills also may be slower than the changing conditions demand. However, in the presence of gill parasites, hyperplasia of lamellar epithelium often occurs as a defensive response, and gill remodeling to increase oxygen uptake may not be possible, or it may come at a much greater cost (Nilsson, 2007). Gill lamellar epithelial hyperplasia was commonly observed in suckers burdened with heavy *Ichthyobodo* sp. infestations in our study, and these fish may not have been able to remodel gills to cope with environmental stressors such as hypoxia.

Although its prevalence has not been specifically studied, *Ichthyobodo* sp. is known to occur in Upper Klamath Lake. *Ichthyobodo* sp. infestations in the gills or skin occurred in larval and juvenile suckers, and other species including tui chub (*Gila bicolor*) and fathead minnow (C. Banner and R. Stocking, Oregon Department of Fish and Wildlife, unpub. data summary CB07-188, 2007; Foott and others, 2007;). Many (14 of 18) live suckers salvaged in 2007 from Caledonia Marsh had heavy *Ichthyobodo* sp. infestations in the gills (C. Banner and R. Stocking, Oregon Department of Fish and Wildlife, unpub. data; summary CB07-188, 2007). More recently, histopathology analysis observed *Ichthyobodo* sp. in 1 (of 87) wild juvenile sucker in Upper Klamath Lake (Burdick and others, 2017). Because the passive sampling gear (trap nets) typically captures healthy fish and less-sensitive laboratory methods (histopathology) rarely detect low-level *Ichthyobodo* sp. infestations, the prevalence of *Ichthyobodo* sp. is likely more widespread than observed by Burdick and others (2017).

Infestations of *Ichthyobodo* sp. in hatcheries typically result in widespread mortality because there are few sublethal distress symptoms or changes in behavior associated with infection (Callahan and others, 2002). In the absence of this parasite, suckers in laboratory stress tests also show few sublethal distress symptoms and little or no change in behavior until they are essentially dead (Saiki and others, 1999; Meyer and Hansen, 2002; Lease and others, 2003). Suckers seem to have a very narrow range in which they show distress symptoms, and this may explain why it has been so difficult to identify causes of juvenile sucker mortality in Upper Klamath Lake. Our study is unique because we were able to collect moribund suckers and assess causes of mortality, and we were able to assess mortality relative to water conditions in three different locations in Upper Klamath Lake.

The seeming high prevalence of homogeneous eosinophilic (hyaline) droplets within the cytoplasm of kidney tubular epithelial cells in moribund fish is suggestive of renal tissue damage or alteration. The presence of hyaline droplets in kidney tubular epithelium is frequently reported in fish (Wolf and others, 2015) and has been associated with exposure to high ammonia levels and various toxicants (Ferguson, 2006). High ammonia concentrations increase the permeability of basement membranes, and some toxicants are reported to cause injuries to the vasculature of kidney glomeruli (injuries that are often invisible in histological sections; Ferguson, 2006). Proteinaceous material that leaks through injured glomeruli (or glomeruli with increased permeability) is taken up by proximal kidney tubules and accumulates as eosinophilic droplets in epithelial cells. However, the presence of hyaline droplets in kidney tubular epithelium must be interpreted with caution, as they often are observed in seemingly healthy fish, normal inter- and intra-species variations are common, and droplets can appear as a result of tissue-preservation artifact (Ferguson, 2006; Wolf and others, 2015). The relatively low un-ionized ammonia concentrations measured in the water during our study were unlikely to have caused renal tissue changes resulting in hyaline droplet accumulation in the tubular epithelium. Svobodová and others (1993) reported that gill damage in carp may render the fish unable to excrete nitrogenous waste (ammonia) through the gills, resulting in high levels of ammonia in the blood and autointoxication. It is uncertain whether the gill lamellar epithelial hyperplasia associated with *Ichthyobodo* sp. infestations in suckers in our study affected ammonia excretion and, consequently, blood ammonia levels, as no blood samples were tested.

Suckers may have been introduced to mesocosms partway through the season, with higher *Ichthyobodo* sp. infestation rates than those at the beginning of the season. Many of the suckers that were introduced to mesocosms throughout our study were found dead or moribund within 1 or 2 weeks of introduction, whereas many of the suckers introduced on July 11 (the beginning of the season) survived. Although these fish were not part of the mortality analysis, mortality, especially at Fish Banks, may have been artificially elevated because of frequent additions of highly parasitized suckers; that is, we may have inadvertently introduced a higher parasite load to the Fish Banks cage because we added more potentially parasitized fish mid-season than at other sites. Water-quality conditions generally were similar or not as extreme later in the season on days when these suckers were introduced, and transportation conditions generally were better (lower densities). Genetic assays and histopathology observations identified severe *Ichthyobodo* sp. infestations in moribund suckers that were introduced to mesocosms later in the season. We first detected *Ichthyobodo* sp. parasites in gill samples collected from suckers in the Klamath Tribes Fish Research Facility in April 2017 while we were preparing for the 2017 field season. One introduction of wild fish to the Fish Research Facility occurred on May 26, 2016 between our initial (negative) *Ichthyobodo* sp. screening in April 2016 and the first *Ichthyobodo* sp. positive result (April 2017). *Ichthyobodo* sp. likely arrived with these fish and slowly spread throughout the system. Suckers introduced at the beginning of the 2016 study may have had low levels of *Ichthyobodo* sp. infestation relative to suckers introduced later in the season. A more thorough investigation of *Ichthyobodo* sp. prevalence and seasonality at the Fish Research Facility and in the wild is necessary before the effect that this parasite has on suckers can be adequately understood.

Interactions among poor water-quality conditions and pathogens may have complex interactions, and fish response to these conditions may vary. Lost River suckers in un-ionized ammonia stress tests had higher survival rates than controls when exposed to *Flavobacterium columnare* (Morris and others, 2006). Morris and others (2006) speculated that immune response may have been elevated for suckers exposed to higher concentrations of un-ionized ammonia or that high concentrations of un-ionized ammonia killed *F. columnare*, resulting in higher survival rates for already stressed suckers. Water quality and pathogens have complex interactions, and numerous pathogens present in Upper Klamath Lake likely have a predominantly negative affect on sucker survival. Although an infection and water-quality interaction might explain why mortality did not always coincide with poor water quality, there also was no consistent delay between poor water-quality and mortality events.

Conclusions

Age-1 mesocosm-held Lost River suckers (*Deltistes luxatus*) in our study seem to have survived relatively well, given indications of high mortality of wild juvenile suckers in Upper Klamath Lake, south-central Oregon. Mortality of age-1 mesocosm-held Lost River suckers ranged from 11.5 percent at Rattlesnake Point to 58.8 percent at Fish Banks. These mortality rates seem to be in contrast with an 84-percent or greater decrease in capture rates for age-0 Lost River suckers from August to September each year, the near absence of age-1 suckers, and a lack of recruitment to the spawning population since the 1991 cohort matured (Burdick and Martin, 2017; Burdick and others, 2017; Hewitt and others, 2018). The difference between wild and mesocom-held sucker survival may be owing to fish size and age or it may indicate that a main source of mortality for wild suckers is predation. If survival in our mesocosms was owing to better survival for age-1 than age-0 suckers, this older age-class also may have relatively good survival in the wild and management might rightly be aimed at rearing fish to age-1 in captivity prior to release in Upper Klamath Lake. However, if predation is the cause of wild mortality, then rearing fish to an even larger size may be preferable. Our ability to link the variation in, survival, growth, and health among sites to water quality likely was obscured by the locations of sondes in the water column. Further investigation may lead to a better understanding of how water quality affects sucker survival. Our results indicate, however, that lakewide summer water quality is unlikely to be the only or primary cause of near complete first-year mortality for this species every year for more than 2 decades. The fact that juvenile suckers survived relatively well in some part of Upper Klamath Lake when protected from predation is positive information for this species that has not produced a cohort that survived to maturity since 1991.

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