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# Spatial and temporal variability of bacterial indicators and pathogens in six California reservoirs during extreme drought

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ABSTRACT

California has one of the largest systems of surface water reservoirs in the world, providing irrigation water to California's agriculturally productive Central Valley. Irrigation water is recognized as a vehicle for the microbial contamination of raw produce and must be monitored according to new federal regulation. The purpose of this study was to further understanding of the variability of fecal indicator bacteria (*Escherichia coli* and fecal coliforms) and pathogens (*E. coli* O157:H7 (O157), non-O157 Shiga toxin-producing *E. coli* (STEC) and *Salmonella*) along both horizontal and vertical profiles within California reservoirs. Monthly sampling was conducted in six reservoirs located in the foothills of the Western Sierra Nevada during the summer irrigation season and extreme drought conditions of 2014 ($n = 257$). Concentrations of fecal indicator bacteria were highly variable between reservoirs ($p < 0.05$) and along the horizontal profile ($p < 0.001$) from upstream to downstream, with higher concentrations typically found outside of the reservoirs than within. Though many of the reservoirs were thermally stratified, bacterial concentrations were not associated with water temperature ($p > 0.05$) or any one particular depth strata ($p < 0.05$). However, prevalence of *Salmonella* and STEC (16/70 and 9/70 respectively) was higher in the deep strata than in mid or surface layers. We found no statistical association between samples collected downstream of reservoirs and those from the reservoirs themselves. Continued monitoring and modeling of both bacterial indicators and enteric pathogens are critical to our ability to estimate the risk of surface irrigation water supplies and make appropriate management decisions.



## 1. Introduction

Management of microbial water quality has a long-standing history for the protection of human health in recreation, aquaculture, and drinking water supplies (Schuster et al., 2005; USEPA, 2004). Until recently, irrigation water supplies, though considered a potential risk to human health via irrigated produce (Emch and Waite-Cusic, 2016; Pachepsky et al., 2011), have escaped regulation and mandatory monitoring. However, in 2011 the Food Safety Modernization Act (FSMA) was passed by Congress tasking the US Food and Drug Administration (FDA) with finalizing rules for produce safety and implementing standards for the monitoring of irrigation water supplies (USFDA, 2011). More specifically, the final rule mandates testing agricultural water for acceptable levels of generic *Escherichia coli;* the geometric mean (GM) is not to exceed 126 CFU/100 mL and the statistical threshold value (STV) is not to exceed 410 CFU/100 mL (USFDA, 2011).

Historically, resource agencies have utilized fecal indicator bacteria (FIB) as a surrogate for potentially harmful pathogenic bacteria in public water supplies (Nevers and Whitman, 2011; Poma et al., 2012; USEPA, 1978). Pathogenic bacteria, such as *Salmonella* and non-O157:H7 Shiga toxin-producing *E. coli* (STEC), are of particular concern given the regularity of cases following exposure to contaminated water and/or consumption of adulterated produce (Centers for Disease Control and Prevention, 2012). However, the value of monitoring for FIB instead of bacterial pathogens continues to be debated (Bradshaw et al., 2016; Busta et al., 2003; Edge et al., 2012; Ferguson et al., 1996; Poma et al., 2012). Pathogens are often rare in surface waters (Partyka et al., 2016) and tend to be time-consuming and expensive to enumerate, necessitating an alternative target, such as generic *E. coli*, for determining the potential human health risk following exposure. While new regulation puts the onus on the grower to monitor their individual water supplies, the variability of microbial water quality in surface

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water sources remains poorly understood; particularly in moving surface waters frequently utilized in the arid Western United States.

California's Central Valley (CV) covers nearly 52,000 km$^2$ of the most productive agricultural region in the world, and produces nearly 65% of the state's agricultural output, estimated at nearly $20 billion a year. It also accounts for nearly 75% of the state's irrigated acreage (Faunt et al., 2016; Hanemann et al., 2016). Much of California is Mediterranean in climate, with long, rainless summers. Agriculture in the CV relies extensively on surface water for irrigation. Most of California's surface water originates from snowmelt in the Sierra Nevada Mountains that is eventually impounded by large state and federal water projects in a series of reservoirs (Hanemann et al., 2016). These reservoirs provide not only irrigation water for the CV but also most of the state's hydroelectric power, drinking water, and water-based recreation (Georgakakos et al., 2012). While local and state agencies have a significant role in all aspects of water deliveries, with over 400 utilities and hundreds of agricultural water districts (Hanak and Lund, 2012), there are no routine bacterial monitoring programs in California's entire 240-reservoir system.

This study took place at the peak of one of the greatest droughts in California history (Maestro et al., 2016), with record high temperatures and record low precipitation (Shukla et al., 2015). Irrigation water supplies, always in great demand, were of limited availability and potentially of reduced quality. As there had been no previous microbiological food safety assessments within the California reservoir system, there was growing concern by the agricultural community that water diverted from publically accessible impoundments imposed additional risk to downstream irrigation water supplies. Bearing these concerns in mind, we sought to understand the variability of FIB and pathogens in a subset of reservoirs in the CV during the peak of the irrigation season, July through October. Specifically, we wanted to examine whether microbiological water quality of irrigation water supplies diverted from reservoir discharge was related to the water quality within the reservoirs and whether reservoir water quality varied by geographical position across horizontal and vertical profiles.

## 2. Material and methods

### 2.1. Site description

Water samples were collected over the course of five months during the summer and fall of 2014 at six managed reservoirs in the Western Sierra Nevada foothills of Eastern California (n = 257). Selection of the reservoirs was based on geographical stratification to cover the southern, mid, and northern sections of the CV. Specifically, we selected Lake Success (LS) and Lake Kaweah (LK) situated in the southern CV; New Hogan (NH) and Woodward (WR) Reservoirs located in central CV; and Camp Far West (CF) and Englebright (EB) Reservoirs located in northern CV (Fig. 1). We grouped these reservoirs in pairs for ease of sampling and roughly to duplicate the effect of regional environmental conditions. While all reservoirs were created by dammed rivers, each had its own unique morphology, capacity, and relationship to the surrounding landscape (Table 1). Generally, as typical of Western Sierra foothills, reservoirs were surrounded by a combination of annual grasslands and oak woodlands. Much of the surrounding landscape is open to mixed uses, including grazing by sheep and cattle. All of the reservoirs were open to the public and were frequented by recreators

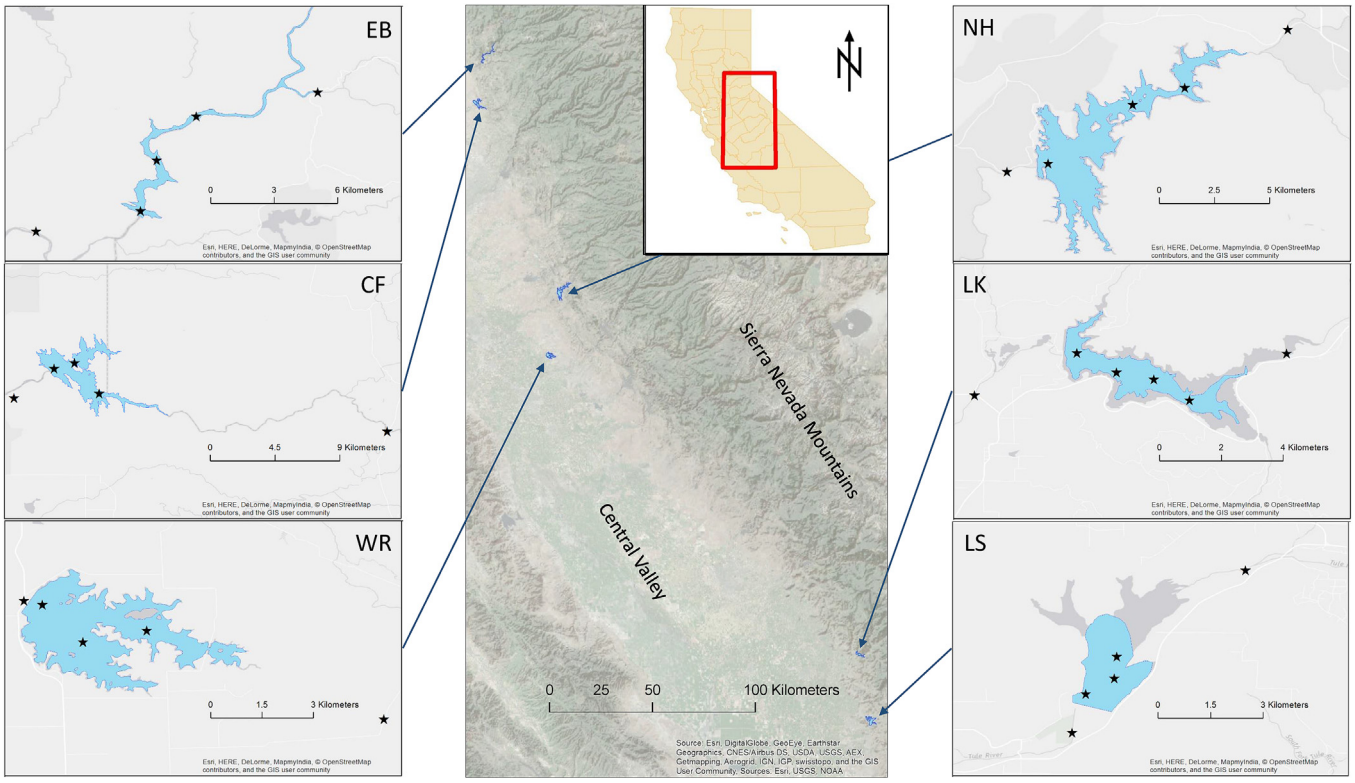


**Fig. 1.** Overview map of California with the portion of the Central Valley included in the study outlined in red. Reservoirs included in the study are shown *in situ* in the central map and with detail in the surrounding insets. Reservoir boundaries in blue are based on the USGS National Hydrography Dataset. Black stars indicate sampling sites at each reservoir along a horizontal gradient from upstream to downstream, generally right to left in each figure. Sampling sites were selected based on a combination of legal accessibility, safety, and adequate stream flow/water depth. CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Summary statistics for each reservoir included in this study. Historical capacity data were not available for Woodward Reservoir.

| Reservoir | Dam Altitude (m) | Dam Type | Surface Area ($km^2$) | Drainage Area ($km^2$) | Max Capacity (AF) | % Capacity Start | % Capacity End |
|---|---|---|---|---|---|---|---|
| Camp Far West | 85.34 | Earthen | 8.09 | 741 | 104500 | 60.5% | 4.4% |
| Engelbright | 167.94 | Variable Curved Arch | 3.29 | 2590 | 70000 | 97.7% | 94.6% |
| Lake Kaweah | 189.58 | Earthen | 7.87 | 1453 | 185600 | 24.7% | 7.7% |
| Lake Success | 188.36 | Earthen | 9.91 | 1017 | 82300 | 14.8% | 3.8% |
| New Hogan | 199.64 | Earthen | 17.85 | 940 | 317000 | 23.8% | 13.0% |
| Woodward | 64.92 | Hydraulic Fill | 13.11 | 260 | 36000 | – | – |

during the study period.

### 2.2. Sampling design

Water samples were collected from each reservoir monthly from June 24th to October 8th in 2014. Two volumes were collected; 1 L for FIB analysis and 20 L for pathogen analysis (see section 2.3. below). One-liter samples were placed on ice in coolers and the 20 L carboys were transported in hard walled bins (204 L) with ice, both were maintained at 4–10 °C until analysis. Samples taken within the reservoir were collected from a boat (explained further below) while samples taken outside the reservoir were collected via grab. There were four sampling events per reservoir. An event consisted of sampling at five horizontal positions (HP) (Fig. 2, $HP_{0\text{-}4}$), beginning upstream of the reservoir ($HP_0$), continuing through the reservoir ($HP_{1\text{-}3}$), and ending at the nearest accessible point downstream of the reservoir ($HP_4$). The HPs within each reservoir were positioned within the historical river channel, as determined by a combination of bathymetric maps (when available) and repeated passes with single-beam sonar (Garmin GPSMAP 547xs, Garmin Ltd. Olathe, KS) $HP_1$ was placed as near to the top of the reservoir as could be accessed by boat while still allowing for vertical profiling, $HP_2$ was placed near the mid-point, and $HP_3$ near the dam face at a safe distance from the point of water off take. The position of horizontal sampling sites was highly reservoir-specific (Fig. 1) and dependent upon safe access and adequate flow.

Within the reservoir, stratified depth samples were collected at each HP at three vertical positions (VP) (Fig. 2 inset): the first was within the epilimnion or well-mixed surface layer ($VP_A$); the second within the metalimnion or thermocline ($VP_B$); and the third within the hypolimnion or well-mixed bottom layer ($VP_C$). Determination of the vertical sampling depths followed a multi-step process. At each reservoir site ($HP_{1\text{-}3}$), four initial vertical conductivity-temperature-depth (CTD) casts were conducted using a Sontek/YSI CastAway CTD (Yellow Springs Instruments, Yellow Springs, OH) attached to a 100 m surveyor's rope (Keson, Aurora, IL). These four casts formed the corners of a box that shared similar depth and vertical stratification characteristics allowing for repeated sampling in an area without the use of an anchor. A single CTD cast was conducted on subsequent visits to determine the depth of the thermocline and hypolimnion layers for $VP_B$ and $VP_C$ sampling, respectively. Briefly, cast data were immediately uploaded to an onboard laptop and evaluated for the presence of a thermocline or thermal gradient. When present, samples were collected near the mid-point of the gradient. The hypolimnion sample was collected at least 2 m deeper than the gradient or at the deepest location possible without disturbing bottom sediments. In

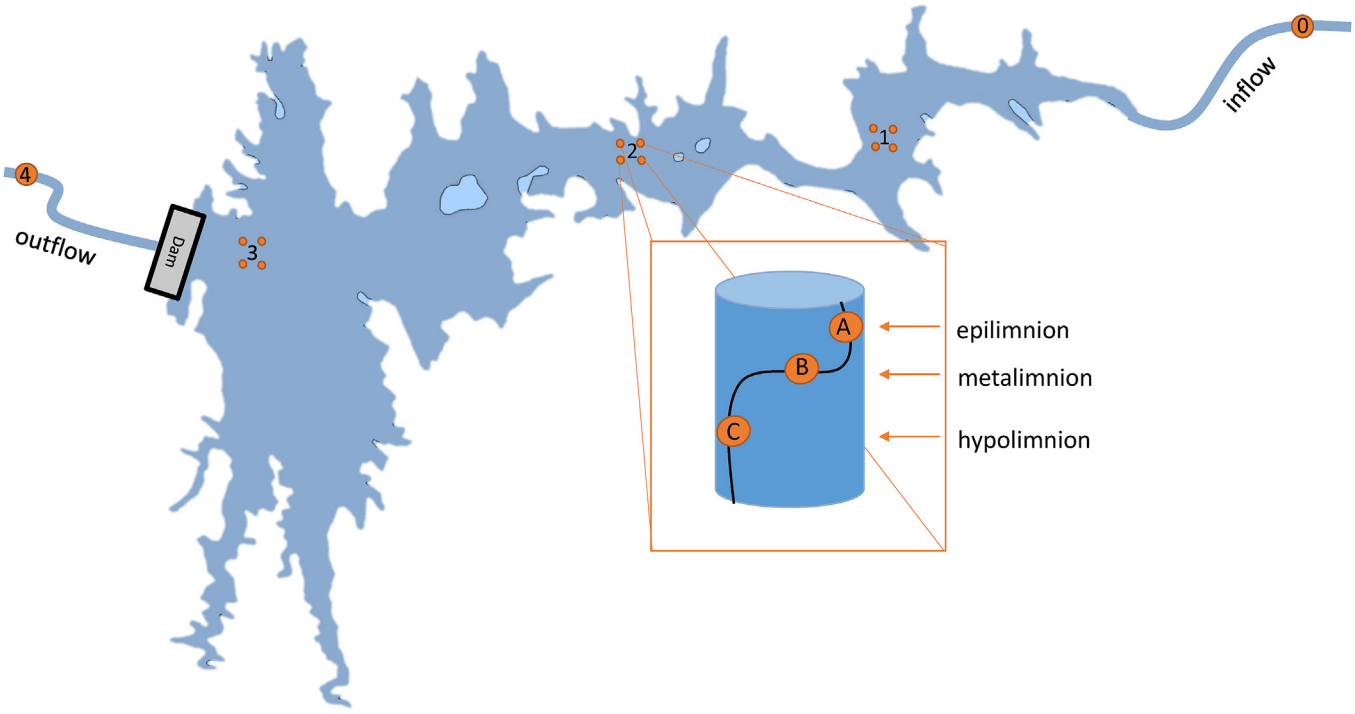


**Fig. 2.** Example schematic of sampling locations at each reservoir. Horizontal positions (HP): (0) inflow, (1) inside reservoir near inflow, (2) inside reservoir near midpoint, (3) inside reservoir near dam and (4) outflow. Inset- Vertical position (VP) sampling sites within reservoir (A) above thermocline, (B) within thermocline and (C) below thermocline.

the absence of a clear thermocline, samples were collected below the surface (1 m), midpoint of water column and near bottom without disturbing sediments.

Samples for vertical profiles were pumped using a Proactive Abyss pump (Proactive Environmental Products, Bradenton, FL) attached to a pre-measured and marked (1 m increments) Teflon lined tube lowered by a 120 m swivel hose reel (Jackson Professional Tools, Camp Hill, PA). The pump was lowered to the desired sampling depth and run long enough to allow approximately 2× the required sample volume ( 2 × 21 L) to be purged (~7 min). In addition to water samples, *in situ* physiochemical measurements (dissolved oxygen, pH, conductivity and temperature) were taken at all surface sites using a YSI ProPlus multiparameter instrument (Yellow Springs Instruments, Yellow Springs, OH) and site specific meteorological measurements (wind speed and direction and air temperature) were taken using a Kestrel 4500 handheld anemometer (Nielsen-Kellerman, Boothwyn, PA). Turbidity was measured following microbiological analysis using a portable turbidity meter (Lamotte Co., Chestertown, MD).

### 2.3. Laboratory analysis

#### 2.3.1. Indicator bacteria

Fecal indicator bacteria (FIB), specifically *E. coli* (EC) and non-*E. coli* fecal coliforms (FC), were enumerated from each water sample (1 L) within 6–8 h of collection using standard membrane filtration techniques (APHA, 2012). Briefly, each sample was homogenized and poured through a 0.45 μm nitrocellulose filter and placed on CHROMagar ECC (CHROMagar Microbiology, Paris, France), a chromogenic selective media, and incubated at 44.5 °C for 18–24 h. Results (EC- blue colonies and FC- mauve colonies) were counted and reported as colony forming units (CFU) per 100 mL.

#### 2.3.2. Ultrafiltration processing and pathogen detection

Each 20 L water sample was concentrated to ≤500 mL using the ultrafiltration method described by Partyka et al. (2016). Briefly, sample water was conveyed via peristaltic pump through a dialyzer filter (Fresenius Medical Care NA, Concord, CA) under pressure to create tangential flow, allowing bacteria-free water to be discarded and the bacteria-laden water to be retained (retentate). Retentates were enriched with irradiated tryptic soy broth pellets (30 g/L retentate; Merck and Co., Kenilworth, NJ) and incubated at 25 °C for 2 h followed by 8 h at 42 °C with orbital shaking at 100 rpm, then held static at 6 °C until pathogen-specific analysis was performed.

Retentates were analyzed for the presence of *Salmonella* spp., *E. coli* O157:H7 (O157), and non-O157 Shiga toxin-producing *E. coli* (STEC) described by Partyka et al. (2016). Immuno-Magnetic Separation (IMS) was preformed using a Dynal BeadRetriever (Invitrogen Carlsbad, Ca USA) according to the manufacturer's instruction to isolate *Salmonella* spp. and O157 from the enriched retentates (Table S1). Up to four presumptive positive colonies per selective agar were further isolated on the same selective agar and then grown on LB agar (Becton Dickinson Company, Franklin Lakes, NJ) for DNA extraction and molecular confirmation by PCR. For detection of STEC, an aliquot (1 mL) of the enriched retentate went through a secondary enrichment in 9 mL mEHEC broth (BioControl Systems, Inc, Bellevue, WA), followed by colony isolation on CHROMagar STEC (CHROMagar Microbiology, Paris, France), (Table S1). Up to six fluorescent (suspect STEC) colonies were isolated then grown on LB agar for DNA extraction and molecular confirmation by PCR.

A simple boiling method was used to extract DNA from suspect isolates (Atwill et al., 2015). *Salmonella* and O157 isolates were PCR confirmed using methods described by Pan et al. (2015). STEC isolates were confirmed using a multiplex-PCR (mPCR) assay designed to detect *E. coli* O157, O145, O121, O111, O103, O45, and O26 (Paddock et al., 2012). Presumptive STEC isolates and positive O157 isolates were further characterized by mPCR for four virulence genes, including Shiga toxin 1 (*stx1*), Shiga toxin 2 (*stx2*), intimin adherence protein (*eae*) and hemolysin (*hlyA*) described by Paton and Paton (2003).

### 2.4. Statistical analysis

Descriptive statistics for environmental parameters and concentrations of indicator bacteria along with all statistical models were calculated using Stata 14 software (StataCorp LP). Microbial indicator counts were $\log_{10}$-transformed prior to parametric analyses to conform with assumptions. Within-group comparisons of environmental, categorical and microbiological results were made using ANOVA followed by post-estimation using the Wald test for linear hypotheses. In this study, we adhered to a detailed model-fitting protocol fully described in Partyka et al. (2017). Briefly, we evaluated the data for distribution shape, residual correlation structure, and autoregressive components prior to examining the presence of multi-level effects or interactions. We used a combination of criteria for determining best model fits, including quasi-likelihood under the independence model criterion (QIC) (Cui, 2007), the Hausman test and the Breusch-Pagan LM test (Rabe-Hesketh and Skrondal, 2012) and comparisons between a combination of AIC score and $R^2$ for final model selection. A univariate significance of $p \leq 0.10$ was used as a threshold for inclusion in preliminary model selection; robust variance estimation was then utilized to calculate p-values within the finalized models. Spatial analyses and mapping were performed using ArcMap 10.4 (ESRI, Inc., Redlands, CA).

## 3. Results

### 3.1. Environmental conditions

Average reservoir depths ranged from 10.7–41.5 m at the start of the study (June/July) to 5.5–41.2 m at the fourth and final sampling visit (September/October). Three of the six reservoirs (CF, LK, and LS) experienced significant ($p < 0.05$) reductions in volume/capacity by the end of the study period; depths within EB remained the most consistent throughout (Table 1). During the study period, there was no measurable precipitation in any of the study systems, greatly reducing any influence of surrounding land uses on subsequent water quality.

Physical and chemical conditions (i.e. air temperature, water temperature, conductivity, pH, dissolved oxygen, and turbidity) varied between all reservoirs, at times significantly (Table S2). Some of these differences followed regional trends; reservoirs in the central part of the CV (NH and WR) were more alkaline on average collectively ($p < 0.01$) and with higher conductivity ($p < 0.05$) than those in the northern CV (EB and CF). Woodward reservoir was the most consistently alkaline of the reservoirs (7.47–8.97) significantly more so ($p < 0.05$) than CF, EB, and LK individually. Both air and water temperatures were significantly warmer in the southern CV (LS and LK) than the central CV ($p < 0.01$ and $p < 0.001$ respectively). Though air temperatures cooled significantly as sampling proceeded from the summer into the fall ($p < 0.0000$ events 2–4 individually compared to event 1), reservoir temperatures did not show significant cooling from starting conditions until the final sample visit in the early fall of 2014 ($p < 0.05$ event 4 compared to event 1). Turbidities varied significantly between all reservoirs ($p < 0.0001$) except LS and CF, and across both horizontal ($p < 0.0001$) and vertical strata ($p < 0.0001$)

with lowest median values found at $HP_0$ for surface samples ($p < 0.05$) and $VP_A$ for samples within reservoirs ($p < 0.001$).

### 3.1.1. Thermal stratification

Clear stratification in water column temperatures was evident in each reservoir at the beginning of the study period, with thermocline width (maximum depth epilimnion − minimum depth hypolimnion) ranging from 2 m to 31.5 m ($\mu \pm sd = 10.9 \pm 8.4$) accompanied by changes in temperature from 3 °C to 14 °C ($\mu \pm sd = 7.8 \pm 3.6$). However, fully developed profiles with a distinct epilimnion, metalimnion, and hypolimnion layers were only measured at sites closest to the dam face ($HP_3$), with the exception of EB reservoir that had defined thermoclines at all sites and all visits. The other five reservoirs slowly became less stratified, with complete loss of the hypolimnion in LK, LS and NH by the fourth and final sampling visit, even at $HP_3$ (Fig. 3). The impact of reservoir drawdown was seen most clearly at CF where the maximum depth decreased from 40 m to <20 m over the 4-month study, yet the minimal temperature of the hypolimnion remained constant (~11.5 °C). Camp Far West also experienced the steepest thermoclines, greatest change in temperature per change in depth, averaging 1.39 °C per m at $HP_3$; significantly steeper than every other reservoir when averaged across visits (LS $p < 0.05$, NH $p < 0.01$, EB, LK, and WR $p < 0.0001$).

## 3.2. Microbial indicators

Bacterial concentrations were highly variable during this study (Table 2) with significant differences between reservoirs ($\log_{10}$ EC $p < 0.001$, $\log_{10}$ FC $p < 0.0001$). Median EC concentrations were greatest in CF and WR reservoirs while highest median FC concentrations were found at LK, LS and WR. Clear differences also existed between samples from the source water feeding the reservoirs ($HP_0$) and the reservoirs themselves (Fig. S1). Median concentrations of EC were >10 times higher at $HP_0$ than surface samples taken within the reservoir ($HP_{1\text{-}3}$) (Table 3) regardless of distance (km) to $HP_0$, while median FC concentrations were >8 times higher at $HP_0$ than $HP_{1\text{-}3}$. For log-transformed EC samples, taken downstream of the dam ($HP_4$), were also significantly higher

**Table 2**
Summary statistics for microbial results for each reservoir: CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir EC = *E. coli* CFU/100 mL.

| Reservoir | | EC[a] | FC[b] | *Salmonella* (PA[c]) | STEC (PA[c]) | O157:H7 (PA[c]) |
|---|---|---|---|---|---|---|
| CF (n = 42) | Mean | 11.69 | 20.62 | 11 | 4 | 0 |
| | Median | 2.33 | 4.33 | 26.2% | 9.5% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 324 | 216 | | | |
| EB (n = 44) | Mean | 2.54 | 5.23 | 27 | 4 | 1 |
| | Median | 1.00 | 2.30 | 61.4% | 9.1% | 2.3% |
| | Min | 0 | 0 | | | |
| | Max | 36 | 40 | | | |
| LK (n = 44) | Mean | 6.10 | 90.26 | 8 | 0 | 1 |
| | Median | 1.17 | 20.17 | 18.2% | 0.0% | 2.3% |
| | Min | 0 | 0 | | | |
| | Max | 84 | 2400 | | | |
| LS (n = 41) | Mean | 45.0 | 5998.7 | 6 | 1 | 0 |
| | Median | 1.0 | 17.6 | 14.6% | 2.4% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 792 | 114000 | | | |
| NH (n = 42) | Mean | 47.05 | 3.23 | 7 | 6 | 0 |
| | Median | 0.20 | 0.67 | 16.7% | 14.3% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 1630 | 28 | | | |
| WR (n = 44) | Mean | 8.62 | 136.45 | 8 | 8 | 1 |
| | Median | 4.00 | 16.50 | 18.2% | 18.2% | 2.3% |
| | Min | 0 | 1 | | | |
| | Max | 44 | 956 | | | |
| Total (n = 257) | Mean | 19.43 | 941.56 | 67 | 23 | 3 |
| | Median | 1.33 | 5.00 | 26.1% | 8.9% | 1.2% |
| | Min | 0 | 0 | | | |
| | Max | 1630 | 114000 | | | |

[a] EC = *E. coli* CFU/100 mL.
[b] FC = fecal coliforms CFU/100 mL.
[c] PA = number positive samples confirmed in presence/absence analysis followed by % samples positive within reservoir.

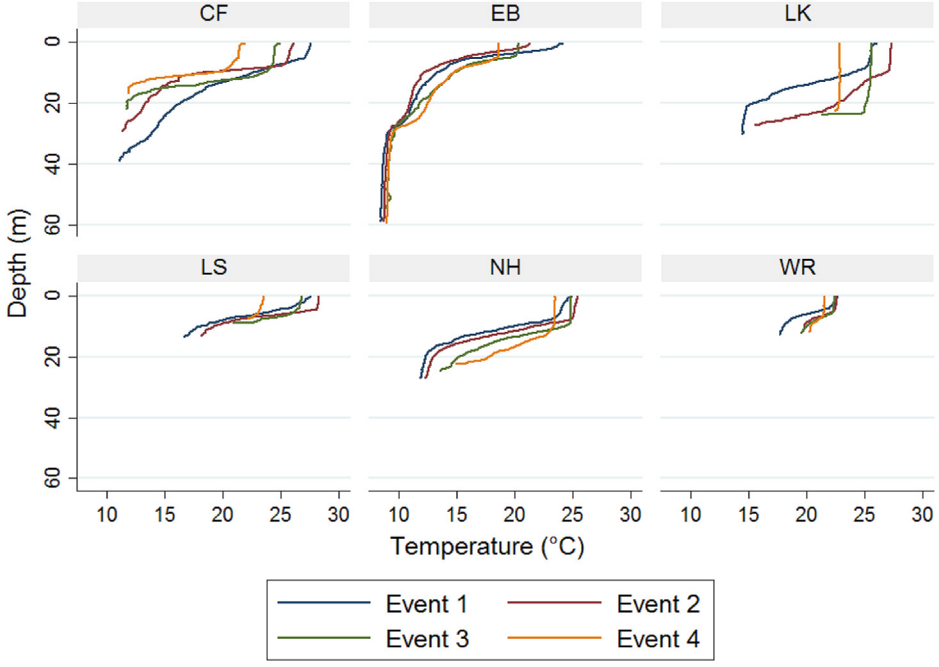


**Fig. 3.** Thermal profiles of each reservoir at site HP3, nearest the dam face, over the course of four sampling events. CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir. See Fig. 2 for relative sampling locations.

**Table 3**
Summary statistics for samples taken from the surface at defined horizontal positions within each system: 0 = river inflow, 1 = within the reservoir closest to inflow, 2 = near mid-point of the reservoir, 3 = near the dam face, and 4 = river discharge below the dam face. During late summer, two source rivers ceased to flow and could not be sampled.

| Horizontal Position | | EC [a] | FC [b] | *Salmonella* (PA[c]) | STEC (PA[c]) | O157:H7 (PA[c]) |
|---|---|---|---|---|---|---|
| 0 (n = 21) | Mean | 120.21 | 59.52 | 15 | 4 | 1 |
| | Median | 13.00 | 41.00 | 71.4% | 19.0% | 4.8% |
| | Min | 1 | 5 | | | |
| | Max | 1630 | 216 | | | |
| 1 (n = 24) | Mean | 12.63 | 1470.40 | 3 | 0 | 0 |
| | Median | 1.04 | 5.50 | 12.5% | 0.0% | 0.0% |
| | Min | 0 | 0.4 | | | |
| | Max | 228 | 34000 | | | |
| 2 (n = 24) | Mean | 5.8 | 4768.8 | 3 | 1 | 0 |
| | Median | 0.84 | 3.83 | 12.5% | 4.2% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 6 | 114000 | | | |
| 3 (n = 24) | Mean | 8.36 | 541.17 | 3 | 3 | 0 |
| | Median | 0.90 | 5.17 | 12.5% | 12.5% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 124.67 | 10100 | | | |
| 4 (n = 24) | Mean | 46.05 | 463.34 | 16 | 2 | 0 |
| | Median | 6.60 | 12.00 | 66.7% | 8.3% | 0.0% |
| | Min | 0.33 | 0 | | | |
| | Max | 792 | 9100 | | | |
| Total (n = 117) | Mean | 35.87 | 1509.47 | 40 | 10 | 1 |
| | Median | 2.20 | 9.50 | 34.2% | 8.5% | 0.9% |
| | Min | 0 | 0 | | | |
| | Max | 1630 | 114000 | | | |

[a] EC = *E. coli* CFU/100 mL.
[b] FC = fecal coliforms CFU/100 mL.
[c] PA = number positive samples confirmed by presence/absence analysis followed by % samples positive within strata.

($p < 0.0001$) than those taken from $HP_{1\text{-}3}$, and were marginally different from $HP_0$ ($p = 0.0456$). The trend in FC was different, however, with no significant difference found between samples from $HP_4$ and those taken from $HP_{1\text{-}3}$ ($p > 0.05$), nor any difference between $HP_0$ samples and $HP_4$ samples ($p > 0.05$) (Fig. S1). When averaged across reservoirs, $\log_{10}$ FC concentrations did not correlate closely with $\log_{10}$ EC ($R^2 = 0.05$); however, stronger correlations were apparent on a reservoir-by-reservoir basis. For example, $\log_{10}$ EC concentrations from NH had a nearly one-to-one relationship with $\log_{10}$ FC ($\beta = 1.011$, $p < 0.0001$, $R^2 = 0.39$) while $\log_{10}$ EC results from WR had essentially no association with $\log_{10}$ FC ($\beta = -0.050$, $p = 0.522$, $R^2 = 0.009$). The variability in the strength of these correlations could result from a combination of different contributing sources, variability in the endemic microbial populations and differential die-off in the microbial populations over a broad geographic scale.

Average concentrations of log-transformed bacteria did not vary significantly ($p > 0.05$) between depths ($VP_{A\text{-}C}$) when averaged across all reservoirs (Table 4). Though vertical position did not have an overall effect, there were significant differences in microbial indicators across depth strata in NH ($\log_{10}$ EC and $\log_{10}$ FC $p < 0.05$) with highest average concentrations at the surface ($VP_A$) compared to thermocline ($VP_B$) and hypolimnion ($VP_C$) samples. Similarly, within CF log-transformed concentrations of FC were significantly higher at $VP_A$ ($p < 0.001$) on average, though this was not always the case at each HP or every sampling event.

### 3.2.1. Linear regression analysis

Following preliminary evaluation using our model fitting protocol (Partyka et al., 2017), FIB results were best-approximated (lowest AIC, highest $R^2$, and smallest residuals) using linear regression of the log-transformed outcomes. Separate models were created for surface waters across the entire horizontal profile and samples at all depths within the reservoirs. None of the models exhibited fixed or random effects as the result of repeated sampling (Hausman > 0.05, Breusch-Pagan LM > 0.05), nor did they show meaningful autoregressive trends, and so were best-modeled using simple multiple regression methods. The final regression model for the horizontal profile included multiple components (Table 5), including factor variables (horizontal position and reservoir), a continuous variable (pH), and an interaction between pH and reservoir (Fig. 4, 1-$\beta = 0.77$, effect size 0.18). In NH, WR, and LS, the three reservoirs with the highest average pH, increased pH was associated with a reduction in $\log_{10}$ EC, while the opposite relationship was demonstrated in the other three reservoirs.

For the within-reservoir model, the width of the thermocline, an indication of how abruptly water temperatures changed through

**Table 4**
Summary statistics for samples taken within the reservoir at three separate vertical positions: A = at the surface (epilimnion), B = within the thermocline, and C = within the hypolimnion. For well-mixed water columns, the B and C strata were taken near the mid-depth and just above the bottom, respectively.

| Vertical Position | | EC[a] | FC[b] | *Salmonella* (PA[c]) | STEC (PA[c]) | O157:H7 (PA[c]) |
|---|---|---|---|---|---|---|
| A (n = 72) | Mean | 8.94 | 2260.14 | 9 | 4 | 0 |
| | Median | 1.00 | 4.62 | 12.5% | 5.6% | 0.0% |
| | Min | 0 | 0 | | | |
| | Max | 228 | 114000 | | | |
| B (n = 70) | Mean | 7.83 | 722.56 | 11 | 4 | 1 |
| | Median | 1.00 | 4.00 | 15.7% | 5.7% | 1.4% |
| | Min | 0 | 0 | | | |
| | Max | 247 | 27000 | | | |
| C (n = 70) | Mean | 8.34 | 192.60 | 16 | 9 | 1 |
| | Median | 1.00 | 2.00 | 22.9% | 12.9% | 1.4% |
| | Min | 0 | 0 | | | |
| | Max | 189 | 4800 | | | |
| Total (n = 212) | Mean | 6.25 | 1085.11 | 36 | 17 | 2 |
| | Median | 1.00 | 4.00 | 17.0% | 8.0% | 0.9% |
| | Min | 0 | 0 | | | |
| | Max | 247 | 114000 | | | |

[a] EC = *E. coli* CFU/100 mL.
[b] FC = fecal coliforms CFU/100 mL.
[c] PA = number positive samples confirmed by presence/absence analysis followed by % samples positive within strata.

**Table 5**
Multiple regression model for the association of $\log_{10}$ *E. coli* in surface water samples with geographical and chemical characteristics of several reservoirs of the California Central Valley. ($R^2 = 0.53$).

| Factor | Coefficient | *P*-value | 95% CI | |
|---|---|---|---|---|
| Intercept | 6.685 | <0.001 | 4.603 | 8.766 |
| Reservoir | | | | |
| Lake Success[a] | 0.000 | | | |
| Camp Far West | −6.364 | <0.001 | −9.837 | −2.891 |
| Englebright | −6.368 | 0.002 | −10.338 | −2.397 |
| Lake Kaweah | −6.587 | 0.003 | −10.842 | −2.333 |
| New Hogan | −3.345 | 0.028 | −6.314 | −0.375 |
| Woodward | −2.677 | 0.303 | −7.805 | 2.451 |
| pH | −0.648 | <0.001 | −0.914 | −0.383 |
| Reservoir*pH | | | | |
| Lake Success[a] | 0.000 | | | |
| Camp Far West | 0.778 | 0.001 | 0.325 | 1.232 |
| Englebright | 0.732 | 0.007 | 0.208 | 1.256 |
| Lake Kaweah | 0.798 | 0.006 | 0.240 | 1.357 |
| New Hogan | 0.396 | 0.038 | 0.021 | 0.771 |
| Woodward | 0.325 | 0.319 | −0.319 | 0.969 |
| Horizontal Position | | | | |
| 0[a] | 0.000 | | | |
| 1 | −0.816 | <0.001 | −1.117 | −0.516 |
| 2 | −0.934 | <0.001 | −1.235 | −0.633 |
| 3 | −0.850 | <0.001 | −1.152 | −0.548 |
| 4 | −0.386 | 0.013 | −0.688 | −0.083 |

[a] Referent condition for the categorical variable, effect is null.

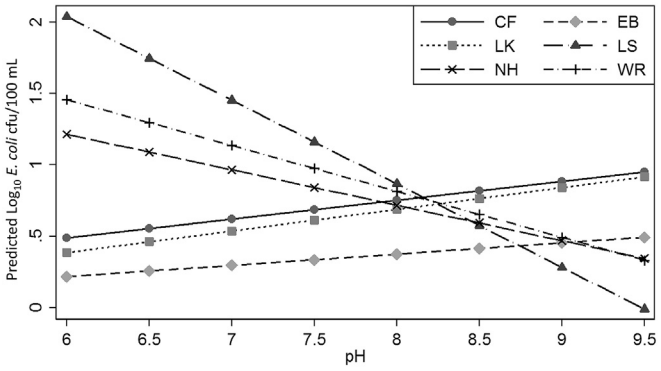


**Fig. 4.** Linear regression model predictions for the distribution of $\log_{10}$ *E. coli* concentrations in surface water samples ($HP_0$-$HP_4$) as a function of reservoir and pH. See Table S2 for measured variability in pH at each reservoir, Fig. 2 for relative sampling locations, and Table 5 for the full model and individual coefficients. CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir.

the water column, was negatively associated with log-transformed EC in a univariate evaluation. However, the shape of the relationship was much more complex within a fully-specified model with strong reservoir-specific interactions (Table 6, 1-β = 0.92, effect size 0.10). For example, LS, NH and WR showed more or less linear associations between thermocline width and $\log_{10}$ EC, yet there appear to be curvilinear associations with thermocline width in CF, EB, and LK (Fig. 5).

As with EC, separate models were generated for FC. The regression model for surface water samples is similar to that for EC, with the replacement of turbidity (NTU) and dissolved oxygen concentration (mg/L) for pH along with a significant interaction between turbidity and reservoir (Table S3, 1-β = 0.75, effect size 0.18). Unlike the model for EC, $\log_{10}$ FC within reservoir showed a seasonal component with each subsequent sampling event exhibiting lower concentrations ($p < 0.001$) than the first event (Table S4. 1-β = 0.87, effect size 0.10).

**Table 6**
Multiple regression model for the association of $\log_{10}$ *E. coli* in samples from within reservoirs as a function of geography and thermal stratification. ($R^2 = 0.22$).

| Factor | Coefficient | *P*-value | 95% CI | |
|---|---|---|---|---|
| Intercept | 0.906 | <0.001 | 0.727 | 1.084 |
| Reservoir | | | | |
| Lake Success[a] | 0.000 | | | |
| Camp Far West | −0.153 | 0.156 | −0.365 | 0.059 |
| Englebright | −0.102 | 0.440 | −0.361 | 0.158 |
| Lake Kaweah | −0.202 | 0.055 | −0.409 | 0.005 |
| New Hogan | −0.420 | <0.001 | −0.629 | −0.212 |
| Woodward | −0.104 | 0.321 | −0.311 | 0.102 |
| Thermocline Width (m) | −0.060 | <0.001 | −0.089 | −0.032 |
| Thermocline Width$^2$ (m) | 0.001 | 0.003 | 0.001 | 0.002 |

[a] Referent condition for the categorical variable, effect is null.

### 3.3. Pathogens

All samples were analyzed for the presence of *Salmonella*, *E. coli* O157:H7 (O157), and non-O157 Shiga toxin-producing *E. coli* (STEC). Presumptive STEC isolates were further analyzed for specific serotype (O45, O145, O103, O111, O121, or O26) and presence of genes associated with virulence and/or toxin production (*stx1, stx2, hylA,* and *eae*). Of the 257 samples collected during this study, over 26% tested positive for *Salmonella* (67/257), 9% were positive for STEC (23/257), and only 1% (3/257) of samples were positive for O157 . The most common STEC serotypes were O26 and O103 each with 17% representation amongst the STEC positive samples (4/23). Of the samples that were positive for STEC, a majority (n = 9) were not differentiated into one of the seven serotypes evaluated by our assay but did contain at least one of the virulence factors associated with pathogenicity in *E. coli*.

Pathogen prevalence did not mirror indicator results; occurrence of *Salmonella* in EB was significantly higher than all other reservoirs ($p < 0.01$) (Table 2), while also having the second lowest overall EC concentration of all reservoirs. Similarly, WR had the lowest median FIB concentrations but had the highest occurrence of STEC positives (~35%, 8/23). For all pathogens, a greater percentage of positive results came from samples within the reservoirs ($HP_{1\text{-}3}$) (*Salmonella* 54%, 36/57; STEC 75%, 12/16; and O157 66%, 2/3), than from source ($HP_0$) or discharge ($HP_4$) samples (Table 3). Within the reservoirs, a higher proportion of both *Salmonella* and STEC positives were found in samples from the bottom of the water column ($VP_C$) (44% and 50% respectively) than the other two depths (Table 4), though this distinction was not significant ($p > 0.05$). When evaluating surface water samples alone, an entirely different trend is seen; the highest occurrence of all pathogens were found outside of the reservoir ($HP_0$ or $HP_4$). This further indicates the importance of understanding which layers of water are being diverted from dams based on their operation and engineering and of monitoring different depth strata when assessing the risk to human health.

#### 3.3.1. Logistic regression analysis

Logistic regression was used to model the binary pathogen outcomes, a positive or negative PCR result. All reservoirs were significantly less likely ($p < 0.01$, O.R.= 0.04–0.13) to test positive for *Salmonella* than samples taken from EB. When accounting for differences in reservoirs, $\log_{10}$ EC was significantly ($p < 0.01$) associated with an increased probability of testing positive for *Salmonella* (Table 7, Fig. 6). According to the model, for every one-log increase in EC, the odds of a sample testing positive for *Salmonella* increased more than 2-fold (O.R. = 2.1). However, the majority of samples testing positive for *Salmonella* had $\log_{10}$ EC

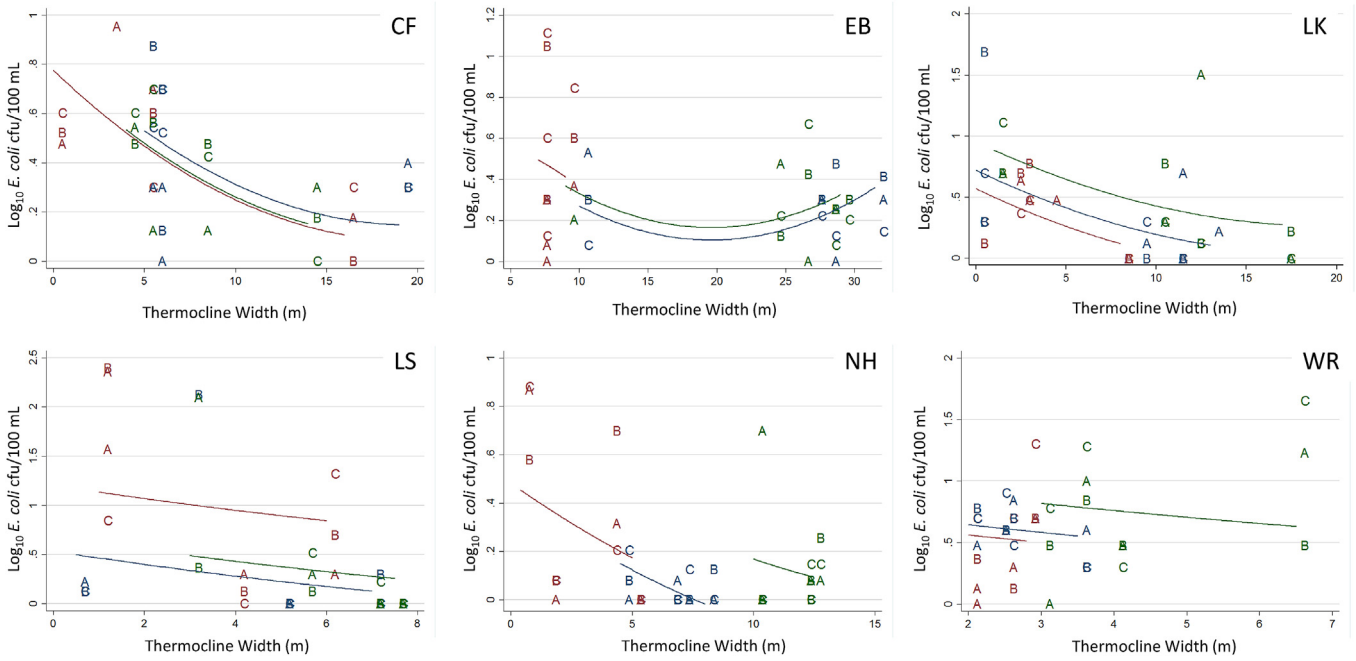


**Fig. 5.** Combination of raw (letters) and linear regression modeled (fit lines) $\log_{10}$ *E. coli* concentrations as a function of reservoir, thermocline width, horizontal and vertical sampling positions. See Table 6 for the full model and individual coefficients. CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir. $HP_1$ = red, $HP_2$ = blue, $HP_3$ = green, $VP_A$ = A, $VP_B$ = B, $VP_C$ = C. See Fig. 2 for relative sampling locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 7**
Multiple logistic regression model for the association of *Salmonella* occurrence with biological and geographical characteristics. ($R^2 = 0.30$).

| Factor | Odds Ratio | *P*-value | 95% CI | |
|---|---|---|---|---|
| Intercept | 9.898 | 0.002 | 2.309 | 42.429 |
| Reservoir | | | | |
| Englebright[a] | 0.000 | | | |
| Camp Far West | 0.133 | <0.001 | 0.046 | 0.386 |
| Lake Kaweah | 0.075 | <0.001 | 0.024 | 0.237 |
| Lake Success | 0.039 | <0.001 | 0.010 | 0.153 |
| New Hogan | 0.077 | <0.001 | 0.022 | 0.263 |
| Woodward | 0.061 | <0.001 | 0.019 | 0.202 |
| $\log_{10}$ *E. coli* | 2.108 | 0.050 | 1.000 | 4.440 |
| Horizontal Position | | | | |
| 0[a] | 0.000 | | | |
| 1 | 0.105 | 0.001 | 0.028 | 0.396 |
| 2 | 0.109 | 0.001 | 0.028 | 0.422 |
| 3 | 0.072 | <0.001 | 0.018 | 0.290 |
| 4 | 0.993 | 0.991 | 0.252 | 3.907 |

[a] Referent condition for the categorical variable, effect is null.

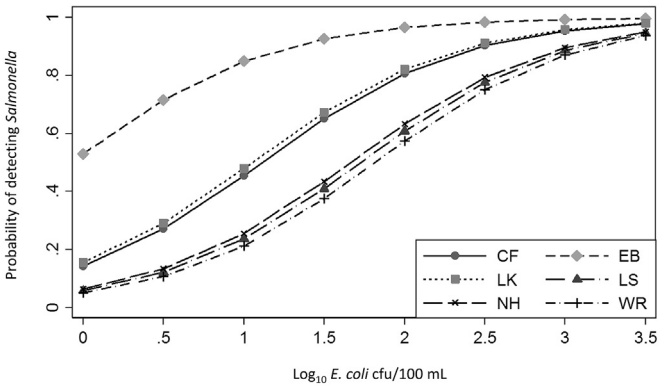


**Fig. 6.** Logistic regression results for the predicted probability of a positive test result for *Salmonella* at each reservoir (all horizontal and vertical positions) as a function of $\log_{10}$ *E. coli* . See Table 7 for the full model and individual coefficients. CF = Camp Far West, EB = Englebright Reservoir, LK = Lake Kaweah, LS = Lake Success, NH = New Hogan Reservoir, and WR = Woodward Reservoir.

concentrations at or below 1, or 10 cfu/100 mL (72%, 48/67). No other environmental or physical attribute was capable of explaining additional variability in *Salmonella* prevalence, including sampling depth, sample temperature, sampling visit, or location within the reservoir. The prevalence of both STEC and *E. coli* O157 were too low to find statistical associations and were not modeled.

## 4. Discussion

Many studies have examined the interaction of physical and biological factors that may influence the distribution and abundance of enteric bacteria in surface waters (Boehm and Soller, 2013; Davis et al., 2005; Olyphant, 2005; Partyka et al., 2017) with varying degrees of agreement on which factors contribute to the greatest understanding of the variability captured through sampling and the subsequent value of statistical models for making predictions. For instance, Olyphant (2005) found that models incorporating meteorological conditions, including wind speed and air temperature, were highly successful at predicting bacterial abundance in fresh water lakes of the mid-west United States. By contrast, Thoe et al. (2015) found that the value of predictive models was highly contingent upon site-specific conditions and the overall quality of the water source being modeled. Further, in a detailed study of surface water quality within the California Central Valley, Partyka et al. (2017) found that the strength and direction of relationships between indicator bacteria and antecedent conditions was highly variable and driven by unmeasured site-specific conditions. With these challenges in mind, we sought to explore the horizontal,

vertical, and temporal trends in microbial water quality within six multi-use reservoirs in order to understand the possible risks imposed on downstream irrigation water supplies. To our knowledge, this is the first published study evaluating three-dimensional distribution and abundance of fecal indicator bacteria and bacterial pathogens in multiple California reservoirs alongside source water inflows and outflows.

We found that regardless of the consistency in our sampling design across all reservoirs, each reservoir posed its own unique set of circumstances and challenges to collecting representative samples. For example, the distance of the inflow sampling location ($HP_0$) varied from ~3 km at Lake Kaweah to over 15 km at Camp Far West (Fig. 1) because of limitations in accessibility. Though we attempted to control for variability in relative site locations, water levels, and overall geographies by the inclusion of these characteristics (like distance to inflow) in our statistical models, none remained in the models individually or in combination. Rather, each model retained a term for reservoir that represents many of the differences (measured and otherwise) inherent in these systems. For example, models for the horizontal distribution of FIB in surface waters retained strong interactions between individual reservoirs and water quality characteristics (pH and turbidity), indicating that each system may be better understood if modeled independently. The horizontal profile from inflow through outflow explained over 90% of the variance in a New Hogan-specific model, a relationship apparent in Fig. S1, yet was non-significant and non-informative in a Lake Success-specific model. However, this disparity was not surprising given Lake Success continually defied analysis.

We also sought to understand the role vertical stratification played in harboring bacterial pathogens during hot, dry California summers. Thermal stratification can have important implications for planktonic succession, fisheries management, and the quality of the water within multi-use reservoirs (Borics et al., 2015; Szelag-Wasielewska et al., 2015; Yu et al., 2014a). Many waterborne bacteria are capable of utilizing a wide range of organic substances during anaerobic respiration; therefore, facultative anaerobes, like fecal indicator bacteria and the pathogens studied here, could contribute to an increase in released nutrients during hypoxic conditions typical of the hypolimnion (Yu et al., 2014a, 2014b). While we lacked the instrumentation to collect physical/chemical characteristics other than temperature and conductivity below the epilimnion, other studies have found that temperature, DO, and pH are lower in the hypolimnion during periods of stratification (Davis et al., 2005; North et al., 2014; Yu et al., 2014a), conditions that typically favor bacterial persistence if not growth. Based on these suppositions, we expected to see clear differences in bacterial concentrations and pathogen occurrence across depth strata when vertical stratification was detected. Surprisingly, while there was clear stratification within all reservoirs at some point in space and time during the study, there was no clear, statistical association between sample depth, presence of stratification, or sample temperature on concentration of fecal indicator bacteria within the study reservoirs. Though not significant, FIB concentrations were actually generally lower at depth than at the surface, contrary to our prediction. The width of the thermocline (m), a measure of the separation between the epilimnion and hypolimnion, was weakly predictive of both indicators; however, this relationship was highly variable across reservoirs (Fig. 5). It also remains difficult to explain biologically, since sites with narrower thermoclines tended to also have the greatest difference in FIB between individual strata ($VP_{A-C}$). Liu et al. (2016) found decreased microbial abundances with depth in vertically stratified lakes of the Tibetan plateau; decreases that were associated with increases in microbial diversity. It is possible that the same processes were taking place within our study reservoirs. However, we failed to capture them when we selected for our study organisms; ones not originating from the aquatic environment and in direct competition with endemic species (Menon et al., 2003).

Surprisingly, pathogen occurrence within the reservoirs was not predictive of pathogen detection in downstream samples ($HP_4$). On the contrary, the majority of samples testing positive for any pathogen were found within the reservoirs, and largely in the deeper strata (Table 4). This trend does seem to be in line with our hypothesis mentioned above, increased persistence in the protective deep water layers, since it is unlikely that pathogens are being sourced at depth. Englebright, the reservoir with the highest prevalence of *Salmonella*, also had the largest drainage area – land area inclusive of streams, creeks or rivers that flow into a reservoir, a relatively small overall capacity, the deepest average depths, and consistent thermal stratification. Perhaps this allowed for increased loading in source river from the surrounding landscape followed by rapid submersion in the reservoir similar to processes described by Hoyer et al. (2015) for pathogen distribution in Lake Tahoe. Reduced downstream prevalence of pathogens in surface water samples from all reservoirs may be a result of rapid exposure to sunlight and increased oxygenation during a highly turbulent discharge. However, FIB concentrations in the reservoirs were not related to bacterial levels in water supplies downstream of the reservoir; perhaps indicating that either additional sources are contributing to the water quality in a short distance between dam face and sample site, or the turbulent flow generated from water release somehow disrupts or disturbs buried sources near the discharge intakes.

This project took place during the summer of 2014 in the midst of one of the deepest droughts that California has ever experienced (Maestro et al., 2016), and prior to the enactment of strict water conservation legislation passed during 2015. Some reservoirs in California had been cut off from the rivers that feed them and many reservoir levels fell well below half of their historical averages (Table 1). Reservoir-specific differences observed in this study may have been driven hydrological differences (CA Department of Water Resources, 2014), intensity of recreational use (Sierra Nevada Alliance, 2006), or even concentrations of domestic/wild animals forced to use the reservoirs as nearby streams began to disappear. Moreover, drought conditions along with rising atmospheric temperatures and anticipated increases in extreme drought events followed by heavier than normal storms conditions are likely to impact management of valuable and vulnerable surface water supplies. Reservoirs, regardless of geographical location or surrounding land uses, may harbor bacterial pathogens. Monitoring for fecal indicator bacteria is unlikely to lead to better understanding of the risks associated with these water sources, as evidenced by the absence of a correlation between regulatory exceedances and pathogen prevalence in this and similar studies. Continued monitoring and modeling of not only bacterial indicators but enteric pathogens is critical to our ability to estimate the risk of exposure to surface water supplies and make appropriate management decisions (Pachepsky et al., 2014; Partyka et al., 2017), particularly when humans may come into direct contact with water supplies through drinking water, recreation, or consumption of irrigated produce.

## 5. Conclusions

- Concentrations of fecal indicator bacteria were highly variable across space and time with riverine samples taken from above and below the impoundments generally higher than samples from within reservoirs.

- Dissolved oxygen, turbidity and pH were the only environmental variables that showed association with bacterial concentrations.
- Thermal stratification was documented within all reservoirs on at least one occasion; however, as the summer progressed and water levels dropped many of the reservoirs became more uniformly mixed. Bacterial concentrations were not associated with any one particular water layer.
- Prevalence of *Salmonella* and non-O157 STEC was highest in reservoirs with the lowest overall concentrations of fecal indicator bacteria; however, *Salmonella* occurrence was best modeled with the inclusion of $\log_{10}$-transformed *E. coli* concentrations.
- Microbial water quality in downstream irrigation supplies was not statistically associated with the conditions within the source reservoir and more closely resembles water quality upstream of reservoirs suggesting effective monitoring of irrigation supplies needs to be conducted downstream of impoundments nearer the point of diversion to irrigation supplies.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.watres.2017.11.038.

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