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Received: 29 March 2023 | Revised: 28 July 2023 | Accepted: 23 August 2023

DOI: 10.1002/wer.10923

RESEARCH ARTICLE

water
ENVIRONMENT RESEARCH

Effects of water turbidity on the survival of *Staphylococcus aureus* in environmental fresh and brackish waters

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Funding information
NIH COBRE P20GM125508; NSF REU 1950353

Abstract

Staphylococcus aureus is an opportunistic pathogen frequently detected in environmental waters and commonly causes skin infections to water users. *S. aureus* concentrations in fresh, brackish, and marine waters are positively correlated with water turbidity. To reduce the risk of *S. aureus* infections from environmental waters, *S. aureus* survival (stability and multiplication) in turbid waters needs to be investigated. The aim of this study was to measure *S. aureus* in turbid fresh and brackish water samples and compare the concentrations over time to determine which conditions are associated with enhanced *S. aureus* survival. Eighteen samples were collected from fresh and brackish water sources from two different sites on the east side of O'ahu, Hawai'i. *S. aureus* was detected in microcosms for up to 71 days with standard microbial culturing techniques. On average, the greatest environmental concentrations of *S. aureus* were in high turbidity fresh waters followed by high turbidity brackish waters. Models demonstrate that salinity and turbidity significantly predict environmental *S. aureus* concentrations. *S. aureus* persistence over the extent of the experiment was the greatest in high turbidity microcosms with T_{90}'s of 147.8 days in brackish waters and 80.8 days in freshwaters. This study indicates that saline, turbid waters, in the absence of sunlight, provides suitable conditions for enhanced persistence of *S. aureus* communities that may increase the risk of exposure in environmental waters.

Practitioner Points

- *Staphylococcus aureus* concentrations, survival, and persistence were assessed in environmental fresh and brackish waters.
- Experimental design preserved in situ conditions to measure *S. aureus* survival.
- Higher initial *S. aureus* concentrations were observed in fresh waters with elevated turbidity, while sustained persistence was greater in brackish waters.

Maria Steadmon is a member of the Water Environment Federation (WEF).

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- Water turbidity and salinity were both positively associated with *S. aureus* concentrations and persistence.
- Climate change leads to more intense rainfall events which increase water turbidity and pathogen loading, heightening the exposure risk to *S. aureus*.

KEYWORDS

persistence, recreational waters, salinity, *Staphylococcus aureus*, survival, turbidity

INTRODUCTION

Staphylococcus aureus, a gram-positive coccus bacterium, is the leading cause of Community-Acquired (CA) skin infections throughout the United States (Akanbi et al., 2017; Elmir et al., 2007). Recreational waters (like coastal beach waters) are likely sources of CA—*S. aureus* infections since pathogens like *S. aureus* have been found in seawater and sand worldwide (Charoenca & Fujioka, 1993; Esiobu et al., 2013; Goodwin et al., 2012; Papadakis et al., 1997). Beaches in Hawai'i, Seattle, Florida, California, Mexico, Israel, Egypt, Spain, and Croatia have all detected *S. aureus* (Abdelzaher et al., 2010; Curiel-Ayala et al., 2012; El-Shenawy, 2005; Gómez et al., 2020; Goodwin et al., 2012; Levin-Edens et al., 2012; Plano et al., 2013; Topić et al., 2021; Yoshpe-Purer & Golderman, 1987). *S. aureus* enters recreational waters through reservoirs such as humans and animals, soils, rainfall, streams, urban runoff, wastewater, and coastal sands (Economy et al., 2019; Gerken et al., 2022; Viau et al., 2011). During storm events, more *S. aureus* is washed into recreational waters from these sources (Economy et al., 2019; Gerken et al., 2022). *S. aureus* concentrations in environmental waters are strongly correlated with physico-chemical parameters such as runoff, river discharge, surf height, salinity, temperature, and turbidity (Curiel-Ayala et al., 2012; Dwight et al., 2004; Economy et al., 2019; Fogarty et al., 2015; Goodwin et al., 2012; Viau et al., 2011). Still, *S. aureus* survival in environmental waters is complex and poorly understood.

Survivability (stability and multiplication) of microorganisms like *S. aureus* is determined by assessing the viability of the organism under hostile conditions through culturing (Filkins et al., 2015; Roszakt & Colwell, 1987). Previous work using pure culture inoculated microcosms have suggested that *S. aureus* and virulent *S. aureus*, such as Methicillin-Resistant *S. aureus* (MRSA), survive longer (ranging from ~1 to 15 days) than fecal indicator bacteria (FIB) like *Enterococcus* spp. and *Clostridium perfringens* (stable from 1 to 5 days) which are used to determine safe recreational water quality (Ahmad et al., 2014; Fujioka & Unutoa, 2006; Gabutti et al., 2000; Levin-Edens et al., 2011; Medema et al., 1997; Zhang et al., 2015). Despite this extended survival in recreational waters compared with FIB, *S. aureus* survival has not been extensively studied despite being suggested as an indicator organism for preventing skin ailments in recreational waters (Curiel-Ayala et al., 2012; Favero et al., 1964). Studies on the survival of *S. aureus* and MRSA in the environment have found that *S. aureus* can survive in fresh, estuarine, and marine waters—with the longest persistence in cold, nutrient rich, saline waters (Fujioka & Unutoa, 2006; Gabutti et al., 2000). However, *S. aureus* populations are significantly reduced when exposed to sunlight—with a 99% reduction within 2 h of exposure (Fujioka & Unutoa, 2006; Levin-Edens et al., 2011). While studies have focused on the impact and dynamics of temperature, salinity, nutrients, beach sands, and swimming pool waters on *S. aureus* survival, research investigating the influence of turbidity on *S. aureus* survival is limited (Fujioka & Unutoa, 2006; Gabutti et al., 2000; Levin-Edens et al., 2011).

The survival of pathogens like *S. aureus* in turbid environmental waters has been an area of focus due to a continual threat to human health that is exacerbated postrainfall events (Economy et al., 2019; Fogarty et al., 2015). Approximately 50% of waterborne disease outbreaks in the United States have long been correlated with poor water quality after heavy rainfall (Coffey et al., 2014). These sporadic rainfall events rapidly flush pathogens accumulated on land during dry periods, and the frequency of these events is predicted to increase with climate change (Coffey et al., 2007, 2014). Based on observations of *S. aureus* in the environment, higher turbidity is often a strong indicator of elevated *S. aureus* concentrations suggesting a positive interaction between *S. aureus* and particles contributing to turbid waters (Steadmon et al., n.d.; Economy et al., 2019; Grobbelaar, 2009). Associations with particulate material in turbid waters offer several advantages to *S. aureus* in terms of survival and persistence including shielding from UV light, protection from phage attack, shelter from predation, and a higher availability of adsorbed organic matter to metabolize (Chamberlim & Mitchell, 1978; Cho et al., 2010; Dutka, 1984; Fujioka et al., 1981; Maugeri et al., 2004). The only study to quantify the impact of

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turbidity on the survival of *S. aureus* focused on potable drinking water (Wen-jun & Yong-ji, 2006). Wen-jun and Yong-ji (2006) demonstrated that higher turbidity in potable water reduced the bactericidal capabilities of UV light on pathogens including *S. aureus* since the suspended particles attenuated light and shielded *S. aureus* from harmful UV rays. Their findings are consistent with other environmental studies (Fujioka & Unutoa, 2006; Levin-Edens et al., 2011).

To further the capacities of applying models to predict the risks associated with *S. aureus* contamination in environmental waters, we determine how turbidity and salinity impact the decay of *S. aureus* at in situ concentrations in the absence of light. This is the first experimental study to quantify survival (stability and multiplication) of *S. aureus* through T_{90}, the time for a 1-log reduction from initial concentrations, in samples of environmental fresh and brackish waters of different turbidity. Understanding these factors will allow us to better understand pathogen transmission and longevity in these waters. As the US-EPA is moving toward more stringent water protection through the statutory authorities of the Clean Water Act and the Safe Drinking Water Act, both the Agency and practitioners need to understand the dynamics of pathogens thoroughly under diverse environmental conditions to better assess their potential effects.

METHODS

Sample collection

In June 2022, water samples were collected in 1 L bottles in triplicate from six freshwater and brackish water sites within the same watershed on the eastern, windward side of O'ahu, Hawai'i, to ensure consistent *S. aureus* source inputs and minimize biogeographical variabilities. To reduce the influence of weather-related environmental variability, samples were collected in the morning within 10 min of each other at three sites in fresh waters and repeated a week later in brackish waters. Sites were selected based upon high community interaction and cultural significance and the fact that they discharge into a popular O'ahu beach. Freshwater samples were collected in stream and spring waters that were classified as low turbidity (5.42 and 5.62 NTU, respectively) and from an agricultural outflow stream with high turbidity (401 NTU). All freshwater sites were approximately 8–22 m above sea level with salinity values of 0 ppt. Twenty-four-hour cumulative precipitation prior to freshwater sample collection was 0 cm (National Weather Service [NWS], 2023). Brackish water samples were collected in a tidally influenced channelized stream near the bottom of the watershed at only 0.1 m above sea level. Brackish water samples were classified as high (>800 NTU), intermediate (66.5 NTU), and low (1.33 NTU) turbidity. Salinity of brackish samples ranged between 18.8 and 19.0 ppt. Twenty-four-hour cumulative precipitation prior to brackish water sample collection was 0.05 cm (NWS, 2023). All samples were kept cool at ambient conditions ($26 \pm 2°C$) in the dark for no more than 3 h in transit to the laboratory before the start of the experiment. After the experiment was completed, particulate matter (PM) and dissolved (colloidal) matter (DM) in each sample were quantified. Since PM and DM contain both inorganic and organic matter, their measurements may have experienced minor fluctuations potentially affecting the accuracy as representations of environmental PM and DM measurements. Aliquots from each sample were filtered through 0.8 μm to capture PM, followed by 0.2 μm pore-size filters to capture DM (Mestre et al., 2017; Schapira et al., 2012). Measurements were carried out using Standard Method 2540D for Total Suspended Solids with modifications described above (Clesceri et al., 1999; Mestre et al., 2017; Schapira et al., 2012).

Microcosm preparation and *S. aureus* enumeration

To constrain the bacterial decay rate of *S. aureus*, water samples were incubated in dark 1 L microcosms under in situ envrionmental watershed conditions. Microcosms were not filter sterilized to preserve in situ turbidity, nutrient sources, minerals, salinities, and the native microbial community structure. This novel experimental design utilized environmentally relevant and tractable abiotic and biotic conditions compared with past experiments. This preserved the naturally occurring microbial diversity at each site (which included a diversity of *S. aureus* strains) at environmentally relevant concentrations (wherein particles were likely colonized with established biofilms) to facilitate the complex ecological interactions that may play important roles in *S. aureus* survival (Levin-Edens et al., 2011). Samples were divided up into a 2×2 factorial design defined by salinity (fresh or brackish) and turbidity (low, intermediate, or high). To isolate potential impacts of turbidity on *S. aureus* persistence and survival in brackish and fresh waters, experiments were conducted in the absence of light. Previous studies have demonstrated that *S. aureus* colonies significantly decrease by approximately 99% within hours of exposure to light, (Fujioka & Unutoa, 2006; Wen-jun & Yong-ji, 2006). If light was included in the experiment, enhanced *S. aureus* survival in turbid waters would be driven by the protective reduction of UV light penetration in higher turbidity treatments,

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while rapid decay in low turbidity treatments would be driven by increased exposure to harmful UV radation (Fujioka & Unutoa, 2006). Thus, microcosms were incubated in the dark (to eliminate confounding light-dependent effects) at in situ water temperatures (26 ± 2°C) and shaken at 144 RPM for the extent of the experiment to reduce settling out of particles, to match stream flow rates, and to ensure adequate aeration.

At each time point, aliquots of 1–5 mL were sampled from each microcosm for culturing. Time zero (t_0) was defined as the start of the experiment and classified as the environmental concentration of that sample. Aliquots were filtered through a 47 mm 0.45 μm pore-size filter for consistency with previously published work (Charoenca & Fujioka, 1993; Economy et al., 2019; Goodwin & Pobuda, 2009; Tice et al., 2010; Viau et al., 2011). Despite the potential for *S. aureus* to pass through 0.45 μm pore-size, staphylococci cell diameters range from 0.5–1.5 μm (Harris et al., 2002) and evidence suggests that *S. aureus* colonies demonstrate limited passage through 0.45 μm pore-size filters (Onyango et al., 2010). Filters were cultured on CHROMagar™ Staph aureus medium and incubated for 24 h at 37 ± 2° C (Goodwin & Pobuda, 2009; Tice et al., 2010). After 24-h incubations, colonies that appeared mauve were counted as *S. aureus*, and selected *S. aureus* colonies were restreaked to isolation to confirm morphologies, consistent with other studies (Economy et al., 2019). The efficacy of culture-based *S. aureus* detected from environmental water samples has been previously tested, demonstrating a percent positive predictive accuracy between 70% and 99% (Goodwin & Pobuda, 2009; Tice et al., 2010). Thus, *S. aureus* colonies in this study are presumptive. Culturing methodologies remained consistent for the extent of the experiment, continuing until most microcosms observed a 1-log reduction (T_{90}) from environmental concentrations.

Calculating the bacterial decay rate and T_{90} of *S. aureus*

The rate of *S. aureus* decay was mathematically described using the Chick-Watson model as follows: $C_f = C_0 e^{-kt}$ where C_f is the concentration at a given time point (t), C_0 is the initial (environmental) concentration, and k is the first-order decay rate constant. Decay rates, or k, for each condition were calculated as the slope from a linear model with natural log-transformed + 1 of *S. aureus* concentrations collected at each time point. This rate constant was then used to calculate the T_{90} using the following relationship: $-1/k = T_{90}$, where T_{90} is the time it takes for a 90% reduction in *S. aureus* concentrations.

Statistical analysis

Prior to analyses, normality tests were run on *S. aureus* concentrations using the Shapiro–Wilks test, where *S. aureus* concentrations were not normal ($W = 0.748$, $p > 0.001$). Significant differences in environmental concentrations of *S. aureus* among samples were then tested using Kruskal–Wallis (KW) and Mann–Whitney Wilcoxon (MWW) tests. Spearman correlation tests revealed a significant positive correlation between turbidity measurements with PM (rho = 0.80, $p < 0.001$) and DM (rho = 0.50, $p < 0.001$). To avoid autocorrelation errors, only turbidity (NTU) was included as a predictor variable in the modeling process. The significance of salinity (fresh and brackish) and turbidity (high, intermediate, or low) on predicting environmental *S. aureus* concentrations in samples was tested through negative binomial generalized linear mixed models (GLMM). Negative binomial GLMMs offer robust modeling for nonparametric count data without a transformation and effectively addresses overdispersion concerns (Fávero & Belfiore, 2019). In these models, salinity and turbidity were both fixed effects, and individual samples were included as a random effect. For model comparisons, a null model (intercept only model) was included (Long & Freese, 2001). The significance of each predictors effect on the response variable in the model was tested through a log-likelihood ratio test (LRT) (Bates et al., 2015). "Corrected" Akaike Information Criterion (AICc), Δ AICc, and Akaike weights were utilized for quantitative model comparisons to determine which model best predicted the observed data (Portet, 2020). Statistical analyses were conducted on R Studio v 2021.09.0. (Affero General Public License, R Studio, Inc.) ($\alpha = 0.05$). Data are accessible from GitHub (https://github.com/labhuiofrank/JWH-Staph-survival-paper).

RESULTS AND DISCUSSION

Environmental *S. aureus* concentrations

In waters we tested with high turbidity, characterized by elevated levels of PM and DM, *S. aureus* concentrations were found to be significantly higher (Figure 1). Average environmental *S. aureus* concentrations were highest in the high turbidity samples for freshwater (9.8×10^3 CFU/100 mL) followed by brackish water (5.1×10^3 CFU/100 mL) (KW, $p < 0.001$). Regardless of turbidity, *S. aureus* concentrations in the environment are often highest in freshwater since they are closer to sources of *S. aureus* such as soils, runoff, and zoonotic shedding (Economy et al., 2019). In lower turbidity samples, *S. aureus* concentrations were roughly an order of

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magnitude lower in the intermediate and low turbidity fresh and brackish water samples (2.3×10^3–9.6×10^2 CFU/100 mL). Intermediate turbidity brackish water was significantly different from low turbidity fresh and brackish water (MWW, $p = 0.001$), but no significant difference was found between low turbidity fresh and brackish waters (MWW, $p = 0.07$, Figure 1). The variability of *S. aureus* concentrations in the water samples positively increased with turbidity. Standard deviations in high turbidity samples were two to four times greater than low and intermediate turbidity samples. This increased variability likely resulted from the heterogeneity of *S. aureus* distribution in samples from potential biofilm formation on particles. Random grab samples were aliquoted in small amounts (1–5 mL) for culturing during each time point possibly contributing to variability in counts (Davies et al., 1995).

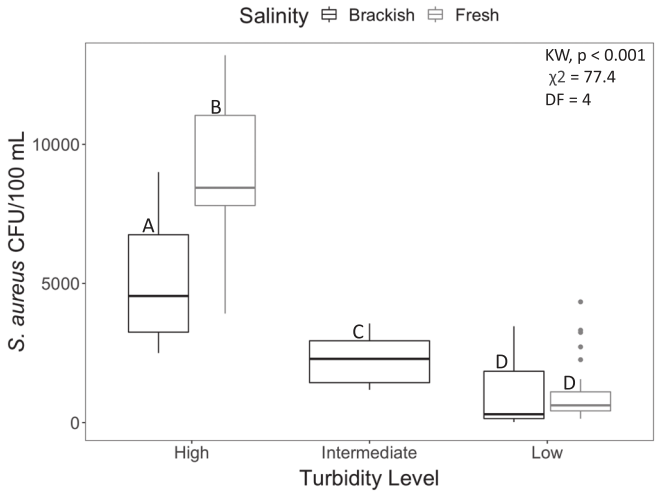

FIGURE 1 Environmental concentrations of *Staphylococcus aureus* (CFU/100 mL) for brackish and fresh waters across high, intermediate, and low levels of turbidity ($n = 108$ total). Concentrations of *S. aureus* were the greatest at highest turbidity. Results from a Kruskal–Wallis (KW) test are shown in upper right corner including degrees of freedom (DF), and letter groupings from a Mann–Whitney Wilcoxon test (MWW) are depicted next to each box ($\alpha = 0.05$). Boxes on the figure are interquartile range, horizontal lines are the median, whiskers are the range, and solid points are outliers.

Turbidity had the strongest effect on *S. aureus* concentrations in the environment. Model results demonstrate that environmental *S. aureus* concentrations in samples were significantly predicted by both salinity and turbidity (LRT, $p < 0.001$, $p < 0.001$, respectively). Model comparisons demonstrate that the model with the best fit includes both turbidity and salinity, followed by only turbidity and only salinity (Table 1). The strong relationship with turbidity in environmental waters detected in this study and others is a consequence of *S. aureus* washing into waters through freshwater runoff, *S. aureus* particle sorption and colonization for protection and nutrients, and light attenuation from particles that protect and extend survival of bacterial cells (Burton et al., 1987; Davies et al., 1995; Mohammed et al., 2012). Sands and other sediments can also easily resuspend *S. aureus* into overlying waters, elevating *S. aureus* concentrations and turbidity of environmental waters (Burton et al., 1987; Davies et al., 1995).

Concentrations of *S. aureus* in this study, on average, were an order of magnitude greater than previous studies in tropical and temperate recreational marine waters, but the range of concentrations was still comparable (Charoenca & Fujioka, 1993; Curiel-Ayala et al., 2012; Economy et al., 2019; El-Shenawy, 2005; Prieto et al., 2001). Still, all environmental samples measured had *S. aureus* concentrations that exceed the Favero proposed titer of 100 staphylococci/100 mL (Favero et al., 1964). Prieto et al. (2001) found that skin ailments have increased by 1.2% when concentrations exceed this titer in marine waters. Given that all our samples had concentrations greater than the titer, the risk of *S. aureus* infection is likely elevated with exposure to fresh and brackish waters.

TABLE 1 Negative binomial generalized linear mixed model (GLMM) comparisons (including null model) for predicting *Staphylococcus aureus* concentrations in the environment with salinity (brackish and fresh) and turbidity (high, intermediate, and low).

Predictors	AICc[a]	Δ AICc	Akaike weight	*p*-value
Salinity + turbidity	1863.5	<0.001	0.903	
Salinity	1970.8	107.3	<0.001	<0.001
Turbidity	1867.9	4.46	0.097	<0.001
Intercept[b]	1971.2	107.8	<0.001	

Note: Sample number was included as a random effect. *P*-values are from log-LRTs to test significance of each predictor ($\alpha = 0.05$). Best-fitting model is based upon the lowest AICc and Δ AICc values and highest Akaike weights (Portet, 2020).

[a]AICc = "Corrected" Akaike Information Criterion.

[b]Null model (intercept only).

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S. aureus persistence over time

S. aureus persistence was the greatest in high turbidity microcosms (independent of salinity) in the absence of sunlight (Figure 2). *S. aureus* was still detected in fresh and brackish water microcosms in the laboratory after 69 and 71 days, respectively. Models fit for each microcosm was statistically significant (F-test, $p < 0.001$). Decay rates, k, were lowest in high turbidity microcosms and steepest in low turbidity microcosms (Table 2). The decrease in decay rates in relation to increasing water turbidity, PM, and DM, suggests that turbid particles have a significant impact on *S. aureus* survival. The decay rates were used to calculate the T_{90} - the time it takes for a 90% reduction in *S. aureus* concentrations. The greatest T_{90} was observed in the high turbidity brackish water microcosms (Table 2). This was almost double (1.8 times) the T_{90} for both the high turbidity freshwater and intermediate turbidity brackish water microcosms. The T_{90} in low turbidity water microcosms was much lower, demonstrating the positive relationship between turbidity and *S. aureus* persistence. The results of this study support other findings that *S. aureus* is associated with PM in turbid waters. Turbid waters offer several advantages to bacterial pathogens in terms of survival and persistence (e.g., shielding from UV light, protection from phage attack, shelter from predation, and a higher availability of adsorbed organic matter) (Chamberlim & Mitchell, 1978; Cho et al., 2010; Dutka, 1984; Fujioka et al., 1981; Maugeri et al., 2004). *S. aureus* extended survival, and colonization on particles has also been observed in wet and dry sand, supporting *S. aureus* affinity to create biofilms in the environment (Mohammed et al., 2012).

Higher salinity was also shown to have an additive influence on increasing the survivability with greater *S. aureus* survival in brackish water microcosms (Figure 2 and Table 2). *S. aureus* is a halotolerant bacteria that can persist in saline waters potentially due to the ions in saline waters, such as Na^+, Cl^-, Ca^{2+}, Mg^{2+}, and SO_4^{2-} (Gabutti et al., 2000; Levin-Edens et al., 2011; Ochiai, 1999; Tolba et al., 2008). These ions can proliferate synthesis and latent potential of cell wall-lytic

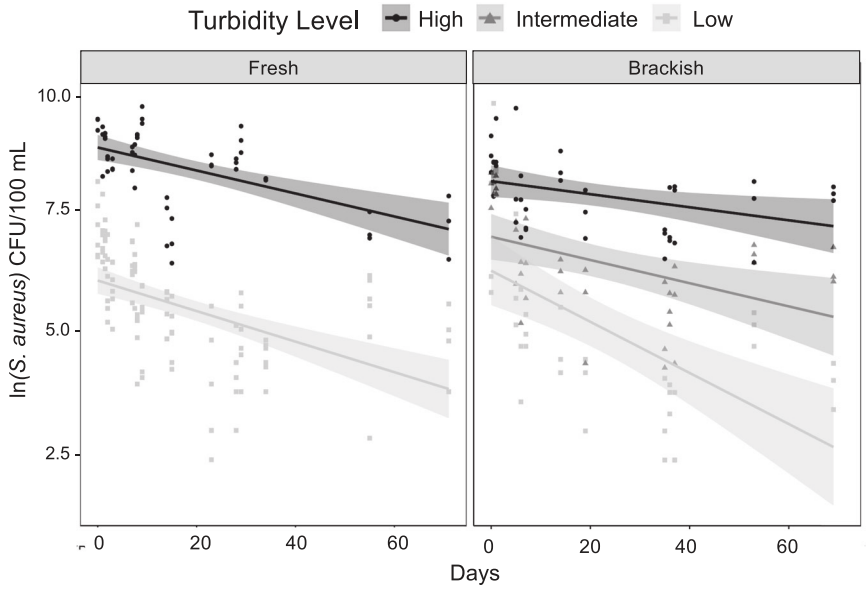

FIGURE 2 Comparative survival of natural log-transformed *Staphylococcus aureus* concentrations over time in brackish and fresh waters across low, intermediate, and high turbidity fit to a linear distribution. The slope of the line represents the decay rate (k) of *S. aureus* in each microcosm. Each point represents the average of six replicates. Concentrations of *S. aureus* decreased over time regardless of salinity and turbidity level but remained the greatest in the high turbidity fresh and brackish water microcosms. Shaded region represents a 95% confidence interval.

TABLE 2 Average *Staphylococcus aureus* 1-log reduction (T_{90}) and decay rates (k) in fresh and brackish samples of different turbidity.

Microcosm	Turbidity level	Turbidity (NTU)	PM[a] (mg L^{-1})	DM[b] (mg L^{-1})	T_{90} (days)	k (day^{-1})
Fresh	Low	5.52	0.387	<0.001	50.3	−0.046
	High	401	749	4.88	80.8	−0.029
Brackish	Low	1.33	2.25	13.1	29.8	−0.077
	Intermediate	66.5	232	15.5	79.5	−0.029
	High	> 800	25,400	104	147.8	−0.016

Abbreviations: DM, dissolved matter; PM, particulate matter.
[a]PM = particulate matter > 0.8 μm.
[b]DM = dissolved matter 0.8–0.2 μm.

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enzymes in *S. aureus* that assist in multiplication, bacterial transformation, and cell wall turnover (Ochiai, 1999; Turner et al., 2004). As such, brackish waters may provide preferable conditions for *S. aureus* survival compared with freshwater.

The T_{90} of 29.8–147.8 days for *S. aureus* in this study was greater than previous reports of 3.3–15.43 days (Fujioka & Unutoa, 2006; Levin-Edens et al., 2011; Tolba et al., 2008). The elevated survival of *S. aureus* observed in this study is most likely because of our inoculation of samples with in situ conditions that included PM. Microcosms composed of varied forms and concentrations of nutrients and established *S. aureus* biofilm communities. Many studies have shown that *S. aureus* creates biofilms to increase fitness, outcompete other microbes, and reduce decay from stressors in environmental waters (Nair et al., 2014) Consequently, the higher T_{90} values observed in this study may be attributed to colonization and growth. *S. aureus* particle sorption and metabolization of accessible nutrients contribute to a prolonged survival in high turbidity microcosms (Fujioka & Unutoa, 2006; Mohammed et al., 2012). The shaking incubation of microcosms during the experiment may have also resuscitated viable but not culturable *S. aureus* cells to become culturable (Ahmad et al., 2014). Lastly, because our microcosms were incubated in the dark (eliminating the potential for cell death by light exposure), *S. aureus* T_{90}'s in this study might be greater than observations in natural systems exposed to consistent light (Fujioka & Unutoa, 2006; Tolba et al., 2008). In the absence of light, this study's decay rates and T_{90} values reveal the impact of turbidity on the potential longevity of *S. aureus* communities in brackish and fresh waters. Furthermore, since experimental parameters closely mimic the conditions found in densely forested areas, subterranean waters, and groundwaters, the results of this study may provide a more relevant estimation on *S. aureus* persistence in environments with limited sunlight exposure. Moreover, in the context of climate change, the reduced UV radiation associated with increased prevalence of storms and increased rainfall will support dark conditions that could contribute to increased survival and potential proliferation of *S. aureus* in environmental waters. Understanding these dynamics sheds light on the resilience of *S. aureus* populations in diverse aquatic settings, especially under reduced light conditions.

S. aureus threat increases with climate change

Our results show that the concentration and persistence of *S. aureus* are strongly correlated with turbidity (and to a lesser extent salinity), consistent with observations of *S. aureus* in the environment (Steadmon et al., n.d.; Economy et al., 2019; Grobbelaar, 2009). Thus, climate change—with the predicted increase in frequency of large rainfall events, sea level rise, and flooding—could drastically amplify the threat of skin ailments like *S. aureus* infections (Mora et al., 2022). Heavy rain events frequently wash high concentrations of fine-grained terrigenous suspended PM as storm runoff into streams, resuspend sand and sediment particles, and further increase the turbidity of waterways—creating turbid conditions to support the colonization and persistence of *S. aureus* (Davies et al., 1995; Mohammed et al., 2012; Yamahara et al., 2007). One day of storm-induced pathogen loading in associated waters could be the equivalent of months, or even years, of dry-weather loading (Krometis et al., 2007). Moreover, as sea level rises and flooding occurs, brackish conditions could further support the survival of *S. aureus*, causing greater health risks to populations in inundation zones (Mora et al., 2022).

Pacific Islands, like Hawai'i, are disproportionally facing many of the unique and unprecedented challenges in association with climate change—including *S. aureus* threats. Hawai'i is recognized as a state with one of the highest rates of staphylococcus infections (Estivariz et al., 2007). Case–control studies have correlated *S. aureus* infection with seawater contact and shown that the diversity of environmental *S. aureus* strains is identical to those isolated from human wounds (Charoenca & Fujioka, 1995; Prieto et al., 2001; Seifried et al., 2007). Clinical studies also indicate that Pacific Islanders are disproportionately affected by *S. aureus* infection, and their traditional lifestyles and cultural practices increase their exposure to potentially contaminated watershed sources (Estivariz et al., 2007). Even though many *S. aureus* infections result from exposure to contaminated fresh and brackish waters, these sources are not monitored, a fact that hinders the ability of public health officials to effectively prevent human exposure. The data herein provide valuable insights into the influence of turbidity and salinity on the abundance and persistence of *S. aureus* in environmental waters. The extended survival of *S. aureus* in turbid waters provides implications for future modeling and prediction of the threat of *S. aureus* exposure in environmental waters.

CONCLUSION

To date, this is the first study to analyze the survival (stability and multiplication) of *S. aureus* in turbid tropical fresh and brackish waters that were not

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manipulated after collection. Environmental concentrations of *S. aureus* were significantly greater in high turbidity waters regardless of salinity. Results from this study highlight that both turbidity and salinity play major roles in mediating pathogen dynamics (i.e., abundance and survival) in recreational waters. Experiments demonstrated that *S. aureus* persisted the longest in high turbidity brackish waters followed by high turbidity fresh waters. Decay rates and T_{90} results were positively associated with turbidity for both fresh and brackish waters. In the absence of sunlight, *S. aureus* can persist for up to several months in turbid environmental waters, increasing the risk of *S. aureus* infections to the public. Climate change can cause more frequent and intense rain events that lead to higher concentrations of *S. aureus* throughout watersheds. Overall, *S. aureus* persistence in turbid brackish and fresh waters is not only a threat for Hawai'i but also a worldwide public health concern.

AUTHOR CONTRIBUTIONS

Maria Steadmon: Conceptualization; data curation; formal analysis; investigation; methodology; software; supervision; validation; visualization; writing—original draft; writing—review and editing. **Kebang Ngiraklang:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing—original draft; writing—review and editing. **Macy Nagata:** Investigation; methodology; writing—review and editing. **Keanu Masga:** Methodology; writing—review and editing; investigation. **Kiana L. Frank:** Project administration; conceptualization; writing—review and editing; funding acquisition; supervision; writing—original draft; data curation; formal analysis; investigation; methodology; resources; software; validation; visualization.

ACKNOWLEDGMENTS

This work was supported by funding from the National Institute of Health (NIH) Centers of Biomedical Research Excellence (COBR P20GM125508. This work was also supported by the National Science Foundation (NSF) Research Experience for Undergraduates (REU) 1950353 and highlights the collaborative training of three undergraduate Native Pacific Island scholars. We also acknowledge the support and collaboration of the community who manage and steward the water resources we sampled. This is SOEST Contribution # (to be determined upon acceptance of publication). The supporting data for the findings presented in this manuscript are openly accessible through JWH-Staph-survival-paper (https://github.com/labhuiofrank/JWH-Staph-survival-paper), with the reference number (592229661).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in JWH-Staph-survival-paper at https://github.com/labhuiofrank/JWH-Staph-survival-paper, reference number 592229661.

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How to cite this article: Steadmon, M., Ngiraklang, K., Nagata, M., Masga, K., & Frank, K. L. (2023). Effects of water turbidity on the survival of *Staphylococcus aureus* in environmental fresh and brackish waters. *Water Environment Research*, *95*(9), e10923. https://doi.org/10.1002/wer.10923

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