Physical Factors Impacting the Survival and Occurrence of *Escherichia coli* in Secondary Habitats

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Abstract: *Escherichia (E.) coli* is a fecal microbe that inhabits the intestines of endotherms (primary habitat) and the natural environment (secondary habitats). Due to prevailing thinking regarding the limited capacity of *E. coli* to survive in the environment, relatively few published investigations exist regarding environmental factors influencing *E. coli*’s survival. To help guide future research in this area, an overview of factors known to impact the survival of *E. coli* in the environment is provided. Notably, the lack of historic field-based research holds two important implications: (1) large knowledge gaps regarding environmental factors influencing *E. coli*’s survival in the environment exist; and (2) the efficacy of implemented management strategies have rarely been assessed on larger field scales, thus leaving their actual impact(s) largely unknown. Moreover, the persistence of *E. coli* in the environment calls into question its widespread and frequent use as a fecal indicator microorganism. To address these shortcomings, future work should include more field-based studies, occurring in diverse physiographical regions and over larger spatial extents. This information will provide scientists and land-use managers with a new understanding regarding factors influencing *E. coli* concentrations in its secondary habitat, thereby providing insight to address problematic fecal contamination effectively.

Keywords: bacteria; water quality; land-use practices; environmental persistence

1. Introduction

*Escherichia coli* (*E. coli*) is a fecal indicator microbe with a life history that cycles between two principal habitats, intestines of endotherms (primary habitat) and environmental water, sediment, and soils (secondary habitats). These habitats differ markedly with respect to physical conditions (e.g., temperature) and nutrient availability [1]. For example, the temperature remains relatively constant (approximately 37 °C) in the primary habitat but can vary greatly in the secondary habitat where annual average temperatures can range from below freezing (0 °C) to approximately 18 °C, or higher [1]. Additionally, the primary habitat is an anaerobic environment [2], whereas the secondary environment varies between aerobic and anaerobic (e.g., deep soil, sediment, and water resources) [3]. Nutrients in the secondary environment are also typically less abundant, especially in soil and sediment [4], which, with respect to bacterial growth, are in a state of constant nutrient deficiency [5]. In water, nutrients can vary from being abundant (e.g., receiving waters in agricultural areas) to scarce (e.g., open ocean) [6,7]. This contrasts primary habitat (i.e., colon) nutrient conditions, comprising consistently high levels that support rapid bacterial growth [1]. Consequently, the secondary habitat
will typically place greater strain on the growth and survival of *E. coli*, as it is not the habitat the *Escherichia* genus predominantly evolved in.

The conditions of the secondary habitat (environment) will, therefore, inhibit the growth and survival of *E. coli* when the microbe’s tolerance thresholds are exceeded. The tolerance thresholds of *E. coli* can be used to predict changes in *E. coli* concentrations based on changes in the conditions of the secondary environment. This can be used by scientists and land-use managers concerned with microbial pollution in the environment.

When present in the environment, fecal microbes, such as the O157:H7 serotype of *E. coli*, can pose considerable health risks to endotherms (humans and animals), particularly if ingested [8]. Exposure to these microbes contributes significantly to morbidity and mortality in the global human population (3.4 million annual deaths) [9]. Therefore, managing the abundance of fecal microbes in the environment is important from a human health perspective. Managing fecal microbe concentrations and, by extension, the water quality of receiving waters requires an understanding of factors influencing the lifecycles and concentrations of these microorganisms in their secondary habitat. Therefore, understanding temperature and solar insolation influences, hydrologic requirements, chemistry, and nutrient availability, and land-use impacts on *E. coli* populations are critical for the proper implementation of effective management strategies.

Historically, *E. coli* was thought to be poorly adapted to survival in the environment and believed to comprise an average half-life of two days [1]. Additionally, it was believed that *E. coli* cells could only originate in the intestines of endotherms before excretion into the secondary habitat. The transfer from primary to secondary habitats was represented by the following two relationships [1]:

\[
\frac{dP}{dt} = \gamma P - \beta P \\
\frac{dS}{dt} = \beta P - \delta S
\]

where \(P\) represents *E. coli* populations in the primary habitat, \(S\) represents *E. coli* populations in the secondary habitat, and \(\gamma, \beta, \text{ and } \delta\) represent effective growth, bulk transfer, and death rate, respectively. Traditional thought surrounding *E. coli*’s limited survival in the secondary habitat held two important implications: (1) deposition of new fecal matter was required to increase *E. coli* populations in the secondary habitat, and (2) the probability of new host colonization was low [1]. Direct deposition of new fecal matter remains an important factor influencing fecal microbe concentrations in the environment, due to the direct proportionality between endotherm population density and fecal contamination (i.e., more animals produce more waste) [10–12]. However, recent investigations have reported on the ability of *E. coli* to persist (survive and reproduce) in the environment for extended periods, thereby increasing the risk of colonizing a new host. This shift in the understanding of the persistence of *E. coli* in the secondary habitat implies that there may be ample time for the microbe to become naturalized into the soil microbiome [13]. Once naturalized, the microbe may become autochthonous and thus, capable of surviving and reproducing in the environment without being directly deposited or replaced by microorganisms from animal feces or water [13]. Given the extended persistence of *E. coli* and its widespread use as a fecal indicator organism [14,15], understanding the relationships between the environment and this microbe will aid land managers and scientists concerned with mitigation of microbial contamination in soil and water resources.

The objective of this review is to provide an overview of factors currently understood to affect *E. coli* lifecycles and concentrations in the secondary habitat (encompassing both soil and water environments), including how those factors can be used to predict *E. coli* population changes quantitatively. Notably, few previous publications have included reviews of quantitative predictive equations used in the estimation of *E. coli* occurrence or survival. A sub-objective was to supply a summary of contemporary management strategies aimed at reducing *E. coli* and fecal microbe concentrations in the environment,
specifically management strategies that can be applied by land-use managers and policy-makers at a sub-catchment scale. The review also includes the identification of research needs and future directions regarding the survival of *E. coli* in the secondary habitat.

2. *E. coli* and the Environment

2.1. Temperature

In nutrient-rich environments (e.g., canned meat products), temperature (approximately 0 to 47 °C) is typically considered the primary factor influencing *E. coli* survival, accounting for up to 61% of *E. coli* population variance (centered on inactivation rates) based on an Arrhenius model [16]. Given its relative importance, temperature must be accounted for when assessing local environmental parameters that influence *E. coli* lifecycles and concentrations in the secondary habitat. Thus, the growth limit and tolerance range of the microbe, 7 °C and −20 °C to 66 °C, respectively, provide insight as to how temperature can alter the bacteria’s lifecycle [17]. Previous investigations reported bacterial temperature dependencies, based on the first-order inactivation rates \( k_c \), defined by the Chick equation [18,19] as

\[
C = C_0 e^{-k_c t}
\]

or alternatively

\[
\ln C = \ln C_0 - k_c t
\]

where \( C \) represents bacterial concentration, \( C_0 \) represents initial bacterial concentration, \( k_c \) represents the inactivation rate, and \( t \) represents time in days [19]. In the above equations, the temperature dependence of bacterial inactivation \( (k_c) \) rates can be expressed using either the \( Q_{10} \) or Mancini equations [19]. The \( Q_{10} \) equation is defined as follows:

\[
\frac{k}{k_*} = Q_{10}^{(T_c - T_{c*})/10}
\]

where \( k \) represents the first-order inactivation at temperature \( T_c \), \( k_* \) represents reference temperature first-order inactivation, \( Q_{10} \) represents the rate of change in the inactivation rate due to temperature increases in 10 °C increments, \( T_c \) represents temperature in °C, and \( T_{c*} \) represents a reference temperature (usually 20 °C) [19]. Conversely, the Mancini equation, frequently implemented in water quality models [19], can be defined as follows:

\[
\frac{k}{k_*} = \theta^{T_c - T_{c*}}
\]

where \( k \) represents first-order inactivation (i.e., die-off) at temperature \( T_c \), \( k_* \) represents reference temperature first-order inactivation, \( \theta \) represents temperature sensitivity of the microbe, \( T_c \) represents temperature in °C, and \( T_{c*} \) represents a reference temperature (usually 20 °C). Consequently, \( Q_{10} \) can be converted to \( \theta \) as follows:

\[
\theta = Q_{10}^{1/10}
\]

Additionally, the temperature dependence of first-order reaction rates can be found through the Arrhenius equation:

\[
k = Ae^{-\frac{E_a}{RT}}
\]

where \( k \) represents the kinetic rate constant at temperature \( T \), \( A \) represents the constant prefactor (collision frequency factor), \( E_a \) represents activation energy, \( R \) represents the gas constant, and \( T \) represents temperature in Kelvin.

Notably, environmental factors, such as water purity, can influence *E. coli* inactivation rates, as pristine water usually comprises higher average \( Q_{10} \) values but lower first-order inactivation rates at 20 °C. For example, based on a review of 450 *E. coli* survival datasets from 70 peer-reviewed investigations by Blaustein et al. [19], pristine water (defined by the authors as water originating from
caves or springs and including fewer impurities) comprised an average $Q_{10}$ of 2.066 ± 0.190 and an average first-order inactivation rate at 20 °C ($k_{20}/\text{day}^{-1}$) of 0.063 ± 0.007. Conversely, groundwater, agricultural waters and wastewater comprised the following $Q_{10}$ and $k_{20}/\text{day}^{-1}$ values: 1.783 ± 0.702, 0.504 ± 0.136; 1.548 ± 0.161, 0.388 ± 0.024, and 1.358 ± 0.238, 0.672 ± 0.114, respectively [19]. Consequently, the source of water can be used to approximate inactivation for aquatic $E. \coli$. However, the impacts of biological and physical survival factor variations can cause variability in site- and source-specific $E. \coli$ survival rates at the same temperature [19]. Therefore, site-specific data (e.g., physicochemical parameters) would greatly improve the accuracy of predictions regarding $E. \coli$ inactivation and survival in water resources.

Based on laboratory investigations, $E. \coli$ was shown to survive for up to 32 days in soil when incubated at 15 °C [13]. In situ investigations also support the extended survival of $E. \coli$ in soils, even at colder temperatures. For example, $E. \coli$ in soil samples extracted from soils surrounding Lake Superior, United States of America (USA), in October 2003 and April 2004 had a 92% DNA fingerprint similarity [13]. This high similarity indicates these $E. \coli$ strains became naturalized. Naturalized, in this context, indicates the process by which non-native $E. \coli$ becomes integrated into the secondary habitat and reproduces at a sufficient rate to maintain its population [20]. Through naturalization, $E. \coli$ become autochthonous members of the soil microbial community, capable of enduring the cold winter months (including numerous freeze–thaw cycles) and growing during the warmer summer months [13]. Additionally, the growth and replication of $E. \coli$ in soils have been verified by laboratory studies. For example, the bacteria grew to high cell densities (4.2 × 10^8 colony forming units (CFU)/g soil) when incubated at 30 °C to 37 °C in nonsterile soils [13]. Additionally, when 9 × 10^2 CFU/g soil $E. \coli$ was inoculated and incubated for 16 days at 15 °C before a temperature increase (37 °C for 8 days), cell density decreased to 1.1 × 10^2 CFU/g soil (during the 16-day period), before increasing 10-fold to 1.04 × 10^3 CFU/g soil 4 days after the temperature increase [13]. However, there was a subsequent decrease in cell numbers to 7.7 CFU/g soil 8 days after the temperature increase, attributed to nutrient depletion (see Section 2.6) [13]. Soil $E. \coli$ population density is also subject to seasonal variation with the highest cell densities, up to 3 × 10^3 CFU/g soil, reported in warmer months (summer to autumn), and the lowest numbers, ≤1 CFU/g soil, reported in the colder months (winter to spring) [13]. Consequently, $E. \coli$ growth is directly influenced by soil temperature fluctuations, with rapid growth increases occurring as soil temperature rises from 15 °C (no growth) to 37 °C [13]. Ultimately, given its reported influence on bacterial survival and growth [13,16,21], temperature constitutes a vital environmental factor influencing $E. \coli$’s survival in the secondary habitat.

2.2. Solar Insolation

Research regarding the impacts of solar insolation on fecal bacteria (e.g., $E. \coli$) survival and inactivation, have been predominantly focused on marine waters [22–24]. However, in a study conducted at Lake Michigan, USA, day length and exposure to insolation during sunny days resulted in an exponential decrease in $E. \coli$ counts [25]. Additionally, diminished $E. \coli$ inactivation was reported during cloudy days [25]. For example, $E. \coli$ concentrations frequently exceeded safe swimming criteria (threshold $E. \coli$ concentration in water at which the bacteria becomes hazardous to human health, approximately >235 CFU 100 mL−1) during partly cloudy or completely cloudy conditions, but rarely exceeded this threshold during sunny conditions [25]. Similarly, results from both a marsh and lagoon in California indicated that first-order $E. \coli$ decay rate constants varied between 1 to 2 days during low light conditions and 6 days during high light conditions [26]. Furthermore, submersion depth also impacted $E. \coli$ decay rates. For example, sunny condition decay rates at 45 cm and 90 cm depths were $Y_{45} = 48091e^{-0.4682t}$ and $Y_{90} = 12746e^{-0.4184t}$, respectively, where $Y$ represents $E. \coli$ concentration (CFU 100 mL−1), and $t$ represents time (hour) [25]. Notably, different components of sunlight can yield different responses in $E. \coli$ [27]. For example, ultraviolet B-ray (UVB) intensity has been reported to impact first-order decay rates, as the two are highly correlated ($α < 0.05$) [26]. Moreover, short exposure (six hours) to UVB was shown to be sufficient to decrease culturability and
reduce the activity of E. coli, thus eliciting similar effects as exposure to sunlight [27]. Conversely, exposing E. coli to ultraviolet A-rays (UVA) or photosynthetically active radiation (PAR) reduces the culturability of the cells to 10%, despite remaining metabolically active [27]. The impact of insolation on E. coli inactivation is also subject to initial bacterial concentrations, with higher concentrations having quicker decay rates [25]. Moreover, lake E. coli density could be more accurately predicted by exposure time (dosage) than insolation [25]. Thus, the impact of extended periods of insolation exceeded the effect of intense insolation over shorter periods. In the Lake Michigan study, insolation was the predominant abiotic factor influencing E. coli inactivation, accounting for 40% of the variance as opposed to 7% by temperature and 8% for relative lake level [25]. Therefore, the results from this study challenge the assumption that temperature is the primary factor influencing E. coli survival, specifically at the surface (upper 90 cm) of freshwater bodies. Consequently, in shallow streams and headwaters, the inactivation of E. coli could be primarily driven by insolation and not temperature.

2.3. Suspended and Settled Solids

The survival of E. coli in water can be influenced by suspended solids concentrations in terms of how readily microbes can attach to those particles [28]. Association can increase nutrient and organic matter availability, particularly when the suspended solids include organic material (e.g., fallen leaf litter), while also providing optimal light exposure [29,30]. In addition, the close proximity of suspended particle-associated microbes to each other can facilitate the horizontal transfer and proliferation of resistance genes [31,32]. The horizontal transfer of genetic material can be expedited when two microbes come into close contact with each other and remain that way until the transfer of genetic material is completed [31,32]. Thus, if two or more microbes associate with the same suspended particle, the likelihood of horizontal genetic transfer increases relative to free-floating microbes. If resistance genes are transferred in this manner, over time, the microbial population may display increased resistance to stressors, such as chemical disinfectants, excessive photosynthetically active radiation (PAR) radiation, ultraviolet (UV) radiation, and predation [33–35]. However, the effect of suspended solids, including sediment, on the inactivation and survival of E. coli in the secondary habitat (the environment) is yet to be quantified as the majority of studies that attempted to quantify this relationship also include temperature fluxes which have a greater impact on E. coli variance [16,36]. Consequently, no equations are available that relate changes in suspended solids to associated changes in E. coli concentrations. Nevertheless, given current understanding, decreased suspended solids in receiving waters will decrease E. coli survivability, thereby decreasing concentrations of this microbe.

The survivability of E. coli in settled sediments has been quantified [37] using an exponential die-off model based on the Chick [18] equation:

\[ \ln C = \ln C_0 - \mu t \]  

(9)

where \( C \) represents current concentration; \( C_0 \) represents initial concentration; \( \mu \) represents inactivation rate, and \( t \) represents time. Different inactivation rates have been reported by previous investigations. For example, settled sediment from the lakes of eastern United States comprised an E. coli inactivation (i.e., die-off) rate (the authors of this work used inactivation rate synonymously with die-off rate) of approximately 0.54 d\(^{-1}\) [37], whereas settled sediments of Southern Ontario creeks included an inactivation rate of 0.15 d\(^{-1}\) [38], and the Hillsborough River in Florida comprised an inactivation rate of 0.07 d\(^{-1}\) [39]. Like other environmental (secondary habitat) variables (see Section 2.1), temperature influences the die-off of E. coli in sediment, with more rapid die-off occurring at warmer temperatures [37]. Additionally, sediment particle size impacts temperature-driven die-off rates, with survival rates being less sensitive to temperature in finer soil. Garzio-Heardick et al. [40] reported the temperature-driven die-off rates relative to soil types as follows:

\[ \text{Sand} : \ \mu = 0.109 \times 1.133^{T-20} \]  

(10)
where \( \mu \) represents the die-off rate, and \( T \) represents the temperature in °C. Ultimately, \( E. coli \)'s survival in settled sediment will vary geographically, due to changes in both temperature and physical soil characteristics. Therefore, to understand \( E. coli \) survival (including changes in survival due to land-use changes or mitigation strategies) in sediment at a specified location, site-specific information would be required, to avoid broad assumptions potentially leading to prediction inaccuracies.

2.4. Hydrologic Conditions

Intense precipitation and subsequent runoff events can increase pollutant transport, thereby deteriorating surface water quality by increasing turbidity, suspended solid concentrations, organic matter, and fecal contamination during stormwater discharge events [11,12]. Similarly, increased overland and streamflow, during storm events, have been linked to increased \( E. coli \) concentrations relative to baseflow conditions [41,42]. The magnitude of the \( E. coli \) concentration increase varies between 15-fold [43] to 1000-fold [12], such that the concentration increase can be represented by the formula below:

\[
C_s \geq C_0 I_s
\]  

where \( C_s \) and \( C_0 \) represent storm and base flow \( E. coli \) concentrations, respectively, and \( I_s \) represents the coefficient of increase ranging between 15.8283 and 1000. Factors impacting \( E. coli \) concentrations during storm-generated overland flow include rainfall intensity and duration, upland agricultural manure application, type and age of fecal deposits, and \( E. coli \) adsorption to soil particles [12]. The coefficient of increase (\( I_s \)) is subject to change based on these factors. Moreover, the relationship between streamflow and \( E. coli \) concentration is not linear, as increases in discharge during stormflow may dilute \( E. coli \) concentrations. For example, in systems where the contribution of groundwater flow to streamflow is high, storm events may result in a decrease in receiving water \( E. coli \) concentrations [12]. This is due to groundwater typically comprising low \( E. coli \) concentrations [44,45]. However, while groundwater can dilute stream water, high groundwater contributions to streamflow can result in increased bed and bank shear stress, increasing resuspension of streambed sediment, and elevating \( E. coli \) concentrations. For example, in systems where the contribution of groundwater flow to streamflow is high, storm events may result in a decrease in receiving water \( E. coli \) concentrations [12]. This is due to groundwater typically comprising low \( E. coli \) concentrations [44,45]. However, while groundwater can dilute stream water, high groundwater contributions to streamflow can result in increased bed and bank shear stress, increasing resuspension of streambed sediment, and elevating \( E. coli \) concentrations. This resuspension can account for approximately 11% of the total \( E. coli \) load during storm events [46]. The concentration of \( E. coli \) that can become resuspended can be calculated as follows [47]:

\[
R_0 = C_s \times E_0 \left( \frac{T_b - \tau_{cn}}{T_c - \tau_{cn}} \right)^{n_s}
\]  

where \( R_0 \) represents resuspended \( E. coli \) (CFU/m²S); \( E_0 \) represents erosion rate (cm/s), \( T_b \) represents bottom shear stress caused by water flow (Pa), \( \tau_{cn} \) represent the critical shear stresses (N/m²) of non-cohesive sediments, \( \tau_c \) represents the critical shear stresses (N/m²) of cohesive sediments, and \( n_s \) represents particle size (diameter < 432 μm, \( n_s =2 \)) [45]. The \( T_b \) can be calculated using the specific gravity of water, \( \gamma \) (N/m²), hydraulic radius, \( R \) (m), and water surface slope, \( S \) (m/m) (\( T_b = \gamma \cdot R \cdot S \)). Conversely, \( \tau_{cn} \) can be calculated using particle size, \( d \) (m), (\( \tau_{cn} = d \cdot 4.14 \times 10^{-3} \)), and \( \tau_c \) can be calculated using Lick’s equation as follows [45]:

\[
\tau_c = \tau_{cn} \left( 1 + a e^{b \frac{p_s}{d^2}} \right)
\]  

where \( a \) and \( b_c \) represent constants of 8.5 \( \times 10^{-16} \) and 9.07 cm³/g, respectively, \( p \) is water density (M L⁻³), and \( d \) is particle size. Resuspension during high flows can be driven by three resuspension mechanisms [48], (1) a steep-fronted wave (caused by the influx of water entering a given stream during a precipitation event resulting in a flashy leading hydrograph edge), with a wave height in excess of the preceding water depth, can lift microbes from the bottom sediment, holding them...
in the turbulent wave front [37,48], (2) a less steep front or falling wave can resuspend microbes without maintaining them in the wave overrun [37,48], and (3) high flow turbulence (decrease in laminar flow due to increased kinetic energy) can cause steady-flow stochastic erosion of bed and bank sources, thereby maintaining elevated microbe concentrations relative to periods of lower flow [37,48]. Currently, equations that describe the general relationships between increased \( E. coli \) concentrations or survival due to storm flow-induced increased suspended solids or increased turbidity are lacking in the literature. This is attributable to the high geographic variation and subsequent site-specificity of this relationship. Subsequently, compiling site-specific data from diverse geophysical environments would be useful for the development of general equations relating to streamflow changes to \( E. coli \) concentrations and survival.

### 2.5. Water Chemistry

Few large-scale published investigations are available regarding the influence of water chemistry on \( E. coli \) in the environment. Therefore, laboratory investigations are most often relied on and extrapolated to determine the growth limits of \( E. coli \) regarding water chemistry variables. However, the sole impact of water chemistry variables of \( E. coli \) is obscured by the inclusion of temperature as an independent variable in addition to the chemical aspect being investigated, by the majority of previous investigations [16,49–51]. These studies invariably conclude that ambient temperature greatly influences water chemistry impacts on \( E. coli \), as, for example, \( E. coli \) can tolerate lower pH at higher temperatures [49]. Additionally, Presser et al. 1997, reported the effects of temperature, pH, water activity and lactic acid and concluded that these factors were synergistic in limiting \( E. coli \) growth [49]. In this investigation water activity (defined as the partial vapor pressure of water in a substance divided by the standard state partial vapor pressure of water) values of 0.985 and 0.975 and temperatures \( \geq 25 \) °C resulted in a minimum \( E. coli \) growth pH of approximately 4. However, temperature decreases raised the minimum pH slightly [49]. Consequently, the growth rate equations presented below assume a constant temperature as temperature fluctuations could impact water chemistry and \( E. coli \) relationships and alter growth and survival thresholds.

Previous investigations reported optimal \( E. coli \) survival between pH 5 and pH 7 with increased acidity or alkalinity resulting in decreased survival [52]. The growth limit of \( E. coli \) is at approximately a pH of 4, however \( E. coli \) in the stationary phase (the period during which the number of viable bacteria cells remains the same) can survive in pH 2 to 3 for several hours [53]. The following equation can be used to estimate the growth rate of \( E. coli \) based on pH, assuming the growth rate is proportional to the amount by which the pH is more than the minimum value which prohibits growth [49]:

\[
rate = \left(c \times 10^{-pH_{\text{min}}}ight) \left(\frac{10^{-pH_{\text{min}}}}{10^{-pH}}\right)
\]

where \( rate \) represents \( E. coli \) growth rate; \( c \) represents a constant of proportionality; \( pH_{\text{min}} \) represents minimum growth tolerable pH, and \( pH \) represents ambient pH [49]. Similar equations have been created for other chemistry variables constituting linear relationships with \( E. coli \) growth. For example, the growth rate of \( E. coli \) as determined by organic acid concentration can be estimated as follows:

\[
rate = c' \times (C_{\text{min}} - C)
\]

where \( c' \) represents a proportionality constant; \( C_{\text{min}} \) represents the theoretical minimum growth inhibitory concentration of the organic acid, and \( C \) is the measured concentration of the organic acid [49]. The equation is predicated on the assumption that the growth rate is proportional to the amount by which the concentration of the organic acid is less than the minimum concentration, which prevents growth. Analogous equations can be created for inorganic acids, water activity chloride, and salinity by applying similar assumptions. The concentrations of inorganic and organic acids capable of preventing the growth of \( E. coli \) is dependent on the specific chemical under consideration.
However, general minimum growth inhibitory concentrations for water activity, chloride concentration, and salinity concentrations are 0.95 [54], 1.5 mg/L [55], and 20% NaCl (complete die-off in 72 h) in nutrient-rich media and 3.5% NaCl (limit for growth) in nutrient-depleted media [56], respectively.

2.6. Nutrients and Nutrient Availability

Environmental nutrient conditions impact *E. coli* growth and survival in secondary habitats. For example, previous investigations reported *E. coli* populations were three times greater in soils rich in organic matter relative to nutrient-depleted sandy soils, suggesting that soil nutrients and organic matter facilitate the growth of bacteria [57]. Additionally, *E. coli* cell density incubated at 30 °C and 37 °C in soils decreased in the days following rapid initial cell growth [13]. This indicates that the final population of the soil *E. coli* was determined predominantly through either the exhaustion of bioavailable nutrients or predation [13]. Nutrient limitation on *E. coli* growth was also evident in laboratory studies where *E. coli* growth in M9 (minimal growth) medium without C and N was limited to a less than one log increase in CFU [21]. In addition to nutrients, soil water potential can also influence the growth of *E. coli* in soil due to its impact on nutrient availability and bacterial movement [21]. For example, regression analysis from previous work indicated that *E. coli* growth (population doubling time) at 37 °C was significantly related to soil water potential ($r^2 = 0.70, p < 0.001$) [21]. Soil water potential can also impact the motility of microbes in soil, as lower water potential ($−1.5$ or $−0.1$ MPa), results in negligible bacterial movement, and decreased solute diffusion (half the rate observed under saturated conditions) and limited nutrient supply [21,58]. In aquatic environments, dissolved nutrients (glucose and peptone) have been shown to greatly increase the survival of *E. coli* [59]. Additionally, nutrient availability, specifically glucose, can alter *E. coli*'s response to stressors [60]. For example, *E. coli* displayed increased sensitivity to secondary stressors and short term nutrient availability following a period of starvation (nutrient deprivation) [60]. Ultimately, nutrient abundance and availability (as determined by factors such as soil water potential) constitute important factors impacting the survival and growth of *E. coli* in the environment.

2.7. Land-Use Practices

Previous work linked land-use practices, including agricultural and urban land uses, to increased *E. coli* concentrations in receiving waters [14,28,61]. In agricultural regions, increased *E. coli* concentrations are primarily driven by manure applications [62] and the population density of endotherms (livestock) [10,12,63]. During manure application, the environmental inactivation or die-off of *E. coli* results in decreasing concentrations with time passed since application. This can be estimated using the equation below:

$$C = C_i - C_i (R_d \times t)$$  \hspace{1cm} (18)

where $C$ represents the current *E. coli* concentration at the soil surface, $C_i$ represents the initial soil *E. coli* concentration immediately after manure application, $R_d$ represents the die-off rate (or rate of inactivation), and $t$ represents the time since the manure was applied. This equation can be adapted to estimate *E. coli* concentrations in associated receiving waters if the *E. coli* transfer rate between the soil and associated receiving waters is known or assuming that 89% of stream *E. coli* concentrations originate directly from surface runoff, as per Ribolzi et al. [46]. Conversely, in agricultural areas comprised primarily of the rearing of livestock, the animal population numbers can be used to approximate the input (addition) of *E. coli* as follows [12]:

$$I = c \times \frac{(N_p \times w)}{A}$$  \hspace{1cm} (19)

where $I$ represents the new input of *E. coli* in a specified area over a specified time period; $c$ represents a constant (which varies based on the type and size of the animals under consideration, assuming larger animals will produce more waste, contributing more *E. coli* to the area), $N_p$ represents the
population number of the animals (endotherms), $W_i$ represents the waste per individual animal, and $A$ represents the area which the animals inhabit. This equation only approximates new additions of $E. coli$ over a specified period and does not approximate total $E. coli$ concentrations, bacterial persistence, bacterial inactivation, or die-off rates. Notably, if the area that an animal population inhabits can be expanded, the concentration of new $E. coli$ inputs will decrease, due to the inverse proportionality between land-use area and $E. coli$ concentration based on animal waste. Thus, the concentrations of $E. coli$ inputs can be reduced without reducing animal population numbers simply by increasing the animal grazing area. The above equation can be adapted to estimate contributions of newly deposited $E. coli$ to associated receiving waters if the $E. coli$ transferal rate between the soil and associated receiving waters is known or assuming that 89% of stream $E. coli$ concentrations originate directly from surface runoff, as per Ribolzi et al. [46].

Predicting $E. coli$ population increases from urban areas is more complex as $E. coli$ concentrations are elevated due to two primary reasons: (1) leaking wastewater infrastructure [10,11,61] and (2) increased runoff during precipitation events due to increased impervious surfaces [10,64]. Predicting leaks from wastewater infrastructure is difficult, and, therefore, the quantitative effect of leaks in urban areas is rarely accounted for, despite potentially contributing significantly to $E. coli$ concentrations in receiving waters [65]. In a simplified form, the contribution of a leak on the $E. coli$ population in a region ($C$) will be impacted by the fecal concentrations of the leak ($C_l$), the specific discharge ($q_l$), and the removal of bacteria in the soil due to the filtering effect of the soil (calculated by the removal rate divided by the distance flowed) ($f_r$):

$$C = C_l \times q_l \times f_r$$  \hspace{1cm} (20)

Assuming saturated conditions, the specific discharge of the leak can be calculated with Darcy’s Law [62]:

$$q_l = \frac{Q_l}{A_l} = -K_{hl} \frac{dh}{dl}$$  \hspace{1cm} (21)

where $q_l$ represents the specific discharge of the leak, $Q_l$ represents the volume discharge of the leak, $K_{hl}$ represents the hydraulic conductivity, and $dh/dl$ is the gradient of the total hydraulic head [66]. Conversely, spatial data software and models, such as the fate transport advection dispersion overland flow modeling approach, can be used to predict the effect of land cover changes on the transport of pollutants (including $E. coli$) during overland flow from precipitation events [67–69]. These models, also known as mass balance water quality models, utilize annual average export coefficients from land use and land cover data to estimate in-stream pollutant (e.g., $E. coli$) loadings [67–69]. An example of an overland flow model is the St. Venant equation [70]:

$$\frac{\delta h(x,t)}{\delta t} + \frac{5(S_0)^{1/2}}{3n_s} h^{5/2} \frac{\delta h(x,t)}{\delta x} = f(t) - i(t)$$  \hspace{1cm} (22)

and

$$q = \frac{(S_0)^{1/2}}{n_s} h^{5/2}$$  \hspace{1cm} (23)

where $h(x,t)$ represents overland flow depth, $q(x,t)$ represents overland flow discharge per unit width, $f(t)$ represents rainfall rate, $i(t)$ represents infiltration rate, $n_s$ represents Manning’s roughness coefficient, and $S_0$ is the channel slope [70]. Notably, complex hydrological equations can be used to predict vertical flow in soil and flow in unsaturated groundwaters, which can include the transport of $E. coli$.

### 3. Mitigation Strategies

Current mitigation strategies to control freshwater $E. coli$ contamination include minimizing the transport of $E. coli$ during overland flow or reducing sources of $E. coli$. Strategies include (1) vegetation management, (2) restricting livestock grazing and movement, (3) altering manure application strategies, and (4) wastewater infrastructure maintenance. The maintenance of adequate vegetation or use of
vegetative filter strips (strips of vegetation planted for the sole purpose of reducing pollutant transport during runoff events) can reduce the rate and energy of runoff, thereby reducing the concentration of pollutants transported to receiving waters [12,71]. Given that 89% of stream E. coli concentrations result from overland flow [46], a reduction in the transport of E. coli from soil surfaces to associated receiving waters will proportionately decrease the concentration of the microbe in the water. Restricting the movement and grazing of cattle, using temporary fencing or active herding will reduce the amount of fecal matter, including E. coli, that is deposited in a specified area over a given period [68]. For example, McDowell et al. [72] reported that restricting the grazing time of dairy cows to three hours decreased E. coli concentrations in associated receiving water to below water quality guidelines of New Zealand and the United States Environmental Protection Agency (126 CFU per 100 mL). Limiting the use of manure in the growing of crops can also decrease E. coli concentrations due to a reduction in the sources of the microbe. Warnemuende and Kanwar [73] investigated the effects of swine manure application on bacterial quality of leachate and reported that “an increase in application rate is more likely to cause greater bacterial contamination”. Therefore, limiting the application rate (frequency) of manure can improve microbial water quality and decrease E. coli concentrations and population numbers in associated receiving waters. Notably, very few large-scale field-based case studies investigating the effect of varying manure application on E. coli or fecal concentrations currently exist in the literature. Thus, the true effectiveness of this form of mitigation remains largely unknown. The same holds true for the precise effect of frequent and proper maintenance of wastewater infrastructure in urban land use areas. Due to the sporadic and unpredictable occurrence of leaks, it is hard to quantify their exact effect on E. coli concentrations. However, studies have reported that in developing nations, leaking wastewater infrastructure contributed significantly to E. coli concentrations in urban receiving waters, specifically during storm events [10,11,65]. Finally, the creation of artificial wetlands can also reduce secondary habitat E. coli populations, as open-water treatment wetlands are effective at reducing fecal indicator organisms present in water, including E. coli, due to increased exposure to solar insolation [74].

4. Future Directions

Currently, there exists a general lack of field-based investigations studying the environmental factors impacting E. coli’s survival in the secondary habitat [75]. Consequently, current understanding is predominantly based on laboratory studies, including many uncertainties and excluding factors that could influence identified relationships in uncontrolled environmental settings. For example, it is known that suspended solids can increase the persistence of E. coli in water resources [38]. Yet, no widely accepted equations are available that relate changes in suspended solids to associated changes in E. coli concentrations. Additionally, the laboratory or small field scale methods implemented by previous investigations [73] imply that large scale work is needed, especially given the processes governing E. coli survival and concentrations could differ by spatial scale. For example, animal population density could be a key consideration in a small agricultural area [59] but could become irrelevant if the surrounding area comprises large cities. In this example, the impact of the physical habitat changes brought about by urbanization may impact the survival of E. coli to a greater extent than the few animals still present in the area. Site-specific modeling techniques, including geophysical characteristics, need to be developed and applied to a wide variety of areas under varying climatic conditions, to improve understanding of the dynamics of the different water masses and their associated E. coli concentrations [12]. This type of work is specifically needed given the contrasting roles of groundwater outflow on stream E. coli concentrations during precipitation events: 1) the dilution of stream E. coli concentrations, 2) and the resuspension of streambed E. coli [12]. Having more fine-scale data also constitutes a fundamental requirement for improving predictive E. coli models [12] and a process-based understanding of E. coli concentration fluctuation in the secondary habitat. Finally, the identification of naturalized soil E. coli communities calls into question the microbe’s use as an indicator of fecal contamination [15,21]. Subsequently, studies are required to investigate the
movement of naturalized *E. coli* strains and their relative contribution to stream *E. coli* concentrations. Environmental effects on this relative contribution also warrant further investigation, as changing climatic or secondary habitat conditions could potentially alter the movement of both naturalized and newly deposited *E. coli* to associated receiving waters. *E. coli* strains can differ in terms of their metabolic and physiological characteristics [76]. Therefore, strain-specific response to physicochemical changes in the secondary habitat also warrants further investigation.

5. Conclusions

Given the health risks posed by the consumption of *E. coli* contaminated stream water (a single exposure exceeding 500 colonies 100 mL$^{-1}$ has a 10% chance to result in gastrointestinal illness [77]) and the bacteria’s widespread use as a fecal indicator organism, understanding the survival of this microbe in the environment is important from a human health perspective. Based on the limited published investigations regarding the environmental requirements of *E. coli* factors, including temperature [13], solar insolation [25], suspended and settled solids [29,30], hydrologic conditions [42], water chemistry [49], nutrient conditions [57], and land-use practices, impact the survival of *E. coli* in the environment [12,78,79]. With more information, the implementation of effective management strategies should be possible and widely applied, given the widespread occurrence of fecal water contamination [9]. However, the effectiveness of implemented management strategies is rarely assessed on large scales, using field-based methods. Therefore, their usefulness remains largely unknown. Consequently, future *E. coli*-focused work should attempt to expand on the current limited number of field-based published works and investigate both the survival of *E. coli* under different environmental conditions in the secondary habitat and the effectiveness of implemented management strategies, specifically on larger scales. This information will provide scientists and land-use managers with new insight to effectively address problematic fecal contamination, thereby aiding in the reduction in disease outbreaks caused by contaminated water.

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