Escherichia coli in Secondary Habitats

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Escherichia (E.) coli are rod shaped, facultative anaerobic, gram-negative, coliform, fecal gammaproteobacteria that inhabit the intestines of endotherms (primary habitat) and the natural environment (secondary habitats). Due to historic thinking regarding the limited capacity of E. coli to survive in the environment, a great deal of research is needed to advance understanding of environmental factors influencing E. coli's survival.

Keywords: E. coli ; Watershed Management ; Hydrology ; Environment ; Aquatic Microbe ; Secondary Habitat ; Nutrients ; Water Quality ; Microbes

1. Introduction

Escherichia coli (E. coli) is a fecal indicator microbe with a life history that includes 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, while temperature remains relatively constant (approximately 37 °C) in the primary habitat, it can vary greatly in the secondary habitat ranging 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, sediment and pelagic aquatic settings [4]. Therefore, the bacteria 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 from 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, especially in the genus' recent evolutionary history.

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 information is useful to scientists and land-use managers concerned with mitigating 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 life cycles and concentrations of these microorganisms in their secondary habitat. Therefore, understanding temperature and solar insolation influences, hydrologic requirements, chemistry, nutrient availability, and land-use impacts on E. coli populations are critical for the proper implementation of effective management strategies.

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 [10]. Given its relative importance, temperature must be accounted for when assessing local environmental parameters that influence E. coli life cycles 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 life cycle [11].

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 [12][13][14]. 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 [15]. Additionally, diminished E. coli inactivation was reported during cloudy days [15]. 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 [15]. 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 [16]. Furthermore, submersion depth also impacted E. coli decay rates. For example, sunny condition decay rates at 45 cm and 90 cm depths were Y45=48091e−0.4682t and Y90=12746e−0.4184t, respectively, where Y represents E. coli concentration (CFU 100 mL^{-1}), and t represents time (hour) [15]. Notably, different wavelengths of sunlight can yield different responses in E. coli [17]. For example, ultraviolet B-ray (UVB) intensity has been reported to impact first-order decay rates, as the two are highly correlated ($\alpha < 0.05$) [16]. 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 [17]. 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 [17]. The impact of insolation on E. coli inactivation is also subject to initial bacterial concentrations, with higher concentrations having quicker decay rates [15]. Moreover, lake E. coli density could be more accurately predicted by exposure time (dosage) than insolation [15]. 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 [15]. 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. It therefore follows that in shallow streams and headwaters, the inactivation of E. coli may 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 [18]. 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 [19][20]. In addition, the close proximity of suspended particle-associated microbes to each other can facilitate the horizontal transfer and proliferation of resistance genes [21][22]. 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 [21][22]. 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 [23][24][25]. 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 [10][26]. Consequently, no equations are available that relate changes in suspended solids to associated changes in E. coli concentrations. Nevertheless, current understanding indicates that decreased suspended solids in receiving waters will decrease E. coli survivability, thereby decreasing concentrations of this microbe.

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 [27][28]. Similarly, increased overland and streamflow, during storm events, have been linked to increased E. coli concentrations relative to baseflow conditions [29][30]. The magnitude of the E. coli concentration increase varies between 15-fold [31] to 1000-fold [28], such that the concentration increase can be represented by the formula below:

$$Cs \geq C0Is \quad (1)$$

where Cs and C0 represent storm and base flow E. coli concentrations, respectively, and Is 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 [28]. The coefficient of increase (Is) 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.

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 on 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 [10][32][33][34]. These studies conclude that ambient temperature greatly influences water chemistry impacts on E. coli, as, for example, E. coli can tolerate lower pH at higher temperatures [32]. 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 [32]. 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 ≥ 25 °C resulted in a minimum E. coli growth pH of approximately 4. However, temperature decreases raised the minimum pH slightly [32]. Consequently, temperature fluctuations can impact water chemistry and E. coli relationships and alter growth and survival thresholds.

2.6. Nutrients and Nutrient Availability

Environmental nutrient conditions can impact E. coli growth and survival in secondary habitats. For example, previous investigations reported E. coli populations that 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 [35]. Additionally, E. coli cell density, incubated at 30 °C and 37 °C, in soils decreased in the days following rapid initial cell growth [36], thus indicating that soil E. coli population density was determined predominantly through either the exhaustion of bioavailable nutrients or predation [36]. 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 [37]. 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 [37]. 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 ($r2 = 0.70$, $p < 0.001$) [37]. 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 [37][38]. In aquatic environments, dissolved nutrients (glucose and peptone) have been shown to greatly increase the survival of E. coli [39]. Additionally, nutrient availability, specifically glucose, can alter E. coli's response to stressors [40]. For example, E. coli displayed increased sensitivity to secondary stressors and short term nutrient availability following a period of starvation (nutrient deprivation) [40]. 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 [18][41][42]. In agricultural regions, increased E. coli concentrations are primarily driven by manure applications [43] and the population density of endotherms (livestock) [28][44][45]. During manure application, the environmental inactivation or die-off of E. coli results in decreasing concentrations with time passed since application. Conversely, in urban areas *E. coli* concentrations are elevated due to two primary reasons: 1) leaking wastewater infrastructure [27][42][44] and 2) increased run-off during precipitation events due to increased impervious surfaces [44][46]. Land-use and land cover changes can also induce changes to the physical characteristics of E. coli habitats [47], thereby impacting the occurrence and survival of fecal microbes. For example, removal of vegetation can result in increased insolation or alteration of soil moisture content and groundwater levels impacting nutrient transport and availability. Consequently, land-use practices and alterations to land cover constitute important variables that must be accounted for when assessing the survival of E. coli in secondary habitats.

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 [28][48]. Given that 89% of stream E. coli concentrations result from overland flow [49], 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 [50]. For example, McDowell et al. [51] 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 [52] 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. 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 [27][44][47]. 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 [53].

4. Conclusion

Given the health risks of E. coli contaminated stream water consumption (a single exposure exceeding 500 colonies 100 mL−1 has a 10% chance to result in gastrointestinal illness [54]) 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 [36], solar insolation [15], suspended and settled solids [19][20], hydrologic conditions [30], water chemistry [32], nutrient conditions [35], and land-use practices, impact the survival of E. coli in the environment [28][55][56]. 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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