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Interactions of *E. coli* with algae and aquatic vegetation in natural waters

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ABSTRACT

Both algae and bacteria are essential inhabitants of surface waters. Their presence is of ecological significance and sometimes of public health concern triggering various control actions. Interactions of microalgae, macroalgae, submerged aquatic vegetation, and bacteria appear to be important phenomena necessitating a deeper understanding by those involved in research and management of microbial water quality. Given the long-standing reliance on *Escherichia coli* as an indicator of the potential presence of pathogens in natural waters, understanding its biology in aquatic systems is necessary. The major effects of algae and aquatic vegetation on *E. coli* growth and survival, including changes in the nutrient supply, modification of water properties and constituents, impact on sunlight radiation penetration, survival as related to substrate attachment, algal mediation of secondary habitats, and survival inhibition due to the release of toxic substances and antibiotics, are discussed in this review. An examination of horizontal gene transfer and antibiotic resistance potential, strain-specific interactions, effects on the microbial, microalgae, and grazer community structure, and hydrodynamic controls is given. Outlooks due to existing and expected consequences of climate change and advances in observation technologies via high-resolution satellite imaging, unmanned aerial vehicles (drones), and mathematical modeling are additionally covered. The multiplicity of interactions among bacteria, algae, and aquatic vegetation as well as multifaceted impacts of these interactions, create a wide spectrum of research opportunities and technology developments.

1. Introduction

Algae, aquatic vegetation, and bacteria are essential inhabitants of the aquatic environment and their presence is of ecological and sometimes public health significance. Total coliforms, and particularly fecal coliforms, have historically been used to monitor for fecal contamination in various water sources and subsequent water treatment efficacy. *Escherichia coli* is part of a larger group of fecal coliforms, an assortment of bacterial species mainly sourced from feces, and the focus of many monitoring and research efforts since numerous *E. coli* serotypes can cause human illness if ingested (Kaper et al., 2004; Jang et al., 2017). Hence, the presence of *E. coli* in natural waters is used as the chief indicator of microbial water quality for recreation, agricultural irrigation, aquaculture, and efficiency of water treatment (Price and Wildeboer, 2017). Monitoring for the presence of *E. coli* is also used to evaluate agricultural, aquacultural, and urban management practices on lands surrounding surface waters (Petersen and Hubbart, 2020). Improvements in understanding interactions of *E. coli* with various constituents in the aquatic environment lead to better interpretation of monitoring results and better decisions for water quality management. Natural waters also contain populations of algae, aquatic vegetation (AV), grazers, and/or nutrients that can change *E. coli* concentrations or alter the aquatic community structure. The aquatic environment constituents considered in this review are algae (including macro- and microalgae, periphyton, benthic algae, and cyanobacteria, also referred to as blue-green algae) and aquatic vegetation (AV).

Algae and AV are known to supply carbon, compete with *E. coli* for nutrients, modify the water chemistry, shelter *E. coli* from solar radiation, and release toxins and stimulants (Vanden Heuvel et al., 2010; Fuentes et al., 2016; Wu et al., 2021). Different types of algae and AV can have different impacts on *E. coli* survival. By altering *E. coli* populations, algae and AV can consequently affect any *E. coli*-based evaluation of the effectiveness of land-based practices, such as waste management, livestock feeding operations, stormwater control, recreational activities,

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and conservation practices on microbial water quality. Conversely, changes in land-based practices (e.g., agricultural practices) may indirectly affect *E. coli* populations via the impact on algae and AV. In particular, practices causing or controlling eutrophication may influence algal populations and consequently affect the conditions *E. coli* has adapted to for survival. Similarly, algicide applications used to control algal populations can influence *E. coli* survival via a change in algal and AV community composition and concentrations.

Climate change and extreme weather events present an additional challenge to resource managers and researchers tasked with monitoring and predicting both algal blooms and pathogenic bacteria movement and concentrations within the aquatic environment. The global warming processes most often considered when assessing aquatic ecosystem impacts are intensified precipitation events that increase nutrient delivery processes via run-off, followed by prolonged droughts that lead to increased water temperatures and thermal stratification over a longer period (Reidmiller et al., 2018). These actions create conditions that favor the growth, development, and maintenance of harmful algal blooms (HABs) and cyanobacteria harmful algal blooms (cyanoHABs) in marine and freshwater environments, such as those used as aquaculture, agriculture, and drinking water sources. CyanoHABs in warmer waters often result in increased thermal stratification and the formation of surface scums, which provide additional competitive advantages for cyanobacteria compared to eukaryotic algae in freshwater systems (Huisman et al., 2004; Kardinaal et al., 2007), a scenario which can promote the growth of *E. coli* (Mezrioui et al., 1994; Vijayavel et al., 2013). Likewise, the risk of transmission of pathogenic bacteria, such as *Cryptosporidium* spp. and *E. coli*, into public drinking and recreational waters is increased with precipitation events as more frequent or extreme storm events, such as predicted with climate change, can overwhelm sewer systems and lead to overflows that contaminate these waters (Patz et al., 2008; 2014), thus providing additional opportunities for synergistic cyanobacteria-pathogenic bacteria interactions.

The predicted increase and intensification of cyanoHABs due to climate change also could create a scenario in which *E. coli* concentrations and occurrences in the aquatic system would increase and require greater resource monitoring efforts for environmental and public health safety. Blaustein et al. (2013) described *E. coli* survival rates across various temperatures in six different types of waters and hypothesized that interactions with algae and algal toxins may influence survival. Work by Lee et al. (2016) and Halac et al. (2019) concluded that hydrographic and water temperature conditions were more important in predicting the occurrence of pathogenic bacteria associated with cyanobacteria than nutrient conditions. Similarly, Bomo et al. (2011) demonstrated that there are species-specific interactions between cyanobacteria and pathogenic bacteria, with the toxigenic cyanobacteria expected to proliferate under predicted climatic changes (e.g., *Microcystis* and *Anabaena*) influencing the growth and survival of *E. coli*. However, other authors have determined that toxic substances, such as microcystins produced by numerous bloom-forming cyanobacteria species, are detrimental to *E. coli* (Dixon et al., 2004; Valdor and Aboal, 2007; Halac et al., 2019). Consequently, while the risk to human health from toxin-producing cyanoHABs may increase under future climate scenarios, the human health risk from pathogenic bacteria may decrease. However, more research is needed with regards to cyanobacteria blooms that do not produce toxins (estimated to be approximately 75% of global cyanobacteria blooms (Groendahl and Fink, 2017), yet would provide the substrate and nutrient sources needed for the proliferation of *E. coli*. In this scenario, the predation of *E. coli* by grazers may be lessened by predicted climate change-driven ecological shifts that promote the growth of cyanobacteria over other algal species as both toxic and non-toxic cyanosHABs often lead to reduced grazer fitness in the natural aquatic environment (Fyda et al., 2010; Paerl and Otten, 2013; Sukenik et al., 2015). It has been noted that some algal and cyanobacterial exudates have a stimulatory effect on bacteria, including stimulation of bacterial DNA synthesis (Murray et al., 1986), enhancement of bacterial horizontal gene transfer (Matsui et al., 2003), increased bacterial biofilm formation (Espeland and Wetzel, 2001), as well as bacteria community composition shifts (van Hannen et al., 1999). However, the impact and extent to which these factors promote or inhibit *E. coli* success in natural waters is largely unexplored.

The community involved in the detection, monitoring, prediction and management of bacterial pathogens and indicators in natural waters is very diverse. It includes not only microbiologists and phycologists; there are many engineering/technical/modeling professionals who are becoming involved in microbial water quality assessments for agricultural irrigation, recreational, and aquaculture water sources. This audience can benefit from a conceptual overview of interactions between *E. coli*, algae, and AV as a knowledge base for elucidating the dynamics of microbial water quality and developing environmental monitoring and management schemes to improve water quality, especially as climate change adds additional human and environmental health and food safety concerns. Providing such an overview is the objective of this paper which summarizes and discusses the state of the knowledge about algae and AV effects on microbial water quality, with an emphasis on *E. coli* as the primary indicator organism used routinely in many monitoring designs and management decisions in the microbial water quality field.

2. Major effects of algae and AV on *E. coli* survival

Fig. 1 presents the major aspects of algae and AV effects on bacteria survival in natural water environments that are reviewed here with a focus on *E. coli*. Gurung et al. (1999), Quero et al. (2015) and Ramanan et al. (2016) detail the role of algae- and AV-derived carbon and other nutrients in the aquatic environment; both algal and AV photosynthetic and decomposition processes release carbon and other nutrients which are used by bacteria in various mutualistic and competitive relationships. Algae and AV provide surfaces for the development of biofilms which become productive habitats for bacteria (Quero et al., 2015; Jang et al., 2017) and can promote or inhibit zooplankton grazer populations (Reche et al., 1997; Paerl and Otten, 2013). Both algae and AV can alter the sunlight energy transfer in water, thus shielding bacteria from radiative damage, but can also cause negative effects on bacteria through photosynthetic processes that change oxygen forms and pH to conditions that are unfavorable for bacteria (summarized in Curtis, 2003). Work demonstrating the toxicity of algal substances to bacteria has been on-going since the 1940s (Pratt et al., 1944), with current research focusing on the effects of cyanobacteria toxins on *E. coli* (Martin et al., 2017). When considering competition between these organisms for nitrogen, phosphorus, carbon, and microelements, and the role that grazers play in the bacterial, algal, and AV community structures, the resulting interactions between these constituents appear to be convoluted with feedback loops and interrelations. This complex system of interactions manifests itself in many controls exerted on *E. coli* populations in natural aquatic environments.

2.1. Changes in the nutrient supply

2.1.1. Carbon in the phycosphere

Algal exudates influence bacteria in the vicinity of algae. The term ‘phycosphere’, used for the first time in 1972, was defined as “a zone that may exist extending outward from an algal cell or colony for an undefined distance, in which the bacterial growth is stimulated by the extracellular products of the alga” (Bell and Mitchell, 1972). The phycosphere is one of the most ignored, yet distinctive, aquatic habitats for bacteria (Cho et al., 2015; Kim et al., 2014; Lee et al., 2013; Ramanan et al., 2015; Sapp et al., 2007). Within the phycosphere, high concentrations of fixed organic carbon are available for consumption as compared to the vast oligotrophic surroundings in marine and fresh waters. Algae release carbon to avoid photoinhibition (Cherrier et al., 2015). As bacteria are usually limited by cell-generated energy for

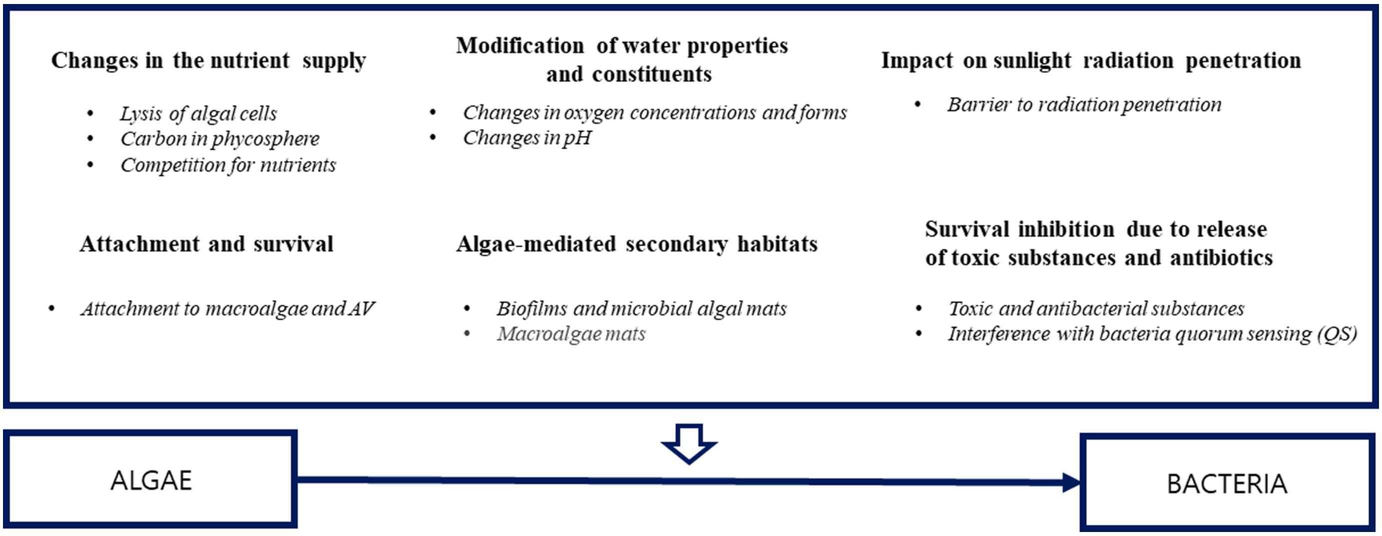

Fig. 1. Synopsis of the review topics.

nutrient transport, they can be highly dependent on algal organic carbon exudates for their energy supply (Jansson, 1988). This relationship has been considered a form of commensalism, in which bacteria growth and survival is limited by carbon produced by the algae more so than nutrient availability in the phycosphere (Gurung et al., 1999).

Microalgae exudate is composed mainly of carbohydrates, followed by different nitrogenous compounds and vitamins (Myklestad, 1995; Underwood et al., 2004; Watanabe et al., 2008). The relationship between the green alga *Chlorella vulgaris* and *E. coli* in nutrient-replete conditions was described as mutualistic by both Delgadillo-Mirquez et al. (2016) and Žitnik et al. (2019), wherein the bacteria used the oxygen produced by the algae to oxidize organic matter and produced CO_2 essential for algal photosynthetic activity in return. Similarly, Cho et al. (2015) demonstrated that algae supply fixed organic carbon to a consortium of mutualistic bacteria, mostly belonging to plant-growth-promoting bacteria, and bacteria, in return, supply dissolved inorganic carbon and low molecular weight organic carbon for algal consumption.

In aquatic systems, bacterial growth is often limited by algal-supplied carbon (Daufresne et al., 2008; Wyatt and Turetsky, 2015). Thus, conditions that prevent or slow algal population development result in low fecal coliform, including *E. coli,* concentrations. Maestre-Valero et al. (2011) reported that in covered reservoirs, where the reduction in water temperature and solar radiation limited algal photosynthetic activity, the shortage of organic matter and cooler water temperature led to a very low concentration of fecal coliforms and *E. coli*. Similarly, suppression of algal biomass due to the presence of duckweed mats led to anoxic and neutral pond conditions and the removal of 99.7% of *E. coli* and 91.8% of enterococci cells (Papadopoulos and Tsihrintzis, 2011).

2.1.2. Competition for nutrients

The relationship between bacteria and algae concerning nutrients has been regarded as competitive (Gurung et al., 1999). At low nutrient concentrations, an increase in algal-derived organic carbon can stimulate the growth of the bacteria community because bacteria are more biologically efficient at low nutrient concentration (Currie and Kalff, 1984; Suttle et al., 1990; Rothhaupt and Giide 1992; Drakare, 2002). At high nutrient concentrations, however, algae can take up nutrients predominantly over bacteria due to greater maximum uptake rates (Gurung et al., 1999).

The type of relationship between bacteria and algae depends on environmental conditions (Gurung et al., 1999). When light is abundant relative to nutrients, algae fix carbon in surplus and subsequently exude large amounts of it (Lancelot, 1983). In such a situation, bacterial growth is nutrient-limited because organic carbon availability is greater than nutrient availability. However, at low light/nutrient ratios algae excrete less organic carbon due to lower photosynthetic rates and bacteria become energy-limited because of an organic carbon deficit (Gurung et al., 1999). Thus, competitive interactions between bacteria and algae are expected to be more intense at higher light/nutrient ratios while commensalism would be promoted at lower light/nutrient ratios.

Phosphorus is the nutrient often used to demonstrate the switch between algae and bacteria relationship types (Bratbak and Thingstad, 1985). When the growth of algae and bacteria is limited only by phosphorus, the interaction between them is competitive. However, when bacterial growth is also limited by organic carbon, the interaction between algae and bacteria becomes more complex (Liu et al., 2012). The interplay between light intensity and phosphorus concentrations as factors determining the relationship between algae and heterotrophic bacteria was elucidated in experiments by Gurung et al. (1999) using the green alga, *Scenedesmus acutus*, and bacteria from a freshwater lake in Japan. Gurung et al. (1999) found that bacteria were carbon-limited at a light intensity < 55 μE m^{-2} s^{-1}, thus indicating a commensal relationship between algae and bacteria (Fig. 2). Above that light intensity, bacteria suffered from an organic carbon deficit, rather than phosphorus-limitation because of low algal biomass which reduced the phosphorus supply. However, at moderate phosphorus supply rates and light intensities$<$ 55 μE m^{-2} $^{s-1}$ bacterial growth was limited by phosphorus rather than organic carbon, because the carbon supply, derived from algae, exceeded the phosphorus supply relative to bacterial demand (Fig. 2C). Further increases in the phosphorus supply reduced or eliminated phosphorus limitation for both algae and bacteria (Fig. 2D). Thus, competitive interaction was most intense at a moderate phosphorus supply rate (Fig. 2C). These results demonstrated that there is a shift between commensalism for carbon and competition for phosphorus depending on light intensity and nutrient supply rate (Gurung et al., 1999).

In mesocosm experiments examining the interactions of algae and heterotrophic bacteria, Liu et al. (2012) found that the addition of carbon, as glucose, immediately resulted in the decline of chlorophyll-*a*; this was attributed to inorganic nutrient competition between the algae and bacteria. Carbon additions, such as glucose, stimulate bacterial growth and activity, which in turn alters the nutrients available to algae and changes the competitive relationships between algae and bacteria. A similar effect was observed by Joint et al. (2002), Danovaro (1998), and Cotner et al. (2010), all of whom noted large increases in bacterial activity with the addition of glucose. The addition of glucose across a range

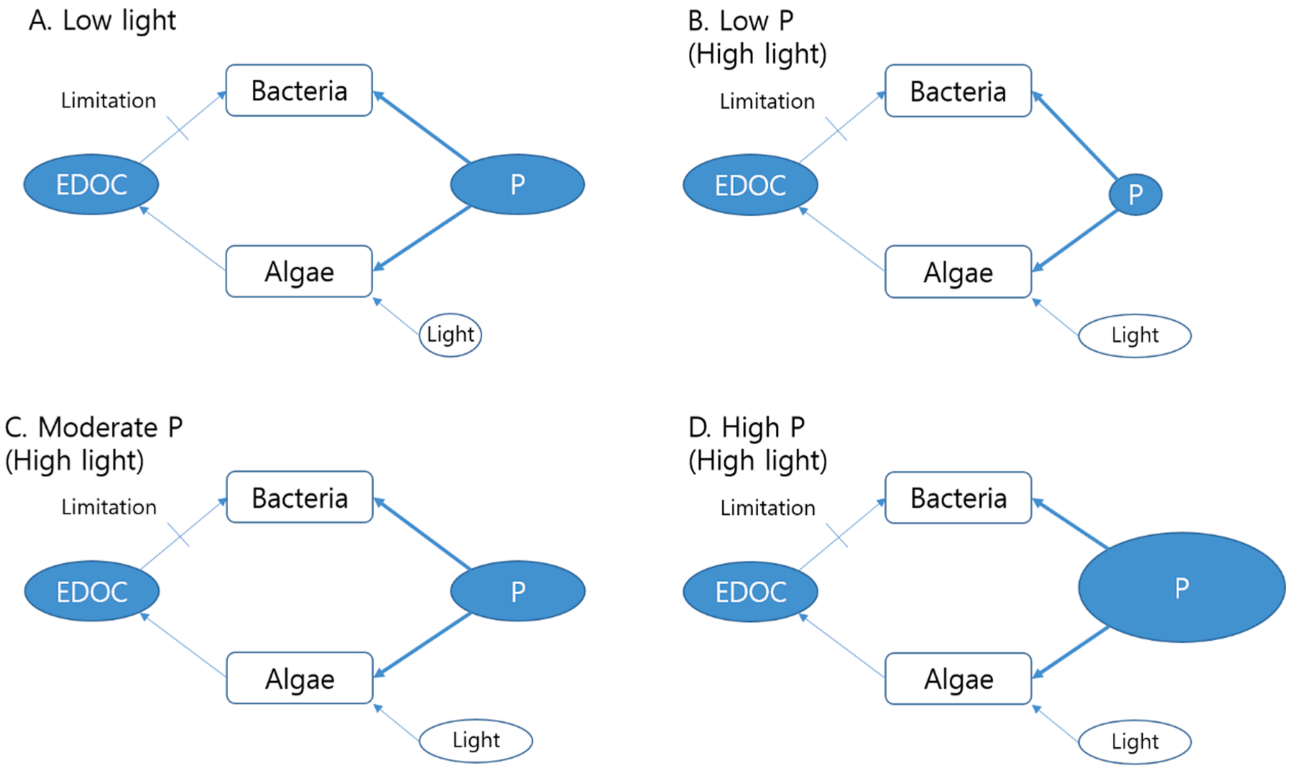

Fig. 2. Effects of light intensity and phosphorus (P) supply rate on the relationship between bacteria and algae (adapted from Gurung et al. 1999). (A) Low light intensity, (B) high light intensity and low P supply, (C) high light intensity and moderate P supply, and (D) high light intensity and high *P* supply. Relative flows of *P* and extracellular dissolved organic carbon (C; energy) is denoted by the thickness of the arrows. The growth of each organism is limited by the resource indicated by a thin arrow.

of concentrations resulted in a decline of algal biomass, which was explained by the ability of heterotrophic bacteria to outcompete the algae for available inorganic nutrients.

Nutrient availability appears to control the switch from mutualism to competition in laboratory experiments designed to examine the relationship between *E. coli* and *C. vulgaris* at a constant temperature, light, and regulated pH (Žitnik et al., 2019). In this laboratory study, the electrical conductance (EC) of the solution was used as the measure of nutrient availability with an EC > 1569 μS/cm indicating a high nutrient concentration. Žitnik et al. (2019) found at an EC > 1569 μS/cm *E. coli* concentrations were high, regardless of the presence of *C. vulgaris*, whereas at an EC < 1569 μS/cm the presence of high concentrations of *C. vulgaris* ($>1 \times 10^7$ cells mL^{-1}) inhibited the growth of *E. coli*, but below this algal cell concentration the ability of *C. vulgaris* to inhibit the growth of *E. coli* declined.

The adaptive response of *E. coli* to being outcompeted in nutrient-deficient conditions involves genetic mutations that increase the efficiency of usage or uptake of the limiting nutrient (Halac et al., 2019; Roose et al., 2020). Halac et al. (2019) described two different forms of adaptive strategies under the nutrient limitation that affect cellular physiology in different ways. Adaptation to nitrogen starvation caused changes that resulted in increased nitrogen scavenging ability of *E. coli*. Adaptation to magnesium starvation initiated restructuring of the cell's outer membrane to a configuration that allows magnesium to be redistributed to other biological processes. Roose et al. (2020) demonstrated the abundance of bacterial *nir* and *nos* genes in response to nitrogen pulses in newly constructed and established wetlands that allowed the bacterial community to compete with benthic algae for limited nitrogen resources.

E. coli competes not only with algae but also with other bacteria in natural freshwater environments. Nutrient additions did not affect microbial concentrations, including *E. coli* concentrations, in the water column in mesocosm experiments conducted by Gregory et al. (2017), however, *E. coli* populations associated with the benthos/sediment did show a growth response. Work by Barnard et al. (2017) showed that the introduction of *Spirogyra grevilleana*, a benthic green alga, to a biofiltration system reduced the concentrations of both *E. coli* and nitrogen constituents. As the interest in benthic algal populations grows for a variety of human and environmental health reasons (Bouma-Gregson et al., 2017) the interplay of benthic algae, benthic cyanobacteria, and the microbiome, including *E. coli*, should be examined more thoroughly.

2.1.3. Lysis of algal cells

At the onset of algal cell death, there is usually a large initial release of soluble materials amounting to 20–50% of the cell's organic content (Depinto and Verhoff, 1977; Cole, 1982). The released dissolved organic matter includes significant carbohydrate (52%) and biodegradable (55 to 74%) fractions (Bouteleux et al., 2005). The organic matter and soluble materials from dead algal cells can be rapidly metabolized by bacteria both in the laboratory and under natural conditions (Iturriaga and Hoppe, 1977; Cole, 1982). These substances are always composed of polysaccharides-glucanes (glucose polymers) belonging to the family of starches or laminarines (Bouteleux et al., 2005).

Biodegradable dissolved organic carbon (BDOC) released by algae was the preferred substrate for *E. coli* growth in the laboratory experiments of Bouteleux et al. (2005). In this study, the addition of algogenic organic matter (AOM) from chlorinated natural waters led to an *E. coli* growth equivalent to that of tap water without addition, while the addition of AOM from ozonated natural waters allowed a 4- to 12-fold increase in *E. coli* growth rates compared to tap water without BDOC addition. Bouteleux et al. (2005) further demonstrated that conditions and reasons for algal cell lysis can affect the suitability of the lysed material to be a nutritious substrate for *E. coli*, specifically after ozonation, in which AOM particles are broken into smaller, biodegradable units that are more quickly assimilated by bacteria. The AOM particles in the Bouteleux et al. (2005) study were composed of a mixture of very diverse organic compounds, of which approximately 50% were identified as sugars. Other nutritive elements, such as growth factors (vitamins, amino acids, siderophores, trace elements, and organic cofactors), are all possibly part of AOM mixes and help facilitate the survival of heterotrophic bacteria, including *E. coli*.

In addition to death and decay processes, algal reproduction can provide a nutrient pool. For example, during mating, *Chlamydomonas reinhardtii*, a species of green algae, releases a lytic factor - a substance that breaks down the cell wall, allowing for fusion of gametes; this digestion releases soluble carbohydrates in amounts up to 3×10^{-6} pg cell^{-1} within a few hours (Solter and Gibor, 1977).

2.2. Modification of water properties and constituents

2.2.1. Changes in oxygen concentrations and forms

Algal photosynthetic activity results in pH elevation and increased oxygenation, but respiration processes and organic matter oxidation also affect the dissolved oxygen (DO) concentrations in aquatic environments on a diurnal cycle (Ansa et al., 2011; Cheng et al., 2013). Limited research regarding the impacts of oxygen concentrations on bacteria has been conducted in natural waters, but increased oxygenation in wastewater treatment ponds (WTPs) or lagoons attributed to algal abundance has been observed to affect fecal bacteria die-off due to the production of toxic oxygen species (Curtis et al., 1992; Liu et al., 2016). This occurs due to the presence of sensitizers, i.e., light absorbing compounds which transfer energy to other molecules. Photooxidation is the process where endogenous or exogenous sensitizers absorb light and transfer energy to other molecules leading to the formation of reactive oxygen species (ROS). When ROS, including singlet oxygen, superoxide, hydrogen peroxide, and hydroxyl radicals are formed through these energy transfer reactions, microorganisms can be damaged (Curtis et al., 1992). Observations of this effect in freshwater environments are scarce; the work by Ansa et al. (2011) for a tropical lake in Ghana presents an example, as do some studies in WTPs. In these examples, an increased efficacy of the removal of bacteria was attributed to algae-mediated elevated oxygen concentrations that lead to photooxidation (Ansa et al., 2011, 2015; Liu et al., 2016). Curtis (1990) and Curtis et al. (1992) showed that pH and ROS concentrations play a proportional role to the survival of *E. coli* in WTPs, with less damage to *E. coli* occurring at pH concentrations below 8. Al-Tameemi and Kadhim (2019) found that the presence of the green algae *Mougeotia* sp. and *Nostochopsis* sp. in WTPs increased the DO (20 mg L^{-1}) and pH (10.6) to concentrations that were detrimental to *E. coli*.

Algae-induced changes in pH and DO have a demonstrated seasonality in temperate and tropical climates creating seasonal patterns in *E. coli* removal efficiency in WTPs. In temperate environments, Liu et al. (2016) and Liang et al. (2018) noted that removal efficiencies of pathogenic microorganisms during wastewater treatment over a year were highly variable, with higher removal efficiencies documented in the summer and fall seasons, correlating with the presence of dense algal blooms. Similarly, in tropical riverine waters Allam and El-Gemaizy (2015) found that when summer algal populations were densest *E. coli* concentrations were lowest.

2.2.2. Changes in pH

Diurnal variation in CO_2 concentration occurs as a result of photosynthesis (Dubinsky and Rotem, 1974). In natural environments (Dubinsky and Rotem, 1974) and laboratory mesocosm experiments (Vasker et al., 2021), this diurnal fluctuation in pH is described as a DO concentration peak in mid-afternoon and falling to a minimum concentration overnight as photosynthesis ceases but respiration continues. More work has been done in WTPs than in natural environments to elucidate this effect on coliform bacteria. In WTPs Gray (2004) and Amengual-Morro et al. (2012) reported that during periods of rapid photosynthesis, algal demand for CO_2 exceeds that produced by bacterial respiration, carbonate and bicarbonate ions dissociate to produce CO_2, which is used by the algae, and hydroxyl ions, which accumulate and can raise the pH to above 10. This pH imbalance between day and night inactivates coliforms due to algal photosynthetic activity exceeding bacterial respiration during the daytime (Amengual-Morro et al., 2012). Diurnal variation in pH in eutrophic lakes may negatively affect *E. coli* survival even if pH does not reach critical basic high values (given as pH = 9.5 by Parhad and Rao (1974) and Awuah (2006)).

Interactions of pH and other factors on *E. coli* survival have not systematically been studied in natural water environments. Davies-Colley et al. (1997, 1999) found that light-related inactivation of *E. coli* is dependent on pH in WTPs. Under elevated pH conditions (pH > 8.5), *E. coli* is inactivated by exogenous mechanisms, while endogenous mechanisms inactivate *E. coli* more slowly under moderate pH conditions. The effects of pH on *E. coli* have been attributed to conformational changes in the membrane of the bacteria. Both Bosshard et al. (2010a,b) and Curtis et al. (1994) found that bacterial inactivation resulted from respiratory chain damage that caused a physical breakdown in the membrane that exposed nucleic acids to environmental stresses.

2.3. Impact of solar radiation penetration

The sunlight-mediated *E. coli* inactivation largely depends on the medium in which bacteria are present and the degree of solar exposure (Dias et al., 2017). Algae can reduce or enhance the harmful effects of sunlight on bacteria by impeding light penetration and increasing DO concentrations (Curtis et al., 1992). Light attenuation by algae can partially compensate for the harm to fecal coliforms caused by algal photosynthesis in the form of increased DO and pH concentrations that cause photooxidation. Curtis et al. (1994) showed that different algal concentrations affected light attenuation with short-wavelength spectra being more impacted by algal biomass than long-wavelength spectra. In turbid aquatic systems, light is attenuated exponentially as a function of chlorophyll-a derived from algae, resulting in an exponential decrease in light penetration in response to a small increase in chlorophyll-a (Grobbelaar, 1989; Curtis et al., 1994; Dokulil, 1994). In natural ponds, solar radiation penetration decreases with increased algal biomass (Van der Steen et al., 2000).

Light attenuation can also impede the *E. coli* inactivation caused by the presence of endogenous sensitizers. Such compounds are present within *E. coli* and other coliform cells (Bolton et al., 2010). The photosensitizer-related inactivation of *E. coli* was first studied for UV-B radiation (Reed, 1997; Davies-Colley et al., 1999), and more recently was determined to occur across the entire visible light spectrum (Kadir and Nelson, 2014). UV-B radiation (290–320 nm) creates direct DNA damage in *E. coli* cells (Shilton, 2005). Typically, damage from UV-B radiation only occurs in the top few centimeters of water because of increasing PAR attenuation rates with depth due to the presence of surface water algal biomass, increased in colored dissolved organic material (CDOM), and turbidity causing materials (Van der Steen et al., 2000; Shilton, 2005; Maraccini et al., 2016; Farrell et al., 2018). Maraccini et al. (2016) noted species specific responses to solar inactivation with *E. coli* being less affected by solar damage in highly turbid waters than *Enterococcus faecalis*. Huber et al. (2011) demonstrated that turbidity causing materials can impact UV inactivation through various mechanisms, including scattering and absorption of incident UV light and shielding of bacteria, protozoa, and viruses, preventing sufficient UV doses for pathogen inactivation.

Diurnal dynamics of *E. coli* concentrations in freshwater sources are complex; Lian et al. (2018) found that the UV-B dose delivery schedule (the combination of dose, rate, and exposure time) influences the inactivation of *E. coli* and MS-2, an *E. coli* bacteriophage, at all UV-B doses investigated in optically-clear water. Through this work two inactivation phases were identified, a UV-B dose rate-limited inactivation phase and a dose rate-saturation inactivation phase. Algae also have unique diurnal cycles (Hansson, 1995) and the synergistic effect of this with *E. coli* diurnal cycles and UV radiation have not been investigated.

Extended survival of *E. coli* and *Salmonella enterica* ser. Typhimurium in the presence of the green alga, *Cladophora*, was attributed to the algae-mediated protection from UV irradiation via the production of exudates (Beckinghausen et al., 2014). The production of secondary metabolites that offer photoprotection is summarized in Klisch and Häder (2008) and Carreto and Carignan (2011). Such effect was observed with mycosporines and mycosporine-like amino acids (MAAs), which are low-molecular-weight, water-soluble molecules that absorb UV radiation in the wavelength range of 310–365 nm and possibly scavenge O_2. These substances exhibited a sunscreen-like function, preventing growth inhibition of *E. coli* in both marine and freshwater (Suh et al., 2003; Oren and Gunde-Cimerman, 2007; Rastogi et al., 2015).

2.4. Algae-mediated secondary habitats

2.4.1. Biofilms

Surfaces of water bodies, rocks, sediments, and submerged aquatic vegetation may be covered with algae-mediated biofilms that present a suitable habitat for bacteria. Mats that form on the surface of water or rocks are typically composed of epiphytic algae, cyanobacteria, detritus, and sediments. Many cyanobacteria species frequently establish biofilms on water surfaces which cause human health risks due to the presence of algal toxins (Paerl et al., 2000; Bomo et al., 2011). These biofilms represent a nutrient-rich environment that promotes the growth and survival of various bacteria. For example, the densities of *E. coli* (MPN), enterococci (MPN) and *Clostridium perfringens* (CFU) attached to mats of the cyanobacteria *Lyngbya wollei* averaged 3.5, 3.2, and 3.2 log g^{-1}, respectively (Vijayavel et al., 2013). Similarly, Dratchev et al. (1957) found that concentrations of *E. coli* in surface films and foams were 100 - 1000 times greater than concentrations in the underlying water.

Phototrophs can survive in natural biofilms formed on a variety of substrates, such as rocks without known organic carbon and energy sources (Cockell et al., 2011), adding a new dimension to studies on the growth of algae and bacteria in extreme environments. Both bacteria and algae survive in extreme conditions by secreting high levels of extracellular polymeric substances (EPS), including organic carbon. Special ice-active substances, like glycoproteins, which change the physicochemical surroundings of the immediate environment, can be secreted to help support biological functions in extreme conditions (Ramanan et al., 2016). Algae and cyanobacteria biofilms form on spider-webs with coastal water evaporation being the sole source of nutrients (Azua-Bustos et al., 2012). Wierzchos et al. (2015) found a diversity of cyanobacteria and bacteria living in gypsum deposits in the Atacama Desert in which the cyanobacteria formed a protective environment for the bacterial community.

Periphyton communities, composed of algae, protozoa, and fungi, that grow attached to benthic surfaces provide a suitable habitat for bacterial growth (Ksoll et al., 2007). Periphyton in sediment biofilms supported a sizable *E. coli* population that exhibited seasonal dynamics ranging from 10^2 to 10^4 CFU gdw^{-1} in the summer and from 10^0 to 10^4 CFU gdw^{-1} in the winter (Stocker et al., 2019). Staley et al. (2011) surmised that decreases in the water column algae populations likely led to the increase of periphyton in the system through mesocosm experiments conducted through lighted and darkened conditions. After the agrochemical atrazine was applied, significantly higher *E. coli* densities were found in the sediments of illuminated microcosms and there was a strong negative trend in the correlation between algae in the water column and *E. coli* densities in the sediments (Staley et al., 2011).

2.4.2. Attachment to micro- and macroalgae

Association of *E. coli* with planktonic microalgae appears to exhibit a complex dependence on species, strains, and level on nutrients in the water (Fang et al., 2022). Results of microcosm research allowed authors to suggest that *E. coli* and enterococci showed little association with three green microalgae species, while three opportunistic pathogen species had the propensity to form such association. In another microcosm study, Perkins et al. (2016) also found no correlation between *E. coli* and particles.

Although detachment of *E. coli* cells from algal surface is plausible, the factors that cause this and rates of detachment have not been elucidated so far. Ansa et al. (2011) simulated the shear stress-caused detachment after one and three days of introduction of *E. coli* in microcosms with algae. Similar numbers of detached cells were found for both days, whereas the *E. coli* concentrations in solution decreased. Attached *E. coli* can receive necessary carbon from the algae it is associated with (Fang et al., 2022), thus algae die-off may initiate the detachment. Since the level of nutrients in water can control the bacteria attachment to algae, a change in this level may also cause detachment. Studies of release of *E. coli* from bottom sediments showed that *E. coli* moves from sediment to water column in absence of shear stress, possibly due to chemotaxis (Pachepsky et al., 2017; Park et al., 2017). It is not known if this type of detachment may occur with *E. coli* associated with algae.

Macroalgae provide excellent attachment conditions for *E. coli*. Attached *E. coli* were abundant, accounting for up to 3250 CFU g^{-1} of algal material in the work of Quero et al. (2015). Macroalgal-associated *E. coli* isolates belonged to all phylogroups, including pathogenic ones, and *Escherichia* cryptic clades (Quero et al., 2015; Mathai et al., 2019). Quero et al. (2019) showed that isolates of *E. coli* obtained from various benthic macroalgae species hadpotential to grow, even at in situ temperatures using only algal extracts as the source of carbon and nutrients. These same isolates also had the ability to produce biofilms in vitro. The genotypic diversity of the attached *E. coli* isolates was high, with significant differences between those found associated with algae and the *E. coli* populations in the overlying water. Quero et al. (2015) found that the algal-attached *E. coli* populations consisted of both resident and transient strains, likely resulting from the heterogeneous input of fecal bacteria from the surrounding urban environment, and that the abundance of algal-attached *E. coli* was positively correlated with *E. coli* abundance in overlying waters.

Much work has been done to study the relationship between fecal indicator bacteria and annual blooms of *Cladophora* in Lake Michigan, and these studies can be used as a reference point for other investigations. High densities of *E. coli*, among other enterococci, have been observed in attached and free-floating *Cladophora* mats at densities often exceeding 100,000 CFU g^{-1} algal material (Byappanahalli et al., 2003; Englebert et al., 2008b; Ishii et al., 2006; Van den Huevel et al., 2010). Within Lake Michigan *Cladophora* appears to stimulate the growth and naturalization of bacteria and concentrations of bacteria significantly decreased with increasing distance from algal mats in nearshore waters (Verhougstraete et al., 2010). Environmental conditions appear to play a role in the movement and survival of *E. coli* and human pathogenic bacteria, *Salmonella* spp., *Campylobacter* spp., *Shigella* spp., and Shiga toxin-producing *E. coli* (STEC), within the lake. Release of *E. coli* from *Cladophora* mats to surrounding water was attributed to wave action (Whitman et al., 2003). Englebert et al. (2008a) also noted that strong wind and wave influences were required to dislodge bacteria from *Cladophora*. During low energy conditions (low wind and wave action) small amounts of bacteria were released from *Cladophora* mats, but these organisms did not show long-term survival when free-floating in the water (Englebert et al., 2008a). The presence of *E. coli* within *Cladophora* mats is correlated with temperature (Whitman et al., 2003; Ksoll et al., 2007). During warmer summer temperatures, bacteria concentrations are highest in *Cladophora* mats and require more intense wave or wind action to dislodge the bacteria from the algal material. As water temperature decreases, the *Cladophora* habitat breaks down resulting in greater numbers of bacteria being released to the surrounding water (Verhougstraete et al., 2010). Whitman et al. (2003) and Englebert et al. (2008b) found that *E. coli* and enterococci survived much longer (45 days) in association with *Cladophora* mats than other pathogenic bacteria species. While other human pathogens, such as

Salmonella spp. and *Shigella* spp., were found in 40 to 100% of *Cladophora* samples collected from Lake Michigan (Ishii et al., 2006) these species were only able to survive outside of the *Cladophora* mats for 10 and 2 days, respectively (Englebert et al., 2008b).

Quero et al. (2015) demonstrated that *E. coli* can be associated with macroalgae other than *Cladophora* and that bacterial abundance was highly variable on both spatial and temporal scales. However, Zulkifly et al. (2012) found microscopic evidence for a diverse bacterial community associated with *Cladophora glomerata* and molecular evidence for ca. 100 distinct sequences classifiable to genus at an 80% confidence level or species at a 96–97% confidence level within nine bacterial phyla, but did not find *E. coli* or related human pathogens. This highlights the importance of considering algal species identifications, as well as life cycle stages, biochemical composition, nutrient availability, and temporal and spatial variability when examining the factors that influence bacteria adhesion.

Attachment to macroalgae (filamentous green algae) decreased populations of bacteria in the water column. Ansa et al. (2011) found that the attachment of fecal bacteria to macroalgae and suspended solids in eutrophic lakes is a potential, natural means of removal of bacterial pathogens. *E. coli* may attach to each other, to algae, and to suspended particles. This aggregate-forming process is commonly viewed as the mechanism that causes the removal of coliforms from the suspended state (Cheng et al., 2013). Settling does not necessarily occur though, but can be mediated when bacteria bind together with large organic molecules forming aggregates (Hess-Erga et al., 2008; Liu et al., 2013; Mamane et al., 2008; Wu et al., 2005).

In the absence of settling, algae-related attachment appeared to stimulate bacterial growth in microcosm experiments (Badgley et al., 2012). In their laboratory study, the increase of algae-attached *E. coli* concentrations did not appear to come from the continuing transition of *E. coli* from the water column to the algal filaments over time. When normalized to the scale of the entire microcosm, the total population of *E. coli* in microcosms containing algae grew more than one order of magnitude over the initial inoculum size. Algal microcosms also allowed for greater persistence of *E. coli* over time when compared to bacterial persistence in microcosms without algae. The observed *E. coli* growth after additional input of nitrogen suggests that algae are capable of supplying enough carbon to support sustained, long-term growth of attached *E. coli* in large-scale systems. This supply of photosynthetically fixed carbon, in addition to protection from other detrimental effects such as ultraviolet light, may be why algae are a favorable substrate for *E. coli* (Bouteleux et al., 2005). Microscopic observations, done using a GFP-labeled *E. coli* strain, supported the hypothesis that the growth of *E. coli* occurred directly on algal filaments (Fig. 3). The number of fluorescent *E. coli* colonies that were observed to be attached to algal filaments increased over time, indicating an increasing population size.

Algal mats washed onto beaches may get buried in the sand by wave action or human activities, where they are protected from sunlight and desiccation. Here, indicator bacteria may multiply due to available nutrients from the decomposing mats; the beach sand can serve as a source of indicator bacteria for the nearshore water, especially when waves resuspend buried mats (Whitman et al., 2003; Byappanahalli et al., 2006). Gubelit and Vainshtein (2011) found similar *Cladophora* - enteric bacteria interactions along the eastern Gulf of Finland shoreline, particularly in regions where water salinities were below 2 ppt.

2.4.3. Submerged aquatic vegetation

Submerged AV have the potential to harbor and disperse *E. coli* and other bacterial pathogens in a large number of water bodies (Staley et al., 2012). Eurasian watermilfoil (EWM) harbored elevated densities of *E. coli* and several potential pathogenic bacteria groups, including *Aeromonas,* Enterobacteriaceae, and *Clostridium* (Mathai et al., 2019). These authors observed that EWM could serve as a temporal source for transmission of microbiota to the water column. A significant difference in chemical composition, distribution pattern, community structure of AV, and bacterial population was attributed to seasonality, geospatial niches, and nutritional potential of several AV species by Othman and Haroon (2020). The presence of wetland plants decreased populations of *E. coli* via mechanisms of filtration, antibiosis, attachment, production of antimicrobial substances, and increases in microbial competition (Karim, 1999). Karim et al. (2008) observed a decrease in populations of *E. coli, S. enterica* ser. Typhimurium, bacteriophages, MS-2, and poliovirus in wetland environments, and attributed the die-off to increased microbial competition or predation. Pitlo and Dawson (1990) noted that the presence of submerged AV in water sources increased the bed and bank roughness, causing decreased flow rates and increased water quality and *E. coli* survival.

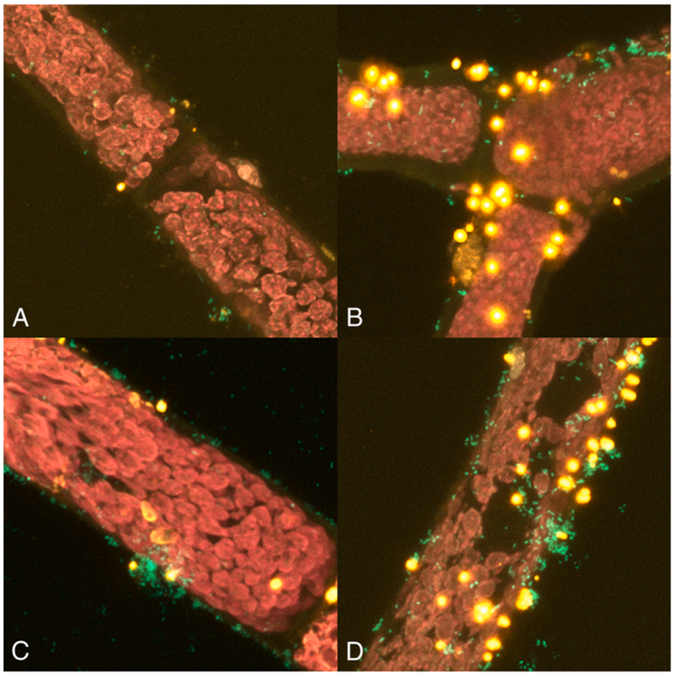

Fig. 3. Micrographs of *E. coli*, labeled with green fluorescent protein (GFP), growing on algal filaments in experimental microcosms (adapted from Badgley et al. 2012). Red indicates algal chloroplasts and bright green cells are labeled *E. coli*. Panels indicate time after inoculation: $A = 2$ h; $B = 24$ h; $C = 48$ h; and $D = 72$ h. All images were viewed at 600× and are presented in equal scale.

2.5. Survival inhibition due to release of toxic substances and antibiotics

2.5.1. Toxic and antibacterial substances

The release of substances toxic to coliform bacteria by algae was first suggested by Sieburth and Pratt (1962) and was often cited as a possible factor of bacterial die-off. Many algal taxa release substances inhibitory to bacteria (Cole, 1982; Ansa et al., 2011). One of the most common algal toxins found in the freshwater environment is microcystin, a hepatotoxin produced by numerous cyanobacteria species (Harke et al., 2016). While this toxin can be lethal to domestic and wild animals and detrimental to humans (Harke et al., 2016), it does not have a strong antibacterial action on *E. coli* (Dixon et al., 2004) and increased concentrations of microcystin may prolong the growth cycle of *E. coli* (Yang et al., 2008).

Cyanobacteria have also been identified as a source of biologically active compounds with antibacterial properties (Østensvik et al., 1998; Abed et al., 2009; Bomo et al., 2011). Aqueous methanol and other organic solvents found in cyanobacteria extracts possess antibacterial properties (Kellam and Walker, 1989; Frankmölle et al., 1992; Falch et al., 1995). Fig. 4 demonstrates this effect using the cyanobacterium *Tychonema bourrellyi* and several bacteria species. Secondary metabolites from cyanobacteria are associated with toxic, hormonal,

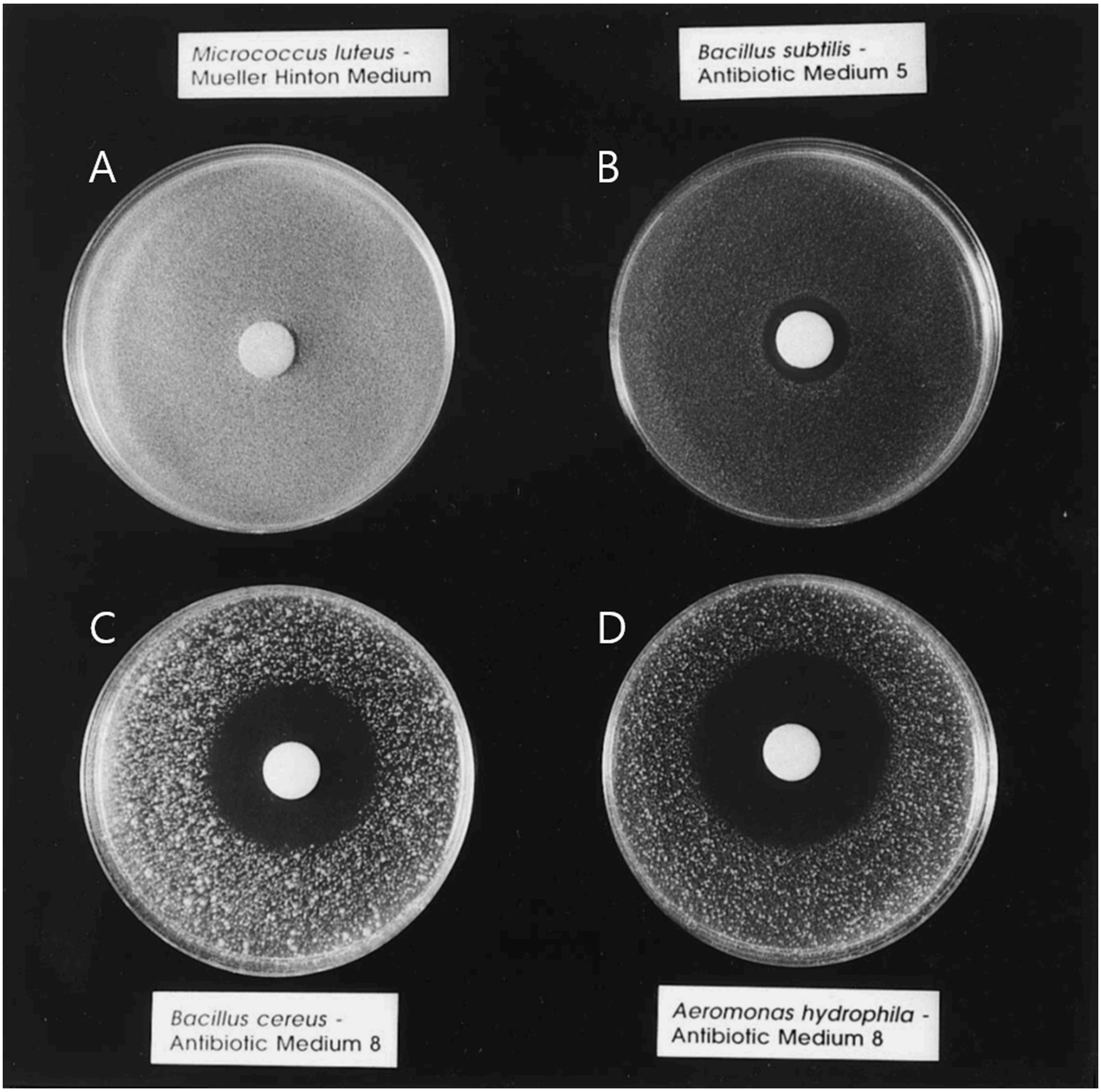

Fig. 4. Demonstration of the antibacterial effect of extracts from the cyanobacterium *Tychonema bourrellyi* in four different bacterial bioassays (adapted from Østensvik et al. 1998). (A) *Micrococcus luteus* inoculated in Mueller Hinton Medium (ML/MH), (B) *Bacillus subtilis* inoculated in Antibiotic Medium 5 (BS/M5), (C) *Bacillus cereus* inoculated in Antibiotic Medium 8 (BC/M8) and (D) *Aeromonas hydrophila* inoculated in Antibiotic Medium 8 (AH/M8). The strongest antibacterial effect is shown in the AH/M8 bioassay. No antibacterial effect is visible in the ML/MH bioassay.

antineoplastic, and antimicrobial effects (Carmichael 1992; Patterson et al., 1994). These antimicrobial substances may target various kinds of microorganisms, including prokaryotes and eukaryotes (Østensvik et al., 1998). However, a negative association between cyanobacteria and fecal coliforms was reported by Halac et al. (2019) for the periods when high (3.2×10^4 to 1.2×10^6 cells mL^{-1}) cyanobacteria cell concentration occurred. Halac et al. (2019) showed that both *E. coli* and *Enterococcus* spp. had decreased growth rates in the presence of the cyanobacterium *Microcystis aeruginosa* leading the authors to hypothesize that the high cell concentration found during *Microcystis* blooms could inhibit bacteria growth. Although both species of bacteria were negatively affected by the presence of *M. aeruginosa, E. coli* was more sensitive than *Enterococcus* spp. Similarly, Martin et al. (2017) exposed *E. coli* to 1 and 10 mg L^{-1} microcystin-LR and found no evidence that this toxin induced oxidative or cell envelope stress. Dziallas and Grossart (2011), Woodhouse et al. (2015), and Su et al. (2017), among others, suggest that the relationship between environmental cyanobacteria blooms and fecal indicator bacteria is complex with temperature, DO concentrations, algal bloom stage, nutrient availability, and co-occurring bacteria community dynamics all playing a role in toxin production and interaction.

Antibiotics are one group of substances that can be released by algae and can affect bacteria survival. The first antibiotic to be isolated from algae (*Chlorella pyrenoidosa* and *C. vulgaris*) was chlorellin, which was effective against both Gram-positive and Gram-negative bacteria including *Staphylococcus aureus, Streptococcus pyogenes, Bacillus subtilis*, and *Pseudomonas aeruginosa* (Pratt et al., 1944). Since this early work, numerous studies have been conducted to elucidate the antibiotic compounds made by algae (summarized in de Morais et al. 2015) and how these compounds may interact with bacteria (summarized in Shannon and Abu-Ghannam 2016).

2.5.2. *Interference with bacteria quorum sensing (QS)*

Quorum sensing (QS) bacteria produce and release chemical signal molecules called autoinducers that increase in concentration as a function of cell density. Gram-positive and Gram-negative bacteria use QS communication circuits to regulate a diverse array of physiological activities that include symbiosis, virulence, competence, conjugation, antibiotic production, motility, sporulation, and biofilm formation (Miller and Bassler, 2001). QS interference has been shown to occur between algae and bacterial biofilms (reviewed in Joint et al. (2007) and Rivas et al. (2010)). QS can be inhibited or stimulated depending on the algal species. QS is well-pronounced in *E. coli* populations (Surette et al., 1999; Sperandino et al., 2003). Tests using *E. coli* JB523 showed that one freshwater and five marine microalgae species exhibited quorum sensing inhibitory activity, whereas two algal species stimulated quorum sensing-regulated gene expression (Natrah et al., 2011). Several marine macroalgae were able to disrupt bacterial QS activities (reviewed in Dobretsov et al. (2009) and Natrah et al. (2011)) and some bacteria have been shown to use QS to regulate algicidal activities against toxigenic cyanobacteria (Wu et al., 2017) but more research needs to be conducted using *E. coli* and algae that typically co-occur with it in natural waters.

2.6. Horizontal gene transfer

The genetic makeup of both bacteria and algae is changing due to horizontal gene transfer (HGT) in the phycosphere (Kouzuma and Watanabe, 2015). A plausible consequence of this evolutionary process can be the acquisition, and subsequent expression of, antibiotic resistant genes in algae. The study of antibiotic resistant gene expression in algae is currently in its infancy and the impact on both human health, through routes of exposure such as recreational water contact, agricultural irrigation waters on fresh produce, or within aquaculture waters, and gene transfer to bacteria cohabitating in the phycosphere has yet to be determined. It is not known whether HABs, which occur throughout all water types, are increasing HGT rates that could lead to antibiotic resistance, though it has been documented that HGT from bacteria to algae aids algae in adapting to environmental extremes (Schönknecht et al., 2013; Raymond and Remias, 2019).

The strain-specific differences in *E. coli* – algae interactions begin with the expression of specific genes. Heo et al. (2019) reported the results of a genome-wide exploration of *E. coli* genes that promote growth in *C. vulgaris*. These authors identified four genes, *ribA, ribD, ribE*, and *ssuE* that exerted a growth-promoting effect on *C. vulgaris*. There is consortia of algae and bacteria that can be efficient in the detoxification of organic and inorganic pollutants, removal of nutrients from wastewaters, and bioenergy production compared to the efficacy of individual microorganisms (Subashchandrabose et al., 2011; Shetty et al., 2019). Thus, it could be beneficial to improve our understanding of which expressed genes influence the efficiency of these processes. The issue of *E. coli* strain variability is not adequately addressed in current environmental studies on algae-AV-*E. coli* interactions and its importance presents a research question to explore.

2.7. Predation of E. coli

Relatively little is known about the effect of algae and AV on the activity of predators controlling the population of *E. coli* in natural waters. Work presented by Ansa et al. (2012) reported that cladocerans were important to the removal of fecal coliforms in WTP systems, whereas Burnet et al. (2017) demonstrated in laboratory assays that these filter-feeding zooplankton did not exert a significant impact on *E. coli* population, even when the zooplankton were in bloom concentrations. Laboratory experiments by Mickalide and Kuehn (2019) demonstrated different survival patterns when *E. coli* was present with algae or ciliate predators versus algae plus ciliates. It is known that AV provide a niche habitat for zooplankton and macroinvertebrates that may prey on various bacteria species (Watkins et al., 1983). Additionally, the quantity and quality of the AV habitat (percentage of co-occurring cyanobacteria) can impact the predator community structure (Bolduc et al., 2016; Henesy et al., 2021) and predator fitness (Fyda et al., 2010; Paerl and Otten, 2013; Sukenik et al., 2015). However, the direct effect algae and/or AV communities and community shifts on *E. coli* predators needs to be further examined in drinking, recreational, agricultural, and aquaculture waters.

3. Outlook

A wide spectrum of research opportunities and technology developments is created by the multiplicity of interactions among *E. coli*, algae, and AV, as well as the multifaceted impacts of these interactions, particularly when global climate change and the need to safeguard environmental and human health from water-borne pathogens is considered. Global climate change is rapidly altering the aquatic environment via temporal and spatial shifts in rain/drought cycle-driven nutrient pulses and temperature anomalies and thus the relationships between aquatic organisms is being altered too (Cavicchioli et al., 2019). With this in mind, researchers, engineers, and resource managers alike need to understand the biological interactions of *E. coli* within the aquatic environment, utilize standard microbial water quality monitoring practices, and incorporate emerging technologies as a means to offer the best environmental and human health safeguards.

With many complex questions surrounding algal-bacterial interactions left largely unresolved, the application of omics approaches will likely surge over the next several years. A diverse omics-based analysis could lead to a collective characterization and insight on biological questions involving genetic alterations, metabolites, and community composition (reviewed in Cooper and Smith 2015). The decreased cost and increased availability of genomic sequencing should aid in the exploration of genetic material sharing by *E. coli* via horizontal gene transfer; an area with limited exploration beyond what Matsui et al. (2003) reported nearly 20 years ago. Metagenomic approaches can shed light on the identification, classification, and relative abundance of bacteria within assorted biotic mixtures without cultivation and may ultimately uncover unrecognized algal-associated *E. coli* populations. For example, Ling et al. (2020) used 16S rDNA sequencing to fully characterize the bacterial diversity found associated with several understudied micro-algal species. Using a more complex functional metagenomics analysis, Nitschke et al. (2020) established bacterial genera present within phenotypically distinct bacterial-algal communities while elucidating differences in metabolic pathways. Similar approaches could uncover factors influencing *E. coli* survival within the phycosphere. Gene expression approaches (i.e., proteomics, transcriptomics, metabolomics) can inform on the micro-scale activities transpiring between bacteria and algae and can complement microbiome compilations by answering not just the question of which bacteria are present and dominant, but the levels of gene expression and functions of the different bacterial taxa. Such detailed datasets have only begun to be assembled and explored. Krohn-Molt et al. (2017) applied these tools to the microalgal-bacterial microbiome of specific phycosphere biofilms to characterize on a community-level bacterial phylogeny, differential gene expression, and functional relevance of proteins found therein.

On larger scales, satellite remote sensing is a fast-developing resource being used to characterize aquatic habitats. Water quality monitoring programs worldwide conduct routine surveillance to protect human health from toxins produced by HABs and from various pathogens, such as *E. coli, Enterococcus* spp. and *Vibrio* spp. Initially monitored by screening discrete water samples for toxins and/or pathogens, this labor- and time-intensive practice is now routinely being augmented through the use of satellite remote sensing coupled with forecasting models developed using data from long-term monitoring programs. In marine and estuarine waters, optical discrimination of absorption, backscatter, and chlorophyll-*a* anomalies are used to identify dinoflagellate and diatom blooms (Tomlinson et al., 2009; Anderson et al., 2011; Soto et al., 2015; Wolny et al., 2020). In freshwater, cyanobacteria blooms are identified in satellite imagery using a spectral shape algorithm (Wynne et al., 2008, 2010). While pathogenic bacteria cannot be monitored directly, the use of satellite-derived temperature, precipitation, solar radiance, turbidity, wave and wind action, and submarine groundwater discharge data in non-linear models coupled with satellite imagery can help identify areas of degraded water quality likely to support pathogenic bacteria populations (Laureano-Rosario et al., 2019; Schollaert Uz et al., 2019; Cheng et al., 2020). A suite of hyperspectral sensors being designed for deployment on several NASA satellite missions launching after 2022 will provide the increased spectral, temporal, and spatial resolution needed for observing algae, bacteria, and their synergistic effects in global waters (Schollaert Uz et al., 2019; Werdell et al., 2019). Ahead of these missions, research should focus on determining the severity and extent of these algae-bacteria interactions and the most useful predictive models for human and environmental health safeguards, such as those in place for the detection of *Vibrio parahaemolyticus* in Chesapeake Bay (DeLuca et al., 2020), bacteria-laden plume waters on the southern California coast (Nezlin et al., 2008), and *E. coli* and diarrhetic shellfish poisoning toxins produced by various HAB species in the UK's coastal shellfish aquaculture facilities (Schmidt et al., 2018). However, there is less data, and consequently fewer predictive models in development, for *E. coli* in agricultural irrigation waters (Pachepsky et al., 2016) though the need is there since the in situ autonomous monitoring devices currently available are cost prohibitive and not designed for long-term deployments (Andres et al., 2018).

Small unmanned aerial systems (sUAS, or drones) provide new opportunities to estimate algal populations and other water quality parameters in *E. coli* habitats. The high spatial and temporal density of measurements, as well as relative low cost, makes using drones very attractive. Two research avenues are emerging with this technology. One consists of applying machine learning methods and building empirical models to estimate *E. coli* concentrations from imagery (Morgan et al., 2020). Another consists of applying bio-optical algorithms to estimate water quality parameters that affect *E. coli* concentrations, including algal population density and then using models that allows for the prediction of *E. coli* populations from the water quality parameters (Giardino et al., 2015; Pyo et al., 2016).

Mathematical modeling of algal-bacterial interactions remains to be developed. A conceptual model, seen in Fig. 5, was presented by Natrah et al. (2014). To date, this conceptual model has not been converted into a mathematical model for conditions in recreational and agricultural irrigation waters. A model such as this is needed for several reasons. First, the variability of data on *E. coli* die-offs in the literature is massive. A large range in *E. coli* inactivation rates, from 0.2 to 43.6 d^{-1}, has been reported for algal systems. This type of model should help to narrow this range by indicating the major factors and interactions for site-specific conditions. Second, because of the complexity of aquatic ecosystems, changes in algal populations create no single, but simultaneously several, effects on *E. coli* survival. Results of model development are encouraging and thought-provoking. For example, mathematical models showed that a mutualistic situation could occur with the introduction of carbon flow from algae to bacteria, even if algae and bacteria compete with each other for inorganic phosphorus (Yasuaki and Hisao, 2001). Zuñiga et al. (2020) have developed a robust modeling framework that quantifies the metabolic drivers of numerous phototrophs. This should help researchers understand the microbial community structure and function. Modeling algae-bacteria consortiums explains the dynamics of wastewater treatment (Solimeno et al., 2019). However, focused work is needed to address differences in site-specific situations in natural water settings.

The conceptual model in Fig. 5 creates an efficient road map for planning experiments that would elucidate reasons for qualitative and quantitative differences in the survival of different bacteria in the presence of various algae. Such differences were observed, for example, with *E. coli* and *Vibrio cholerae* (Mezrioui et al., 1994) and Enterococci taxa and *C. perfringens* (Al-Tameemi and Kadhim, 2019) in the presence of green algae in the wastewater environment. However, future research should turn attention to natural waters to test the applicability of the conceptual model of Natrah et al. (2014) to cyanobacteria species where there is less certainty about positive or negative algal-bacterial interactions and a growing global concern over cyanobacteria-induced declines in water quality.

4. Conclusions

Interactions of algal populations and AV with *E. coli* occur via a multitude of mechanisms. These mechanisms have been studied and understood to different extents and will be impacted by predicted climate change scenarios.

Algae and AV can provide nutrition and shelter to *E. coli* but can also make water quality unfavorable for *E. coli*. Predicting the site-specific outcome of these trends is the grand challenge for microbial water quality theory and applications.

Interactions of *E. coli* with algae and AV need to be considered on different scales. Scales of interest encompass the range from the molecular scale, where horizontal gene transfer and strain differences are important, to the landscape scale, where monitoring is needed to delineate zones of different favorability for *E. coli*. Similarly, temporal scales of interest span an extensive range that include diurnal oscillations and seasonality.

Research in *E. coli*-algae interactions has a great number of possible directions. The expansion of predictive abilities regarding the fate of *E. coli* appears to be one of the critical success metrics. With many potentially significant predictors and uncertainty in their relative importance, machine-learning methods should have many successful

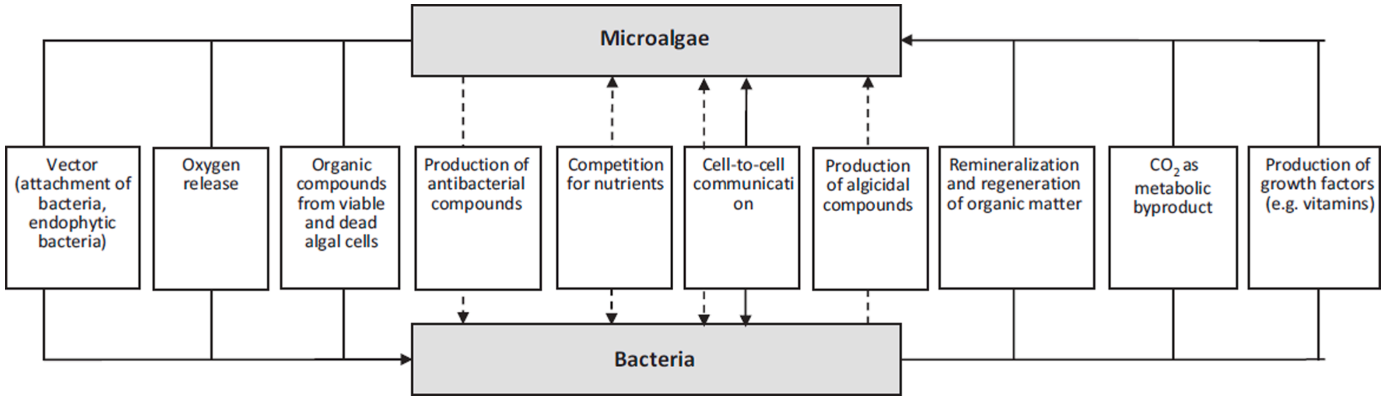

Fig. 5. Conceptual model of interactions that can occur between algae and bacteria (adapted from Natrah et al. 2014). Solid line arrow: positive interaction, leading to bacterial cell survival; dashed line arrow: negative.

applications.

The effect of algae and AV on *E. coli* is a matter of public health in most situations. Progress in this field requires a multidisciplinary effort. The authors hope that this review will facilitate interactions between specialists of different backgrounds working on microbial water quality.

Declaration of Competing Interest

The authors have no competing interests to declare.

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