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Salmonella in the environment: A review on ecology, antimicrobial resistance, seafood contaminations, and human health implications^{*}

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ABSTRACT

Salmonella is a genus of Gram-negative bacteria that is responsible for numerous food poisoning outbreaks worldwide. With 93.8 million food-borne illnesses and 155,000 fatalities annually, it has emerged as a significant global public health issue. There are currently more than 2,500 distinct Salmonella serotypes, and more than half of them are associated with Salmonella enterica. An increasing global public health concern for humans and animals is antimicrobial resistance by Salmonella species worldwide. Salmonella infections can be lethal; conditioned with an increased prevalence of multi-drug resistant (MDR) strains in the future. The emergence of MDR Salmonella serotypes is considerably impacting the efficacy of antibiotic treatments. There is a potential association between Salmonella growth and proliferation with different environmental factors such as temperature, precipitation, pollution, nutrient availability, and other climate change-induced phenomena. Seafood and shellfish are common vectors for salmonellosis in humans and other animals and are responsible for food poisoning-related deaths every year. Effective food hygiene, water sanitation, and limiting the use of antibiotics in food animals must be upheld to reduce Salmonella infections. This article provides an overview of pathogenesis, epidemiology, antibiotic resistance, seafood contamination, and environmental factors affecting Salmonella proliferation, in addition to providing an outline of Salmonella infection.

Introduction

Salmonella stands out as the predominant microorganism among numerous foodborne pathogens, contributing to a significant number of fatalities worldwide (Eng et al., 2015; de Melo et al., 2021). Food-borne illnesses are one of the many potential sources of diseases that represent a significant risk to human health across the world. A recent survey claims that 420,000 people die yearly, and 1 in 10 individuals get sick after eating food contaminated with pathogens (Soubeiga et al., 2022). Among the most prevalent food-borne microorganisms that cause zoonotic infections in aquatic and terrestrial animals including humans, one of the most common isolates is Salmonella (Coburn et al., 2007; Eng et al., 2015; Jajere, 2019; Ehuwa et al., 2021). Salmonella infection is a significant public health concern worldwide along with financial strain due to the expenses of disease prevention, and treatment (Crump et al., 2004; Helms et al., 2005; Mkangara, 2023). The phenomenon of *Salmonella* contamination in food or water causes salmonellosis, resulting from consuming contaminated foods (Gonçalves-Tenório et al., 2018).

Salmonella is a Gram-negative, facultatively anaerobic, nonsporulating, rod-shaped bacterium that belongs to the family *Enterobacteriaceae* (Agbaje et al., 2011; Waldman et al., 2020). They are mesophilic and can grow within 5 to 46 °C with an optimal growth temperature between 35 and 37 °C (Keerthirathne et al., 2016). They cannot multiply at an Aw (water activity) of 0.94, especially when combined with a pH of 5.5 or lower and are less tolerant to pH 4.5 or below (Bibek, 2001; Keerthirathne 2016; Gautam et al., 2020). The cells

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Abbreviations: AMR, antimicrobial resistance; ATR, acid tolerance response; CDC, Centers for Disease Control and Prevention; GI, gastrointestinal; IPCC, Intergovernmental Panel on Climate Change; MDR, multi-drug resistant; NARMS, National Antimicrobial Resistance Monitoring System; NTS, non-typhoidal Salmonella; RES, reticuloendothelial system; RTE, ready-to-eat; SCV, Salmonella containing vacuole; SPIs, Salmonella pathogenicity islands; T3SS, type III protein secretion system.

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of this bacteria can multiply in numerous foods and endure being frozen or dried for an extended period without losing their ability to be pathogenic. Additionally, evidence suggests that *Salmonella* can even survive in environments with excessive salt (Petrin et al., 2022).

Salmonella can be divided into typhoidal and nontyphoidal (NTS) serovars. There are two typhoidal serovars: Salmonella Typhi and Salmonella Paratyphi A. (Johnson et al., 2018) causing typhoid and paratyphoid fever, respectively. In addition, these infectious disorders can cause neurological symptoms, leukopenia, septicemia, and immunological signs. These complications can sometimes lead to deaths in severe cases (Majowicz et al., 2010; Andino and Hanning, 2015; Chong et al., 2017). Typhimurium and Enteritidis are two non-typhoidal Salmonella (NTS) serovars that have a wide range of host specificity while some serovars use humans as their exclusive niche like Sendai, Typhi, Paratyphi (A, B, or C). NTS can induce mild to severe gastroenteritis (e. g., vomiting, diarrhea, nausea, etc.) or rare bacteremia (i.e., dissemination of infection in the body) (Andino and Hanning, 2015). Mainly there are three distinct clinical manifestations of salmonellosis: gastroenteritis, septicemia, and enteric fevers (Crump et al., 2015).

Environmental factors alterations due to climate change impact the spread and survivalism of zoonotic pathogens and exert an influence on more than half of all infectious diseases (Morgado et al., 2021; Mora et al., 2022; Dietrich et al., 2023). The development of the genus Salmonella, a zoonotic agent, is influenced by the ambient temperature at different stages in the food chain. Among different food sources, ready-to-eat seafood is an important one in Salmonella outbreak in the United States (Ehuwa et al., 2021). Recently, Billah and Rahman (2021) demonstrated a correlation between higher temperatures and the proliferation of Escherichia coli in the American oyster, an important seafood, in a laboratory study. Salmonella also multiplies faster at higher temperatures and this correlation between the Salmonella outbreaks and the outdoor temperature has been known for some time (Akil et al., 2014; Zhang et al., 2018). Besides, precipitation, humidity, soil properties, and pH are influential in the spread, reproduction, and survival of Salmonella (Dieterich et al., 2018; Robinson et al., 2022). According to a recent report, mean global warming will be increased from 1.5 to 5.8 °C and a rise in the mean global precipitation has been predicted from 5 to 15 % by the end of the century (Duchenne-Moutien and Neetoo, 2021). Therefore, it is indispensable to learn the impact of climate change and pathogen survivalism on food safety, health risks, and vulnerabilities of food systems. This comprehensive review is primarily focused on exploring Salmonella as a significant foodborne pathogen, with special emphasis on its incidence in seafood. The review also delved into the critical issues of antibiotic resistance in Salmonella strains and explored the impact of global climate change, especially temperature rise on the proliferation of this bacterium. Furthermore, the review offers an extensive and pertinent background encompassing the nomenclature, classification, epidemiology, and pathogenesis of Salmonella to provide a comprehensive reference point for researchers, public health professionals, and policy makers.

Methodology

A literature review was carried out utilizing a variety of online resources (e.g., Google Scholar, PubMed, Springer Nature, Science Direct, Taylor & Francis, and John Wiley) to provide the recent existing information regarding our chosen topics on *Salmonella* to prepare a comprehensive and updated review article. The keywords used were mainly *Salmonella*, environmental factors, antimicrobial resistance, fish, and shellfish. In addition, the contents and citations in scholarly journals ratify the excellence of the selected literatures for the article. In our study, we used immunohistological method to show the expression of *Salmonella* in the gills of oysters collected from field sites (e.g., polluted sites) and experimental study (i.e., oysters were exposed to 24, 28, and 32 °C according to the method described by Billah and Rahman (2021) using highly specific anti-mouse *Salmonella* primary antibody according to the method described by Morrison et al. (2012), Rieger et al. (2015), and Billah and Rahman (2021).

Nomenclature and classification

Salmonella nomenclature has been a source of scientific controversy among bacteriologists until recently because the genus's original classification was not based on DNA relatedness, but on clinical considerations (Brenner et al., 2000; Todar, 2006). Theobald Smith first discovered and isolated Salmonella for the first time from the classical swine fever-infected intestines of pigs in 1855, and the bacterial strain was named after Dr. Daniel Elmer Salmon (Schultz, 2008; Eng et al., 2015). The classification of Salmonella strains has evolved afterward (Euzéby, 1999).

The phylogeny of bacteria can also be used to classify them by comparing 16S rRNA or other gene sequences and constructing a phylogenetic tree. Based on 16S rRNA sequence analysis, the genus Salmonella has been classified into two species, Salmonella enterica (2443 serotypes) and Salmonella bongori (20 serotypes). The World Health Organization (WHO) Collaborating Centre, Centers for Disease Control and Prevention (Centers for Disease Control and Prevention (CDC) 2023), and other organizations are currently using this system (Popoff et al., 2003). Six additional subspecies of S. enterica have been identified based on genetic similarities and biochemical characteristics, including, S. enterica subsp. enterica, S. enterica subsp. salamae, S. enterica subsp. arizonae, S. enterica subsp. diarizonae, S. enterica subsp. Houtenae and S. enterica subsp. Indica (Andino and Hanning, 2015). Notably, more than 2500 serovars, considered potential pathogens for both animals and humans, reflect the antigenic diversity caused by variations in flagellar and lipopolysaccharide architecture (Wan Norhana et al., 2010; Ibrahim and Morin, 2018).

Epidemiology of Salmonella

Every year *Salmonella* causes approximately 200 million to over 1 billion infections globally. This includes 93 million cases of gastroenteritis and 155,000 deaths. Shockingly, 85 % of these illnesses are exclusively related to contaminated food (He et al., 2023). Moreover, domestic food poisoning with salmonellosis accounts for 11 % of infectious cases in the United States, 35 % hospitalization, and 28 % death (Scallan et al., 2011; CDC, 2023).

Only five serotypes: Salmonella Enteritidis, S. Typhimurium, Salmonella Infantis, Salmonella Newport, and Salmonella Heidelberg are responsible for 74 % of the 87,923 verified human cases identified in 2019 (EFSA and ECDC, 2019). The most prevalent species of Salmonella is S. enterica, which contains roughly 1500 serotypes, and is responsible for 99 % of human and other warm-blooded animal infections (Park et al., 2009; Guibourdenche et al., 2010). Enteric infections caused an estimated 4.5 billion episodes and 1.7 million fatalities (22 deaths per 100,000) worldwide in 2016 (Troeger et al., 2018). On the other hand, S. Enteritidis and S. Typhimurium are the two most frequent non-typhoid serotypes causing human salmonellosis, among more than 200 serotypes that have been discovered as capable agents of causing disease in humans (Greig and Ravel, 2009; Xu et al., 2021; Xue et al., 2021). The primary cause of bacterial enteritis in humans is non-typhoidal Salmonella (NTS), which accounts for 93.8 million cases of gastroenteritis worldwide (Ngogo et al., 2020), the second most prevalent causative agent of salmonellosis (after Norovirus) from food poisoning (Todd, 2014, 2020). NTS is also very common in Sub-Saharan Africa, and they are linked to a 20-25 % case fatality rate in children and adults (Feasey et al., 2012). Besides, a recent multistate outbreak of Salmonella Paratyphi B and Salmonella weltevreden involving 11 states, 65 patients, and 11 hospitalizations was reported in the United States in 2015 (Hassan et al., 2019). Despite the continued high burden of enteric infections, significant reductions, particularly in mortality, have been achieved recently (Troeger et al., 2018; Foreman et al., 2018) though

overall *Salmonella* outbreaks have not shown any remarkable downturn in the last decades. In addition, anti-microbial resistant (AMR) *Salmonella* spp. has been evolved as a formidable global health concern. The estimated yearly death toll from AMR *Salmonella* is currently 700,000; by 2050, it is anticipated to increase to 10 million, resulting in a \$100 trillion economic loss (Balbin et al., 2020). In the United States alone, AMR affects 2 million people each year, and as a result, 23,000 people die annually as a consequence (Dadgostar, 2019). Recently, Medalla et al. (2021) reported that an estimated yearly occurrence of 1200,000 illnesses is linked to NTS, with at least 100,000 infections being caused by antibiotic-resistant *Salmonella*. The additional healthcare costs associated with the anti-microbial resistant *Salmonella*-derived illnesses is \$20 billion, and the US economy suffers a \$35 billion productivity loss (Weiner et al., 2016).

Salmonella as a food-borne pathogen

One in six citizens in the United States is prone to being infected with food-borne pathogens (Scallan et al., 2011). Salmonella is a vital microorganism responsible for food-borne diseases, and non-typhoidal Salmonella spp. are more prevalent food-associated pathogens (Martinez-Urtaza et al., 2003). Salmonella is mostly present in food items derived from animals, with a particular emphasis on uncooked chicken, raw meat, eggs, and their byproducts, and act as major sources of human salmonellosis (Silva et al., 2011; Carstens et al., 2019), with almost 6 % of all cases linked to pig and/or pork products in the USA (Trinetta et al., 2020). Slaughtering food animals at slaughterhouses is another common source of Salmonella contamination from organs and carcasses and slaughter houses contribute to about 12 % of Salmonella infections (Gillespie et al., 2005; Akil and Ahmad, 2019). In a research investigation examining the prevalence of Salmonella within poultry company-associated slaughterhouses in Europe (EFSA, and ECDP, 2019), it was observed that among the many batches that were sampled, a significant number of fecal samples, specifically 69.4 % (25 out of 36), demonstrated evidence of Salmonella shedding. Additionally, Salmonella contamination was detected in 46.3 % (100 out of 216) of the carcass samples, encompassing the neck skin and internal cavity (Marin et al., 2022). Salmonella can also be transmitted through vegetables and fresh fruits contaminated by animal microflora (Pui et al., 2011; Wu et al., 2015; Jajere, 2019; Carstens et al., 2019). Fresh foods such as spinach, herbs, and leafy greens, are commonly contaminated with coliform bacteria. In a recent study, Salmonella was found in 0.3 % of the 360 fresh produce samples, comprising 129 imported and 231 locally grown samples, while 0.8 % of the fresh fruit was imported to the United States (Liu and Kilonzo-Nthenge, 2017). Salmonellosis is a more common phenomenon in developed and developing countries, caused by eating contaminated meat, fruits, and vegetables (Carstens et al., 2019). Salmonella is also very pervasive in marine ecosystems and resident animals. The occurrence of Salmonella spp. in marine organisms, especially in seafood, mostly arises from terrestrial pollution sources originating from human activities and animals (Billah and Rahman, 2021).

Seafood is a highly nutritional food source but can also come with potential hazards, particularly those related to microbial contamination. A number of outbreaks of *Salmonella* have been linked to seafood in the United States, Europe, and other countries (FDA 2007; EFSA and ECDP, 2019; Popa and Popa, 2021; Porto et al., 2022) especially when consumed raw (Chakroun et al., 2021). *Salmonella* has been found in a wide range of fish and shellfish species such as crabs, clams, lobsters, mussels, scallops, shrimps, oysters, etc. While most types of fish and shellfish are eaten fried, baked, or steamed, some species are ready-to-eat (RTE) and consumed raw (Heinitz et al., 2000; Brands et al., 2019). Fish and shellfish can acquire *Salmonella*, and other pathogens from contaminated waters, or during processing and storage (Panisello et al., 2000; Prabhakar et al., 2020; Atwill and Jeamsripong, 2021; Billah and Rahman, 2021).

Incidence of Salmonella in seafood

Salmonella is not a native aquatic environment resident, however, multiple Salmonella serovars are widely distributed in waters (e.g., sea, estuarine, and river) and seafood such as mollusks, shrimp, clams, and different fish species showing the highest prevalence (de Abreu Correa et al., 2007; Kumar et al., 2015; Novoslavskij et al., 2016; Liu et al., 2018). Salmonella is a more common filter-feeding organism because it filters water throughout its life cycle, which causes the pathogen to build up in its tissues (Kumar et al., 2009; Billah and Rahman, 2021). For example wild-caught American oyster (also called Eastern oyster, Atlantic oyster, or Virginia oyster; Crassostrea virginica), has been shown to include foodborne pathogens such as Salmonella, and E. coli (Todd, 2014; Billah and Rahman, 2021). Salmonella was found in 7.4 % of the ovsters taken from American bays, with S. newport being the predominant serovar (Brands et al., 2005). Salmonella contamination of seafood can frequently occur from contaminated coastal areas and contaminated surroundings where fish is handled, even though environmental conditions and human activities can largely affect the incidence of Salmonella in seafood (Martinez-Urtaza et al., 2003; Ehuwa et al., 2021). For example, a high intensity of Salmonella was found in the gills of American ovsters collected from polluted sites in the southern Gulf of Mexico (Fig. 1). Because of improper sanitation practices and human and animal waste disposal, Salmonella can potentially pollute water sources (Amagliani et al., 2012; Pandey et al., 2014; Mkangara, 2023). Salmonella can live for extended periods, months, or even years if they enter the soil and aquatic ambiance, which facilitate their entrance into new hosts (Winfield and Groisman, 2003; Waldner et al., 2012). Salmonella contamination can come from various sources, ranging from diseased animal flesh to polluted water (Majowicz et al., 2010).

Because of its nutritional content, which includes high-quality protein, omega-3 fatty acids, vital vitamins, and minerals, shellfish is regarded by consumers all over the world as a healthy dietary component (Venugopal and Gopakumar, 2017; Billah and Rahman, 2021). Simultaneously, shellfish are potential hosts of viral and bacterial pathogens (Beuret et al., 2003; Rincé et al., 2018), and Salmonella species are prevalent in shellfish harvested and consumed raw in many countries in the world including the United States (Hamilton et al., 2018; Billah and Rahman, 2021). Since the 1980s, there has been a sharp increase in the prevalence of Salmonella infections, which results in an annual productivity loss of millions of dollars, and many cases have been connected to eating seafood, especially shellfish (Heinitz et al., 2000; Khan et al., 2009; Kumar et al., 2015; Elbashir et al., 2018; Atwill and Jeamsripong, 2021). In shellfish fisheries in the United States, the presence of fecal coliform was assessed to determine the risk of exposure to pathogens through shellfish consumption, and a notable amount of Salmonella was found in the mollusks (FDA, 2007). A significant amount of Salmonella has been found in live oysters gathered from water bodies where shellfish harvesting is allowed in the United States which is a matter of concern (Brands et al., 2005; DePaola et al., 2010). Oysters are important shellfish species that ingest and concentrate particle debris from water during filter feeding including harmful bacteria and viruses (Martinez-Urtaza et al., 2003). The accumulation of pathogenic bacteria and viruses within the oysters makes them hazardous for human consumption.

In United States market surveys, 7.4 to 8.6 % of raw, market-ready oysters tested positive for *Salmonella*, with infection rates as high as 77 % locally (Cox et al., 2015). In another study, *S. enterica* serovars from six different species were discovered in the oysters from U.S. restaurants, indicating multiple instances of *Salmonella* contamination of American oyster supplies. Notably, 12 (43 %) of the 28 infected oysters reported the presence of *S. enterica* serovar Newport strain (Brillhart and Joens, 2011). *S.* Typhimurium has been reported to have a larger concentration in Pacific oysters (*Crassostrea gigas*) than bacteria in a healthy state, even after thirty days of infection (Chakroun et al., 2021). The presence of pathogenic bacteria like *E. coli* and *Salmonella* in the oyster

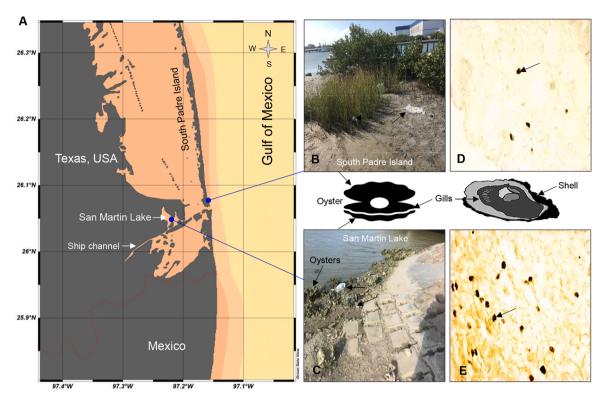


Fig. 1. Oyster collection sites on the southern Texas coast. (A) Gulf of Mexico, a marginal sea basin largely surrounded by the North American continent (modified from Billah and Rahman, 2021), (B) Sampling sites at South Padre Island (location: 26°04'30"N, 97°09'59"W), and (C) San Martine Lake (location: 26°00'10"N, 97°17'56"W) with pictures. (B, C) Arrows indicate source of pollutions (e.g., plastics, containers, bottles, etc.). Blue dots indicate sampling sites. (D, E) Immunohistological detection of representative photographs of gills in oysters collected from South Padre Island (D) and San Martine Lake (E). Expression of *Salmonella* in gills of oysters determined by immunohistochemical analysis using anti-mouse *Salmonella* primary antibody according to the method described by Morrison et al. (2012), Rieger et al. (2015), and Billah (2020). Arrows indicate colonies of *Salmonella*. Magnification = 10X.

habitat is assumed to be a reason for the higher bacterial contamination of oysters (Billah and Rahman, 2021). For instance, *Salmonella* with the highest virulence and antibiotic resistance were found to be present in saltwater microcosms after a year, which may have an impact on the occurrence of *Salmonella* in seafood such as oysters (Chandran and Hatha, 2005). Runoff from agricultural crops may potentially contribute to the summertime increase in *Salmonella* contamination, as most crops are irrigated with recycled water, which may include *Salmonella* and other fecal contamination (Harris et al., 2018).

Environmental conditions like elevated temperatures due to climate change have been found to modulate the pathogen count in seafood species (Billah and Rahman, 2021). The temperature of the water may play a role in the differences in *Salmonella* isolation between summer and winter, with colder waters lowering bacterial presence and warmer waters potentially promoting bacterial survival (Flores Monter et al., 2021). This is supported by recent reports that showed fecal coliform and *Salmonella* spp. contamination levels vary between the summer and winter in fish and shellfish species. *Salmonella*'s movement, fate, growth, and multiplication in the environment can be influenced by several elements, such as temperature, pH, soil moisture, nutrients, microbial competition, water activity of food matrix, and contact surface (Erickson et al., 2014; Alegbeleye et al., 2018; Trinetta et al., 2020; Roy et al., 2021).

Pathogenesis of Salmonella

Many pathogenic bacteria infect large domains of host organisms and *Salmonella* spp. is no exception in this regard (Hernández-Reyes and Schikora, 2013). The intensity of salmonellosis in humans depends on the serotype and immune status of the respective host. Compared to healthy individuals, young children, and older people with weak immune defense systems are highly vulnerable to *Salmonella* (Coburn et al., 2007; Kurtz et al., 2017). *Salmonella* is highly pathogenic and can cause potentially fatal diseases because of its probable capacity to penetrate, multiply, and survive in human host cells. *Salmonella* invades non-phagocytic human host cells by inducing its phagocytic host cells to get easy access (Hansen-Wester et al., 2002).

The Salmonella pathogenicity islands are virulence gene clusters responsible for invasion, survival, and extraintestinal transmission. They are considered "quantum leaps" in bacterial evolution (i.e., Salmonella pathogenicity islands, SPIs). These gene collections are situated in chromosomal DNA regions that encode for determinants required in the invasion phase and are assumed to be acquired by horizontal gene transfer (Eswarappa et al., 2008; Grassl and Finlay, 2008; Siriken, 2013). Salmonella penetrates the intestinal epithelium during host infections and causes gastrointestinal disease when contaminated food or drink is consumed (Fàbrega and Vila, 2013; Dieterich et al., 2018). Salmonella pathogenicity island-1 (SPI-1) encodes the type III protein secretion system (T3SS), which produces the effector proteins needed for intestinal invasion and the development of enteritis (Lou et al., 2019; Azimi et al., 2020). The ability of Salmonella to modulate actin cytoskeletons of nonphagocytic cells is key to its pathogenicity. It is caused by the coordinated actions of several bacterial effector proteins that alternately stimulate and down-regulate host cell responses (Alto and Orth, 2012; Galán and Zhou, 2000). Intracellular pathogens have two options for surviving: either reside in the host cell's cytoplasm or create a self-contained vacuole. In order to become pathogenic or virulent, Salmonella typically creates an intracellular vacuole known as Salmonella containing vacuole (SCV) (Garai et al., 2012; Castanheira and Garcia-del Portillo, 2017). After entering the host cell, Salmonella manipulates inflammatory pathways and autophagy processes. Salmonella also evades the adaptive immune system through its interactions with dendritic

cells, and T and B lymphocytes (Bernal-Bayard and Ramos-Morales, 2018). Upon detecting *Salmonella* as a foreign body, the host cell's immune response would secrete the lysosomes and enzymes responsible for bacterial degradation (Sachdeva and Sundaramurthy, 2020). However, the remodeled vacuole prevents the lysosomes from fusing, allowing the bacteria to survive and replicate within the host cells. The bacteria's capacity to thrive Inside macrophages permits them to go through the reticuloendothelial system (RES) (Behnsen et al., 2015).

Salmonella as an antibiotic-resistant bacterium

The upsurge of antibiotic-resistant bacteria is a rapidly growing global public health concern as antibiotic-resistant pathogens are insensitive to clinically significant antibiotics (Esperón et al., 2018; Chaudhari et al., 2023). Antimicrobial resistance (AMR) in Salmonella has been emerging as a severe health problem worldwide, and a remarkable increase in antibiotic resistance among non-typhoidal Salmonella has been elevated in recent times (Chiu et al., 2002; Haeusler and Curtis, 2013; Bell et al., 2014; Higgins et al., 2020; Marchello et al., 2020) Antibiotics including ampicillin, chloramphenicol, trimethoprim-sulfamethoxazole, and other types are typically used as first-line treatments for salmonellosis (Marchello et al., 2020). Early in the 1960s, the first instance of Salmonella resistance to a single antibiotic, chloramphenicol, was documented (Montville and Matthews, 2008). Since then, there has been an upsurge in the isolation of Salmonella strains that are resistant to one or more antimicrobial treatments in many countries, including the United States, the United Kingdom, and Saudi Arabia (Yoke-Kqueen et al., 2008).

A significant number of drug-resistant Salmonella outbreaks in the United States have been found linked to food poisoning. For instance, an intermediate tetracycline and streptomycin-resistant Salmonella serovar called Salmonella Urbana was discovered in 2017 spreading through papayas (Nair et al., 2018). There was an outbreak in 2015 of the serovar Salmonella Poona, isolated from ready-to-eat shrimp, and the isolates were nalidixic acid- or tetracycline-resistant (Nair et al., 2018). In 2018–2019, an outbreak of multidrug-resistant Salmonella Heidelberg, S. Typhimurium, and Salmonella Hadar took place in the United States via contaminated ground turkey, beef, and turkey burgers (Hassan et al., 2018, 2019). In 2014, there was a Salmonella Heidelberg outbreak linked to mechanically separated chicken, and 67 % of isolates were antibiotic-resistant across various classes (Punchihewage-Don et al., 2022). In a study conducted by Elhadi (2014) from Saudi Arabia, the Salmonella species isolated from seafood exhibited the highest levels of antibiotic resistance to amoxicillin-clavulanic acid (45 %), ampicillin (70 %) and tetracycline (90.71 %). Meanwhile, in a report by Rahimi et al. (2013) in Iran found a predominant resistance rate of 47.4 % of Salmonella isolates to nalidixic acid.

The rise of antibiotic-resistant foodborne pathogens has sparked public concern, as these diseases are more virulent, resulting in a higher fatality rate among infected individuals. The extensive use of antibiotics in intensive aquaculture practices increases the emergence of antimicrobial-resistant (AMR) *Salmonella* in the aquatic ecosystem as well. For instance, in a 12-month study across 32 aquaculture farms in Malaysian states, *Salmonella* showed high resistance to antibiotics like ampicillin and streptomycin. In this study, *Salmonella* showed a resistance rate of 20 % to vitally essential human therapeutic antibiotics such

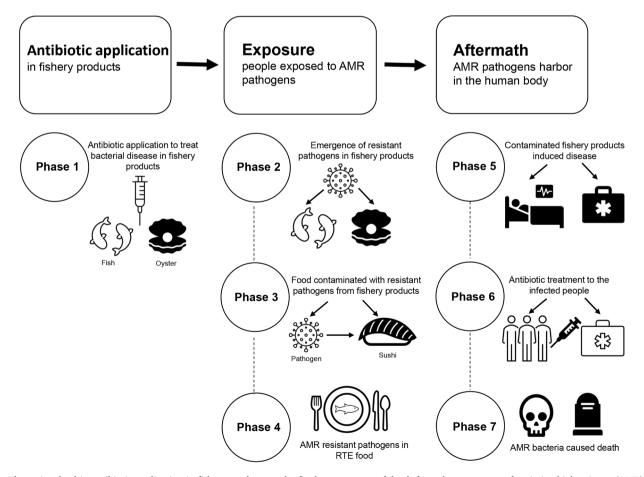


Fig. 2. Phases involved in antibiotic application in fishery products to the final consequence of death from the emergence of antimicrobial resistant (AMR) pathogens. Phase 1: Application of antibiotics in fishery farms to treat pathogens. Phase 2–4: Exposure of AMR to human beings through fish/shellfish or ready-to-eat (RTE) food. Phase 5–7: Aftermath of AMR pathogens accumulation in the human body.

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as Colistin. Moreover, multi-drug resistant (MDR) Salmonella in tilapia demonstrated a high MDR level of 77.8 %. This underscores the growing public health challenge of antibiotic-resistant Salmonella occurring from seafood and aquaculture (Dewi et al., 2022). Fig. 2 represents a schematic pathway of antibiotic application in fishery farms and its final consequence for human beings. Marine and estuarine environments are frequently affected by antibiotic-resistant Salmonella contamination that severely impacts human health. Ampicillin, amoxicillin, and chloramphenicol-resistant Salmonella strains were previously isolated from marine environment (Chahouri et al., 2022). Seafood is frequently referred to as a means of spreading bacteria resistant to antibiotics (Feldhusen, 2000; Brands et al., 2005), and more than 80 % of the seafood consumed in the United States is imported (Elbashir et al., 2018). In addition, a significant number of dengue fever (7%), malaria outbreaks (6 %), and diarrhea outbreaks (2.4 %) in industrial countries worldwide are caused by climate change (Campbell-Lendrum et al., 2015). Moreover, climate change-related deaths accounted for 0.3 % of all deaths, while illness burden accounted for 0.4 % (Kendrovski and Gjorgjev, 2012).

Effects of environmental factors on *Salmonella* growth and proliferation

Temperature

Environmental factors such as high temperatures or heat waves significantly impact the emergence of many infectious diseases (Mills et al., 2010; Kumar et al., 2015). According to estimates, the impact of climate change is responsible for 4.6 % of all risks and diseases originating from the environment (Kendrovski and Gjorgjev, 2012). Salmonella grows best at temperatures between 35 and 37 °C, though at <15 °C, growth is substantially reduced (Juneja et al., 2007; Zhang et al., 2010). High temperatures can affect the spread of infectious diseases, especially for heat-sensitive bacteria like Salmonella (Robinson et al., 2022). Warmer temperatures facilitate faster reproduction of Salmonella; hence increase in ambient temperature is positively correlated with gastrointestinal infections caused by bacterial pathogens (Akil et al., 2014). The rate of Salmonella cases has been found positively and linearly related to the average temperature of the previous week or month, with the rate peaking in the summer each year (Bentham and Langford, 2001; Russell et al., 2010).

Robust linear relationships between temperature and salmonellosis

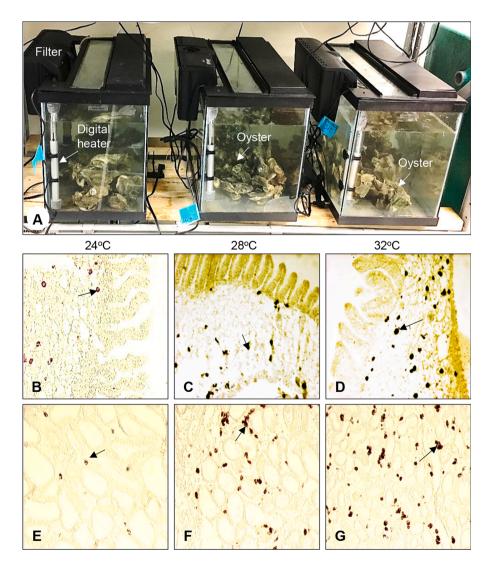


Fig. 3. (A) Experimental setup and heat-exposure experiment for laboratory study in oysters described previously by Billah and Rahman (2021). (B-G) Effects of one-week heat exposure (B: 24 °C, C: 28 °C, and D: 32 °C) on expression of *Salmonella* in gills (B-D) and digestive glands (E-G) of oysters determined by immunohistochemical analysis using anti-mouse *Salmonella* primary antibody according to the method described by Morrison et al. (2012), Rieger et al. (2015), and Billah (2020). Arrows indicate colony of *Salmonella*. Magnification = 10X.

occurrence have been observed in Australia and European countries, with a seasonal relationship for Campylobacter (McMichael et al., 2006). The implications of climatic variation on Salmonella infections in Mississippi were investigated in a prior study. Results indicated that elevated temperatures are linked to the Salmonella outbreak. This study also found a seasonal tendency, with the largest outbreaks occurring in the summer and early fall (Akil et al., 2014). Recent findings from Asia, Australia, Europe, and North America with similar trends showing a positive relationship between temperature and Salmonella infections are similar to those found in this study using regression and neural networks (D'Souza et al., 2008; Taylor et al., 2010; Zhang et al., 2010; Akil et al., 2014; Robinson et al., 2022). Because Salmonella grows better at higher temperatures, there is a higher concentration of Salmonella in seafood during the summer months. In a recent study, we observed that Salmonella count was consistently increased in the gills and digestive glands of wild-caught oysters exposed to high temperatures (28 °C and 32 °C) (Fig. 3). Similarly, a member of Enterobacteriaceae and facultative anaerobe, E. coli, showed a similar trend of proliferation in oyster tissues under high temperatures (Billah and Rahman, 2021). Elevated temperatures have the potential to impact the dissemination of Salmonella in a range of ways, including direct and indirect effects on bacterial multiplication along with seasonal eating behaviors (Keerthirathne et al., 2016). For example, seasonal variations in eating habits can be seen in the increased consumption of leafy green vegetables during the warmer months, which is a leading cause of salmonellosis (Liu et al., 2018). After accounting for seasonal and long-term patterns, the frequency of enteric bacterial illnesses usually rises along with the weekly temperature (Fleury et al., 2006). The number of cases could increase by 8.8 % with a 1 °C increase in the mean weekly maximum temperature, while the number of cases could increase by 5.8 % with a 1 $^\circ C$ increase in the mean weekly minimum temperature (Zhang et al., 2010).

Salmonella growth is influenced by the ambient temperature at several points in food processing, including the bacterial burden in raw foods, manufacturing, and transportation practices, and storage conditions. The proliferation of Salmonella and Vibrio cholerae is heavily influenced by ambient climatic conditions, as they multiply quickly at warmer temperatures: *V. cholerae* in water and Salmonella in food and animal guts (Akil et al., 2014). It is believed that, within certain bounds, ambient temperature favorably influences the survival and spread of specific intestinal diseases (Fleury et al., 2006). Furthermore, it was discovered that enteric diseases had a seasonal pattern in temperate latitudes, with the maximum prevalence of illnesses occurring during summer (Dietrich et al., 2023).

Consequently, recent studies empirically predict that salmonellosis rates will likely rise in the future because temperatures are expected to rise above historical norms due to climate change, contributing to an additional 1000 cases per year. By 2050, this will equate to an increase of approximately 1200 lost workdays per year and an estimated \$120,000 will be spent on health care and surveillance (Bambrick et al., 2008; Akil et al., 2014).

Precipitation

Rainfall patterns may affect the survival and movement of environmental *Salmonella*, which in turn may impact the spread of the disease (Lee et al., 2019; Robinson et al., 2022). Numerous studies have found that precipitation and temperature have an impact on patterns of enteric disease occurrence (Carlton et al., 2016; Levy et al., 2016; Stephen and Barnett, 2016). According to other studies, temperature extremity, rainfall, and relative humidity were all positively related to the frequency of *Salmonella* cases. Notably in Canada and the United States, outbreaks of water-borne diseases have been connected to periods of intense rainfall (Curriero et al., 2001; Rose et al., 2001; Cann et al., 2013; Jiang et al., 2015). Studies using daily or weekly precipitation rates found a better correlation with *Salmonella* outbreaks (Akil et al., 2014). In addition, 2–4-week lags between a high temperature or heavy precipitation event increase in salmonellosis (D'Souza et al., 2008; Zhang et al., 2010). Moreover, extreme rainfall was associated with substantially increased salmonellosis (5 %) compared with no excessive rainfall. In addition, salmonellosis risk was also found notably increased (13 %) in moderate rainfall compared with antecedent dry periods (Jiang et al., 2015; Lee et al., 2019). Along with precipitation, the quality of drinking water has also been linked to gastroenteritis (Zhang et al., 2010; Wolkoff et al., 2021).

Nutrient availability

The growth and virulence of pathogens, the development of the illness, and the disease progression all depend on the pathogen's ability to access host nutrients in infected tissues (Steeb et al., 2013). The nutritional composition of the growth medium significantly affects DNA, proteins, lipid and carbohydrate content, cellular forms and structure, transcriptome, and phenotype of Salmonella (Galdiereo et al., 1994; Blair et al., 2013). A previous study shows that cultivation in minimal media inhibits S. Typhimurium's capacity to penetrate epithelial cells in an SPI-1 (Salmonella Pathogenicity Island-1) and SPI-2 (Salmonella Pathogenicity Island-2) independent way. This study suggests that nutritional deficiency can reduce the pathogenicity of *S*. Typhimurium (Sridhar and Steele-Mortimer, 2016). In an in vivo model, S. Typhimurium growth in minimum media did not significantly affect intestinal pathogen loads, inflammation, or pathogen transfer in humans (Yurist-Doutsch et al., 2016). However, S. Typhimurium can be affected by nutrient deficiency in different ways. Starvation-induced selective pressure can result in genetic heterogeneity in the pathogen population and chromosomal gene duplication (Sonti and Roth, 1989). Furthermore, malnutrition has been demonstrated to promote acid tolerance in some enterobacteria which can be a leading cause of in vivo virulence (Antunes et al., 2011). Findings from previous studies indicate that prior to infection, short-term fasting has little effect on S. Typhimurium's potential to induce gastrointestinal and systemic illness. In comparison to S. Typhimurium cultured in rich media, S. Typhimurium cultured in minimal media resulted in a different post-infection GI microbiota composition, including an increase in Bacteroidetes species and a decrease in Enterobacteriaceae microbiota members (Singh et al., 2015), and consequently, in relation to this finding, it is believed that rich media-cultured S. Typhimurium is a better model for human disease (Yurist-Doutsch et al., 2016).

The processes behind GI microbiota compositional alterations caused by minimal versus rich media-grown pathogens are still unknown. Conventional colitis symptoms, such as the amount of pro-inflammatory cytokines in the gut, may not change depending on the type of infection present, the host's reaction to the infection may vary, and the GI microbiota may be affected differently. Alternately, metabolic alterations in S. Typhimurium that occur during cultivation in different media may alter the composition of the microbiota through direct bacterial interactions. The metabolic profiles of various organisms have been shown to change when grown in a minimal versus rich medium (Saito et al., 2010), in turn, a pathogen's interaction with the GI microbiota may be influenced by the pathogen's metabolic state. Increases in the availability of external nutrients speed up intracellular Salmonella's growth, which is dependent on the bacteria's capacity to use particular nutrients (Steeb et al., 2013). For instance, S. Typhimurium is shown to be an unusually virulent pathogen that can overcome nutritional limitation and virulence gene inhibition to successfully colonize the host using restricted media cultivation as a model of infection originating from fecal contamination or water-borne disease. Additionally, decreased invasion in human epithelial cells due to this environment causes significant alterations in the bacterium's genetic program and influences its ability to affect the makeup of the host microbiota (Sridhar and Steele-Mortimer, 2016; Yurist-Doutsch et al., 2016).

pH

In bacterial cells, biological and physiological processes can be regulated by both internal and external pH (Lund et al., 2020), and viability loss may result from adverse pH conditions (Choi and Groisman, 2016). Surprisingly, Salmonella has strategies for adapting to low pH conditions and maintaining pH homeostasis (Krulwich et al., 2011; Keerthirathne et al., 2019). Salmonella can lessen membrane proton conductance and proton extrusion, which also protects the cell from acid stress. The acid tolerance response (ATR) is the mechanism by which S. Typhimurium detects an acidic environment and adjusts to endure at low pH (Ryan et al., 2015). The ATR protects Salmonella spp. at pH values between 3 and 4, but it becomes active at pH values between 5.5 and 6 in the environment and when pH homeostasis is disrupted. The terms "postshock stage" and "preshock stage" apply to these pH levels. In order to stop and repair acidic damage to macromolecules, 43 acid shock proteins are stimulated during the postshock phase (Foster and Hall, 1991). This feature of Salmonella has made the control of the pathogen a complicated task. For instance, pH has an impact on the consistency and stability of mayonnaise, which is mostly formed of eggs, oil, and vinegar (Depree and Savage, 2001). S. enterica cells given an initial acid shock at pH 4.5 and 5.8 before inoculating mayonnaise (pH 4.2-4.5) improved the organism's survival and persistence at 4 °C (Leuschner and Boughtflower, 2001).

Although pH has a significant impact on Salmonella's capacity to create biofilm, most strains are unable to do so at pH 4.5 except for S. dublin. On the other hand, in tryptic soy broth with 10 % NaCl and pH 7, S. senftenberg and the monophasic variety of S. Typhimurium demonstrated the highest biofilm development (Petrin et al., 2022). On the other hand, filamentous bacteria appeared to be more tolerant of low pH than planktonic cells after being exposed to pH 2 for 10 min and able to thrive in 10 % bile salts after a 24-hr period of exposure (Stackhouse et al., 2012). The Government of New South Wales (NSW), Australia, suggests in their food safety guidelines that a pH at or below 4.2 has been demonstrated to be helpful in limiting Salmonella in raw egg products. Besides the impacts of other factors, the effects of the type of acid, temperature, and water quality on Salmonella growth have been described in various literature (Jung and Beuchat, 2000; Mattick et al., 2000; Indu et al., 2006; Zhu et al., 2012; Yang et al., 2014). While environmental stress can trigger reactions in a wide variety of bacterial species (Alvarez-Ordóñez et al., 2015), Salmonella spp. can develop cross-tolerance to different stimuli when they are stressed (Hiramatsu et al., 2005).

Conclusion and recommendation

Around the world, *Salmonella* infection is a significant public health concern. This pervasive pathogen can adapt to various habitats, including those with human, animal, and non-animal hosts due to their genetic makeup. According to findings from earlier studies, Salmonella infection is not only related to poor hygiene, and it may not be possible to eliminate Salmonella contamination in seafood and fisheries products by simply controlling indicator organism levels. Additionally, the development of MDR Salmonella strains presents a significant difficulty in treating infections brought on by these strains. On top of that, the anticipated climate change and perturbation of environmental factors will increasingly threaten the safety of the food supply and a gradual rise in the incidence of foodborne infection and intoxication in the coming years. In this context, more stringent preventive and control measures must be adopted. One of the most effective preventive measures is to limit the indiscriminate use of antibiotics in food animals that have been suggested to curb the spread of Salmonella infection. Besides, to curb the health risk from foodborne infections, a ubiquitous sanitation measure should be adopted in every sphere of food preparation before consumption. We also recommend utilizing new innovative technologies to trace every step of supply chains including processing and preservation.

On a large scale, a stronger level of cooperation between public health authorities within and between countries is required, in addition to continued funding for human health perspectives.

Data availability

The representative photographs used in this review paper are available from the corresponding author upon reasonable request.

Consent to publish

Both authors have approved the submission of the final version of the manuscript.

Conflict of interest

The authors declare that there is no conflict of interest that could impact or influence the research work reported in this manuscript.

Ethics approval

There was no need to obtain permission from the UTRGV IACUC committee to conduct laboratory experiments on invertebrates including oysters. All wild-caught oysters, however, were collected according to the approved wildlife species capture rules and regulations by the Texas Park & Wildlife Department (scientific permit number: SPR1018–274).

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CRediT authorship contribution statement

Mohammad Maruf Billah: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Md Saydur Rahman:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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