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Managing the risk of *Vibrio parahaemolyticus* infections associated with oyster consumption: A review

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Abstract

Vibrio parahaemolyticus is a Gram-negative bacterium that is naturally present in the marine environment. Oysters, which are water filter feeders, may accumulate this pathogen in their soft tissues, thus increasing the risk of *V. parahaemolyticus* infection among people who consume oysters. In this review, factors affecting *V. parahaemolyticus* accumulation in oysters, the route of the pathogen from primary production to consumption, and the potential effects of climate change were discussed. In addition, intervention strategies for reducing accumulation of *V. parahaemolyticus* in oysters were presented. A literature review revealed the following information relevant to the present study: (a) managing the safety of oysters (for human consumption) from primary production to consumption remains a challenge, (b) there are multiple factors that influence the concentration of *V. parahaemolyticus* in oysters from primary production to consumption, (c) climate change could possibly affect the safety of oysters, both directly and indirectly, placing public health at risk, (d) many intervention strategies have been developed to control and/or reduce the concentration of *V. parahaemolyticus* in oysters to acceptable levels, but most of them are mainly focused on the downstream steps of the oyster supply chain, and (c) although available regulation and/or guidelines governing the safety of oyster consumption are mostly available in developed countries, limited food safety information is available in developing countries. The information provided in this review may serve as an early warning for managing the future effects of climate change on the safety of oyster consumption.

KEYWORDS

climate change, food poisoning, oyster, risk, *Vibrio parahaemolyticus*

1 | INTRODUCTION

Oysters are among the most appreciated seafood products worldwide because of their nutritive value and flavor. Oyster consumers are willing to pay a higher price for high-quality and safe oysters. An increasing trend was observed in the production and trade of oysters during the past decade (FAO, 2019). According to the FAO report, the global production of oysters from wild capture fishery and aquaculture increased from 4.5 million tons in 2010 to 5.9 million tons in 2017 (Figure 1a). Asia was the most productive oyster area (Figure 1b). Currently, China, the Republic of Korea, the United States, Japan, Mexico, France, Taiwan, the Philippines, Canada, and Thailand are the top 10 oyster producers globally (Figure 2). Regarding oyster trade, the FAO report showed that the import value of oysters increased from USD 324.8 million in 2010 to USD 432.8 million in 2016, whereas the export value increased from USD 298.9 million in 2010 to USD 505.5 million in 2016 (FAO, 2019).

Oysters are part of a healthful diet, but eating oysters is not risk free. Oysters may contain foodborne pathogens, such as *Vibrio parahaemolyticus*. *Vibrio parahaemolyticus*, a

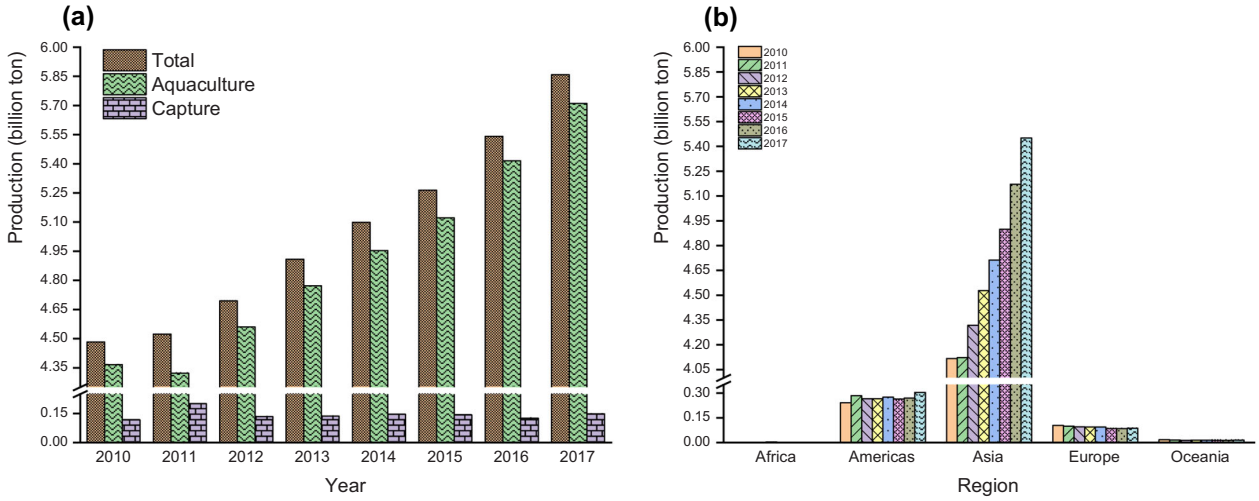

FIGURE 1 Global production of oysters by the capture fishery and aquaculture (a), and by the production regions (b). Data from FAO FishStat (2010 to 2017)

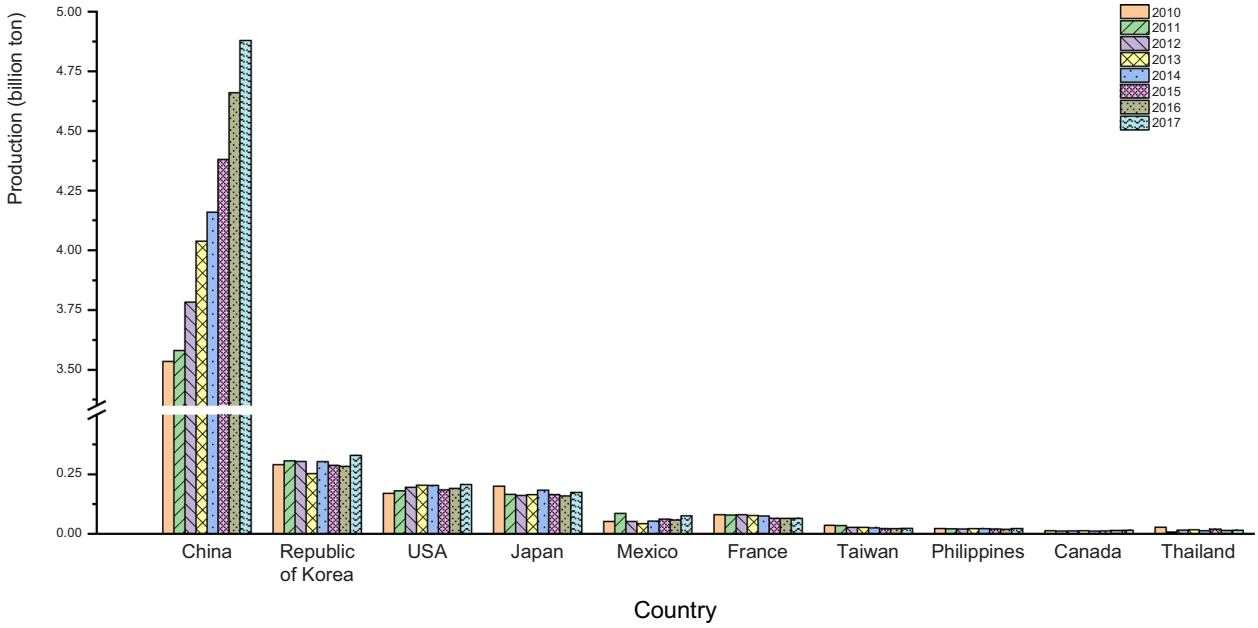

FIGURE 2 Top 10 countries producing oysters. Data from FAO FishStat (2010 to 2017)

foodborne pathogen that is naturally present in the aquatic marine environment, can contaminate the surface or enter the tissues of oysters (Baker-Austin et al., 2018; Taylor, Cheng, et al., 2018). *Vibrio parahaemolyticus*, a Gram-negative bacterium, was first isolated in 1950, and has become a pathogen of global concern following the appearance of the first pandemic O3:K6 strain in 1996 (Nair et al., 2007). This pathogen is typically isolated in warm seawater and is rarely isolated when the temperature of seawater is under 13 to 15 °C (Kaneko & Colwell, 1975). Significant investigation and analysis of the presence of *V. parahaemolyticus* in seafood were presented by Odeyemi (2016) recently in a systematic review and meta-analysis of 48 studies published between 2003 and 2015. The author revealed that the concentration of *V. parahaemolyticus* was higher in oysters than in other seafood products; the presence of *V. parahaemolyticus* in oysters, clams,[1] fish,[2] shrimp,[3] and mussels [4] was 63.4%, 52.9%, 51.0%, 48.3%, and 28.0%, respectively (Odeyemi, 2016). A high concentration of *V. parahaemolyticus* is expected because oysters are aquatic filter feeders; consequently, they accumulate high

[1] Including clams and cockles.

[2] Including fish, squids, and cephalopods.

[3] Including shrimp, prawns, and crabs.

[4] Including mussels, scallops, and periwinkles.

concentrations of the bacterial pathogen *V. parahaemolyticus*. Hence, consuming oysters is associated with a higher risk of *V. parahaemolyticus* infection than is consuming other types of seafood. Furthermore, contamination of oysters with *V. parahaemolyticus* also occurred during handling, processing, and preparation or by cross-contamination through contact between oysters and other contaminated seafood products or seawater. Studies have shown that gastroenteritis is the most common disease resulting from *V. parahaemolyticus* infection (Butt, Aldridge, & Sanders, 2004; Iwamoto, Ayers, Mahon, & Swerdlow, 2010; Makino et al., 2003; Shimohata & Takahashi, 2010). The most common symptoms include watery diarrhea, abdominal cramps, nausea, vomiting, headache, fever, and chills (Humphries & Linscott, 2015). Nevertheless, the risk caused by the presence of *V. parahaemolyticus* in oysters can be easily reduced or eliminated by adequate cooking. However, in many cases, *V. parahaemolyticus* infection occurs because of the consumption of raw or undercooked oysters that may be contaminated by *V. parahaemolyticus* (Huang, Hwang, Huang, Wu, & Hsiao, 2018; Sobrinho, Destro, Franco, & Landgraf, 2014; Taylor, Cheng, et al., 2018). In a report, even with consumer who reported eating only thoroughly cooked (grilled, stewed, or fried) oysters were as likely to become ill as those who ate raw oysters due to the failure of cooking (McDonnell et al., 1997). The incidence of gastroenteritis caused by *V. parahaemolyticus* associated with the consumption of oysters has been reported in the United States (Drake, DePaola, & Jaykus, 2007; Iwamoto et al., 2010; McLaughlin et al., 2005), Canada (Taylor, Cheng, et al., 2018), China (Chen et al., 2017; Ma et al., 2014; Wu, Wen, Ma, Ma, & Chen, 2014), Taiwan (Hsiao, Jan, & Chi, 2016; Lin, Lin, Kou, Hong, & Wu, 2015), Spain (Lozano-León, Torres, Osorio, & Martínez-Urtaza, 2003), Italy (Ottaviani et al., 2008), Chile (Garcia et al., 2009), Peru (Gil et al., 2007), and Brazil (Leal et al., 2008). Recently, the Centers for Disease Control and Prevention (CDC) in the United States also reported two cases of *V. parahaemolyticus* infection resulting from the consumption of oysters imported from Mexico (U.S. CDC, 2019). In Canada, 82 cases of *V. parahaemolyticus* infection associated with the consumption of raw oysters were reported by Taylor, Cheng, et al. (2018).

Seafood companies and food safety authorities are under considerable pressure to ensure that consumption of seafood, such as oysters, does not harm consumers when they are prepared and/or eaten because these organizations are not only required to ensure the safety of oysters but also to protect their overall reputation (Hussain & Dawson, 2013; Marques, Nunes, Moore, & Strom, 2010; Reardon, 2001). Food companies involved in the production, processing, or distribution of oysters should be able to identify risk factors affecting food safety in their operations; hence, they have developed appropriate control and mitigation strategies. These strategies are important because many factors can affect food safety, including that of oysters, from primary production to consumption (Racicot et al., 2019; Zanabria et al., 2018). Climate change, which involves changes in global or regional climate patterns, is one of multiple factors that can affect the safety of oysters (Adler, Leiker, & Levine, 2009; Brucet et al., 2012; Wu, Lu, Zhou, Chen, & Xu, 2016). Climate change is thought to affect the weather, which results in changes in temperature, precipitation, wind, and sunshine. Therefore, the concern of climate change affecting food safety arises because it can affect the establishment and growth of foodborne pathogens and affect interactions among hosts, pathogens, and their environment (Watts et al., 2018). Climate change may affect these food safety in various ways, such as exacerbating the presence of biological contaminants in the environment and foods (Alava, Cheung, Ross, & Sumaila, 2017; Watts et al., 2018); thus, it may increase the occurrence of foodborne diseases.

Despite the controversy surrounding climate change, evidence suggesting that climatic conditions affect the level of pathogens in seafood (Marques et al., 2010; Smith et al., 2015) and that they are correlated with the occurrence of foodborne illnesses is available (Aik et al., 2018; Choi et al., 2015; Jiang et al., 2015; Lake, 2017; Park, Park, & Bahk, 2018). The World Health Organization recently suggested that its member nations should increase awareness of the increase in foodborne diseases associated with climate change and urged relevant authorities and stakeholders to incorporate food safety measures for mitigating the effect of climate change on health (WHO, 2019). Similarly, the European Food Safety Authority in Europe identified that an increase in seawater temperature because of climate change could be a potential food safety concern because it may affect the survival, growth, and proliferation of foodborne pathogens, particularly *Vibrio* spp. This finding suggests that climate change could be a significant factor directly or indirectly affecting the food safety of oysters and may cause a threat to human health.

Against the background of the aforementioned concerns, we reviewed the risk of *V. parahaemolyticus* infection associated with the consumption of oysters. In this review, the risk was defined as "a function of the probability of an adverse health effect and the severity of that effect, consequential to a hazard(or hazards) in food" (Heilandt, Mulholland, & Younes, 2014, p. 345). We focused on the risk of getting *V. parahaemolyticus* infection associated with eating raw oysters. In our literature review, we referred to previously published studies (Smith, 2018; Torraco, 2016; Winchester & Salji, 2016) to understand the topic, discover the gaps, determine a possible solution, and draw a conclusion. A literature research was performed using online databases, including Web of Science, Science Direct, and Google Scholar. Pertinent information was obtained by searching for predefined keywords, namely, "oysters" and "*Vibrio parahaemolyticus*" in combination with "outbreaks," "foodborne," "gastroenteritis," "infection,"

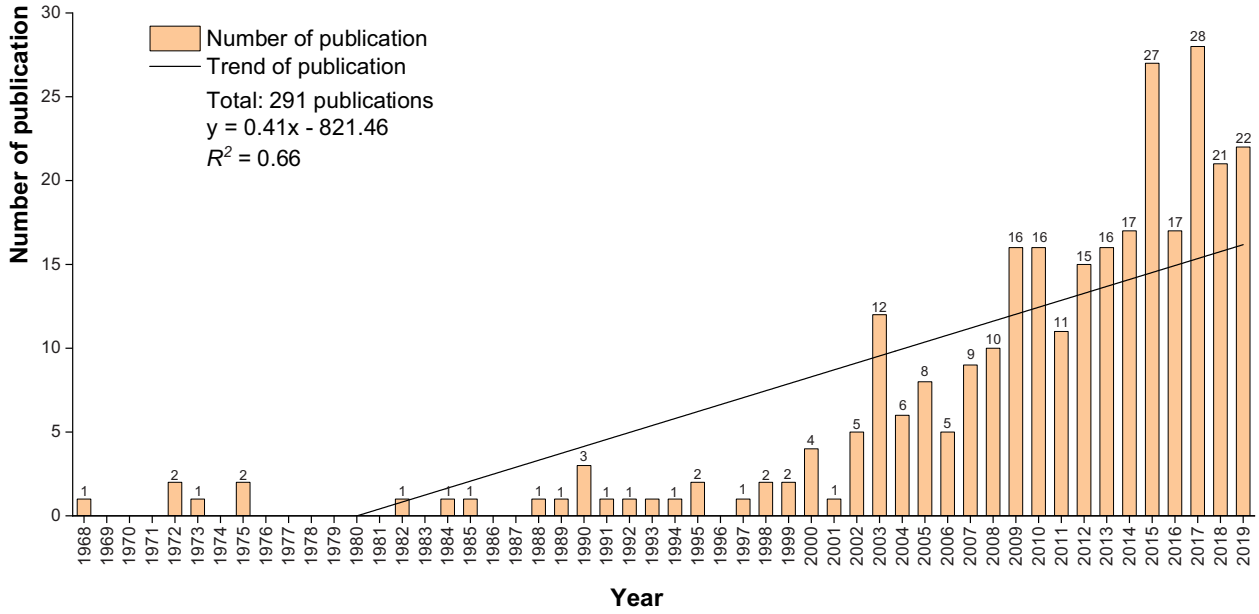

FIGURE 3 Distribution of publications per year across the period studied

"prevalence," "predictive model," "growth rate," "risk," "virulence factor," "risk assessment," "culturing method," "climate change," "climatic variation," "extreme events," "cross-contamination," "handling," "processing," "cold chain," "food safety management," or "risk-based food safety management." Relevance of each article was screened using the following criteria: (a) articles published in English, with preference for peer-reviewed articles, book, or book chapters, and (2) the document, or part of the document, is relevant to the objective of this review. No restriction to a specific range of years was applied. In addition, we reviewed the bibliography sections of retrieved articles to identify relevant studies. We also used Google search engine to search for information related to policies, legal requirements, and/or guidelines governing the safety of oysters published by the relevant professional organizations (e.g., FAO/WHO) and food safety authorities. Finally, we identified and included 291 references that were most relevant to the topic in this review (see Figure 3). In general, the distribution showed an increase in the number of studies related to *V. parahaemolyticus* concentrations in oysters since 2000, which indicated that the risk of contracting *V. parahaemolyticus* infections because of oyster consumption has been gradually receiving increasing attention. With respect to publication scope, the obtained references were categorized into the following 10 themes to simplify data analysis: (a) agricultural and biological sciences; (b) medicine, pharmacology, toxicology, and pharmaceutics; (c) immunology and microbiology; (d) biochemistry, genetics, and molecular biology; (e) environmental science; (f) multidisciplinary; (g) earth and planetary science; (h) business, management, and accounting; (i) engineering and computer science; and (j) others (e.g., policies, legal requirements, and/or guidelines)

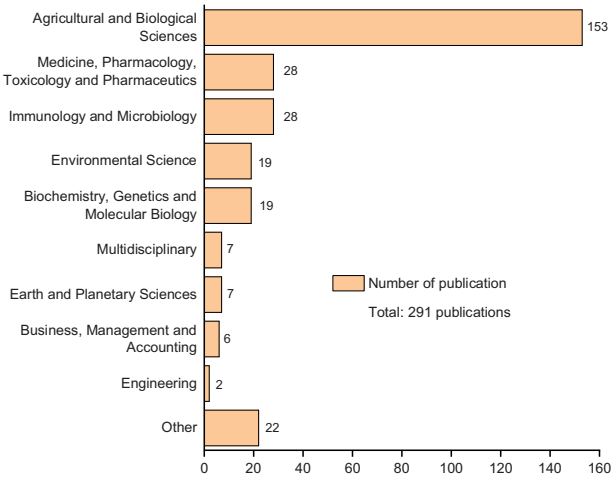

FIGURE 4 Distribution of references in publication field in paper review

(see Figure 4). Most of the academic material was found in publications devoted to agricultural and biological sciences. Most of the articles were published in the *Journal of Food Protection*, *Applied and Environmental Microbiology*, *Food Control*, and *International Journal of Food Microbiology*.

The remainder of this review is arranged in various sections. Section 2 provides a basic overview of the effects of environmental conditions for the survival and growth of *V. parahaemolyticus*. Section 3 presents the distribution of *V. parahaemolyticus* in oysters. Section 4 discusses factors affecting the risk of infection caused by the consumption of oysters. Section 5 reviews the pressures of climate change on the risk of *V. parahaemolyticus* infection and discusses the projection of the future effects of climate change.

Section 6 discusses potential intervention strategies for reducing *V. parahaemolyticus* concentrations in oysters and decontaminating oysters by considering climate change factors. Section 7 presents the existing policies, legal requirements, and/or guidelines regarding the food safety of oysters. Finally, Section 8 presents a conclusion and prospects for future research. Data presented in this review were not comprehensive; however, sufficient information was provided in the present study to serve as early warning information for public health. Furthermore, the critical analysis used in this review may be applicable for assessing the potential effects of climate change on other types of food.

2 | EFFECT OF ENVIRONMENTAL CONDITIONS ON THE GROWTH RATE OF *V. PARAHAEMOLYTICUS* IN OYSTERS

Several studies have attempted to develop predictive models describing the effects of environmental conditions on the growth rate of *V. parahaemolyticus* in oysters (Fernandez-Piquer, Bowman, Ross, & Tamplin, 2011; Kim, Lee, Hwang, & Yoon, 2012; Parveen et al., 2013; Tang et al., 2015; Yang et al., 2009; Yoon et al., 2008). Experimental data showed that temperature is among other environmental conditions that considerably affect the survival and growth rates of *V. parahaemolyticus*. Notably, the survival and growth rates of this pathogen are also affected by factors such as pH and salinity. In general, *V. parahaemolyticus* prefers an alkaline pH of 7.9 to 8.6 and 3% NaCl for growth (Beuchat, 1975). Several studies have reported that the growth of this microorganism is favored at temperatures higher than 15 °C; the optimum temperature for growth is 35 to 37 °C (Fernandez-Piquer et al., 2011; Kim et al., 2012; Parveen et al., 2013; Tang et al., 2015; Yang et al., 2009; Yoon et al., 2008). This pathogen dies or at least becomes inactive at temperatures of <10 °C (Fernandez-Piquer et al., 2011; Parveen et al., 2013; Shen et al., 2009). The concentration of this pathogen was found to remain stable at 15 °C in live oysters (Yoon et al., 2008) and oyster slurry (Fernandez-Piquer et al., 2011) but was reduced by 0.002 and 0.001 log CFU/hr in shell-stock oyster at 5 and 10 °C, respectively (Parveen et al., 2013). However, Thomson and Thacker (1973) and Shen et al. (2009) observed that *V. parahaemolyticus* continued growing in oyster slurry and shell-stock oysters at a temperature of 10 °C. Variations in the minimum temperatures required for *V. parahaemolyticus* growth are probably related to inoculation techniques that affect the distribution of this pathogen in oyster tissues, variations in *V. parahaemolyticus* strains used in these studies, growth substrates and habitats, and competing microbiota living in oyster-growing regions (Beuchat, 1975; Fernandez-Piquer et al., 2011).

Increasing temperatures can accelerate the multiplication of *V. parahaemolyticus* and shorten the incubation period. Gooch, DePaola, Bowers, and Marshall (2002) reported that this microorganism could increase up to 50-fold and 790-fold in live oysters after 10 and 24 hr of storage, respectively, at 26 °C. Yoon et al. (2008) reported that this pathogen multiplied rapidly in oyster slurry at temperatures higher than 20 °C. Shen et al. (2009) revealed that this pathogen rapidly grew in either shucked or shell-stock oysters from undetectable concentrations (<3 most probable number [MPN]/g) to 4.72 log MPN/g, 5.04 log MPN/g, 5.72 log MPN/g, and 6.66 log MPN/g at 16, 20, 26, and 32 °C, respectively, after 32 hr of exposure to contaminated artificial seawater (ASW). Parveen et al. (2013) reported that the growth rate of this pathogen in shell-stock oysters at 15, 20, 25, and 30 °C was 0.038, 0.082, 0.228, and 0.219 log CFU/hr, respectively. However, an excessive increase in temperature (>45 °C) increased the mortality rate of this pathogen (Fernandez-Piquer et al., 2011; Kim et al., 2012; Parveen et al., 2013; Yoon et al., 2008).

Studies presented thus far have provided evidence of the effect of environmental conditions on the survival, growth rate, and concentration of *V. parahaemolyticus* in oysters (Fernandez-Piquer et al., 2011; Gooch et al., 2002; Parveen et al., 2013; Shen et al., 2009; Yang et al., 2009; Yoon et al., 2008). Because the concentration of *V. parahaemolyticus* in oysters indicates the potential risk of infection by this pathogen following consumption of oysters, controlling environmental conditions can control the potential risk of *V. parahaemolyticus* infection. Therefore, the development of models predicting the growth of *V. parahaemolyticus* in oysters is critical for improving risk management practices by identifying conditions that should be controlled for controlling the survival and growth rate of this pathogen, particularly during postharvest processing, storage, and transport. However, studies presented thus far were performed using artificially contaminated oyster homogenates or live oysters, except for the studies by Parveen et al. (2013) and Kim et al. (2012) who have examined the effects of temperature on the natural concentration of *V. parahaemolyticus* in live oysters and oyster slurry, respectively. Inoculated *V. parahaemolyticus* in a homogenate or live oysters may not reflect the diversity of the natural population of *V. parahaemolyticus* observed in live oysters (Kim et al., 2012; Parveen et al., 2013; U.S. FDA, 2005). Thus, the use of predictive models that were developed using inoculated *V. parahaemolyticus* in homogenates or live oysters in a risk assessment may not provide an accurate estimation of the potential risk of *V. parahaemolyticus* infection. Furthermore, the diversity, growth, and survival of naturally occurring *V. parahaemolyticus* may differ among oyster species (Parveen et al., 2013).

3 | DISTRIBUTION OF *V. PARAHAEMOLYTICUS* IN OYSTERS

3.1 | Detection of *V. parahaemolyticus*

Systematic reviews of methods for detecting *V. parahaemolyticus* in seafood, including oysters, have been presented by Letchumanan, Chan, and Lee (2014) as well as Bisha, Simonson, Janes, Bauman, and Goodridge (2012). Generally, the presence of *V. parahaemolyticus* in samples is detected using culture-based or molecular-based methods. In culture-based methods, the presence of *V. parahaemolyticus* in samples is enumerated using the MPN method or colony-forming count method on an agar plate, followed by the identification test (e.g., analysis of oxidase activity, Gram staining, NaCl triple sugar iron test, halophilism tests, analytical profile index test, and slide agglutination test) (Deepanjali, Kumar, Karunasagar, & Karunasagar, 2005; Jones et al., 2014; Mok, Ryu, Kwon, Kim, & Park, 2019; Sobrinho, Destro, Franco, & Landgraf, 2010, 2011; Zulkifli et al., 2009). The results of culture-based methods are expressed as MPN per unit volume or sample weight. However, the use of traditional methods to detect this pathogen in samples and complete identification takes a long time (7 to 10 days), results in a heavy workload, and requires the use of multiple reagents. Furthermore, these methods cannot be used to detect low numbers of *V. parahaemolyticus* in samples.

Technological advancement in the past two decades has considerably improved detection (high sensitivity, high specificity, and simplicity) of *V. parahaemolyticus* in seafood samples based on molecular-based techniques (Chen & Ge, 2010; Letchumanan et al., 2014). Species-specific polymerase chain reaction (PCR) by using specific primers is one of the most popular molecular-based methods used by many researchers to allow fast, accurate, and highly specific detection of *V. parahaemolyticus* in seafood samples. In the PCR method, a specific DNA segment is amplified by a factor of at least six orders of magnitude within hours; therefore, the PCR method enables the detection of an extremely low concentrations of bacterial cells. The presence of *V. parahaemolyticus* strains in samples is detected by targeting the presence of *ToxR* gene (Deepanjali et al., 2005; Suffredini et al., 2014; Taiwo et al., 2017). Another reliable marker for this pathogen is the thermolabile hemolysin (*tlh*) gene (Suffredini et al., 2014; Taiwo et al., 2017). The presence of *ToxR* or *tlh* gene does not indicate the presence of a virulence factor; in fact, these genes are used to determine the presence of the total concentrations of *V. parahaemolyticus* in samples (Bej et al., 1999; Letchumanan et al., 2014; López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, & Rendón-Castro, 2015). Many studies have reported that the presence of pathogenic strains was identified by targeting the thermostable direct hemolysin (TDH) (*tdh*) and/or TDH-related hemolysin (*trh*) gene (Barrera-Escorcia et al., 2016; Bej et al., 1999; Mok et al., 2019; Paranjpye, Hamel, Stojanovski, & Liermann, 2012; Sobrinho, Destro, Franco, & Landgraf, 2011). The presence of a specific gene in *V. parahaemolyticus* in samples is confirmed by visualizing the PCR product on an agarose gel. Combining the traditional method (i.e., MPN method) with PCR amplification enables the identification and highly accurate detection of total and pathogenic *V. parahaemolyticus* in oyster samples; the entire identification process is completed within 2 days. Jones et al. (2014), López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, and Rendón-Castro (2015), and Cruz, Hedderley, and Fletcher (2015) have reported that the lowest detection limits of the MPN–PCR method for detecting *V. parahaemolyticus* in oyster samples were 0.30, 0.30, and 0.36 MPN/g. A crucial feature of the PCR method is that it can detect multiple specific genes in a single reaction; these reactions are called multiplex PCRs. They increase output speeds and reduce reagent costs (Bej et al., 1999; Sobrinho et al., 2011; Whistler et al., 2015).

An advancement over conventional PCR, known as real-time PCR, allows the detection of *V. parahaemolyticus* in samples in real time (Davis et al., 2017; Paranjpye et al., 2015). This method is also often referred to as quantitative PCR (qPCR). This method allows fast, accurate, and consistent detection of specific genes simultaneously in large numbers of samples. Real-time PCR does not require post-PCR steps, and results are expressed as a number of genome equivalents or copies per unit volume or weight samples (Davis et al., 2017; Paranjpye et al., 2015). Several studies have successfully used multiplex real-time PCR using primers that target multiple species-specific genes for detecting and enumerating total and pathogenic *V. parahaemolyticus* in oyster samples, including Kim, Lee, Kim, Kwon, and Kwon (2008), Nordstrom, Vickery, Blackstone, Murray, and DePaola (2007), Panicker, Call, Krug, and Bej (2004), Xu, Ji, Wu, Yan, and Chen (2018), and Blackstone et al. (2003). Other molecular methods, including DNA hybridization (Givens, Bowers, DePaola, Hollibaugh, & Jones, 2014; Jones, Noe, Byars, & Depaola, 2009; Nordstrom & DePaola, 2003) and the loop-mediated isothermal amplification assay (Cao et al., 2019; Kampeera et al., 2019; Malcolm et al., 2015), have been employed to detect and identify this pathogen in oysters.

Considerable improvements have been made in detecting *V. parahaemolyticus* in samples over the past two decades because of technological advancements. However, the detection of *V. parahaemolyticus* in samples is affected by numerous factors, including the substrate used for isolation, isolation methods, detection methods, and sampling period (Anupama et al., 2019; Givens et al., 2014; Lopez-Joven, de Blas, Furones, & Roque, 2015; Pinto, Terio, Novello, & Tantillo, 2011). For example, the use of the

chromogenic medium (CHROMagar *Vibrio* or Bio-Chrome *Vibrio* medium) was found to be more effective than that of thiosulfate citrate bile salts sucrose (TCBS) agar for isolating colonies of *V. parahaemolyticus* (Duan & Su, 2005a; Pinto et al., 2011). Duan and Su (2005a) reported that the accuracy and specificity of the chromogenic medium for detecting *V. parahaemolyticus* were 84% and 94%, respectively, whereas the accuracy and specificity of TCBS agar were only 54% and 77%, respectively. Similarly, Pinto et al. (2011) also observed that the accuracy and specificity of the chromogenic medium were 88% and 95%, respectively, whereas those with TCBS agar were only 51% and 71%, respectively. Moreover, culture-based methods may not be effective to detect and enumerate *V. parahaemolyticus* in a special physiological state, the so-called "viable but nonculturable (VBNC)" state (Coutard et al., 2007; Wong & Wang, 2004). The state of VBNC refers to the condition of bacterial cells that are metabolically active, but cannot grow on conventional culture media. *Vibrio parahaemolyticus* may enter the VBNC state due to unfavorable environmental conditions, such as extreme temperature, low salinity, and nutrient deprivation (Coutard et al., 2007; Wong & Wang, 2004). Furthermore, the use of the MPN method followed by conventional phenotyping and biochemical identification test required more time, required more material, and created a greater workload for detecting *V. parahaemolyticus* in the samples than MPN followed by PCR (Letchumanan et al., 2014). The use of real-time PCR is faster and more accurate than conventional PCR (Niu et al., 2018; Takahashi, Iwade, Konuma, & Hara-Kudo, 2005). Because speed and accuracy are critical in assessing the risk of *V. parahaemolyticus* infection caused by consuming oysters, variations in detection results can affect the accuracy of food safety risk estimation (FAO/WHO, 2011; Nauta, 2000).

3.2 | Virulence factor of *V. parahaemolyticus*

The identification of virulence factors in *V. parahaemolyticus* is one of the major topics that have drawn considerable scientific attention. A comprehensive review of virulence factors in *V. parahaemolyticus* was presented by Li, Meng, Gu, Li, and Jia (2019). Many studies have considered the presence of TDH encoded by the *tdh* gene and TDH-related hemolysis (TRH) encoded by *trh* gene as major virulence factors in *V. parahaemolyticus* that could cause an infection (Honda, Ni, & Miwatani, 1988; Li, Tang, et al., 2017; Matsuda et al., 2019; Nishibuchi & Kaper, 1995; Park, Ono, Rokuda, Jang, Iida, et al., 2004). Although these two proteins were mostly detected in clinical isolates of *V. parahaemolyticus* from samples isolated from human samples (Iida et al., 1998; Li, Tang, et al., 2017; Saito et al., 2015; Sakazaki et al., 1968), extremely few environmental isolates (e.g., from oysters, seawater, and sediment) contained the *tdh* and/or *trh* genes (Theethakaew et al., 2013).

Other than *tdh* and *trh* genes, several studies have suggested that the Type 3 Secretion System (T3SS1 and T3SS2) is also responsible for pathogenicity of *V. parahaemolyticus* (Broberg, Calder, & Orth, 2011; Burdette, Yarbrough, Orvedahl, Gilpin, & Orth, 2008; Hiyoshi et al., 2015; Makino et al., 2003; Matsuda et al., 2019; Park, Ono, Rokuda, Jang, Okada, et al., 2004). The study of Hiyoshi, Kodama, Iida, and Honda (2010) showed that T3SS2 is often associated with enteropathogenic strains. A recent study by Matsuda et al. (2019) reported the export of *tdh* through the T3SS and caused an infection in an animal model. However, Jones et al. (2012) found that clinical isolates of *V. parahaemolyticus* strains that were submitted to the U.S. CDC in 2007 from wound infection or foodborne illness exhibited the presence of neither *trh* and *tdh* nor T3SS. This indicated that an unknown virulence factor could be responsible for pathogenicity. Other studies have suggested that the pathogenicity of this microorganism is probably also related to the Type 6 Secretion System (T6SS1 and T6SS2) (Li, Kinch, et al., 2017; Zhang, Gao, et al., 2017; Zhang, Osei-Adjei, et al., 2017), adhesion factors (Jiang et al., 2014; Liu & Chen, 2015; Zhang, Osei-Adjei, et al., 2017), iron-uptake system (León-Sicairos et al., 2015), lipopolysaccharide content (Guvener & McCarter, 2003; Zhang et al., 2018), proteases (Lee, Cheng, Yu, & Pan, 2002; Osei-Adjei et al., 2017), and outer membrane proteins (Zha, Li, Li, Ye, & Pan, 2016). These studies have reported that the mechanism underlying the pathogenicity of *V. parahaemolyticus* and contributing factors is not completely understood.

3.3 | Presence and concentration of *V. parahaemolyticus* in oysters

Table 1 shows examples of studies that have investigated the presence of *V. parahaemolyticus* in oysters collected from either culturing environments or markets in either tropical, subtropical, or temperate areas. Oyster samples collected from tropical or subtropical areas (Cook et al., 2002; Deepanjali et al., 2005; DePaola, Nordstrom, Bowers, Wells, & Cook, 2003; Han et al., 2017; Johnson et al., 2010, 2012; López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, & Rendón-Castro, 2015; Matté, Matté, Rivera, & Martins, 1994; New et al., 2014; Sanjeev & Stephen, 1993; Sobrinho et al., 2010, 2011; Ward & Bej, 2006; Yang et al., 2017; Yu et al., 2013, 2016; Zimmerman et al., 2007) are generally considered to exhibit higher concentrations of *V. parahaemolyticus* than those obtained from temperate areas (Cruz et al., 2015; Duan & Su, 2005b; Fletcher, 1985; Jones et al., 2014; Kaysner, Abeyta, Stott, Krane, & Wekell, 1990; Kaysner, Abeyta, Stott, Lilja, & Wekell, 1990; Kirs et al., 2011; Lopatek, Wieczorek, & Osek, 2015; Lopez-Joven et al., 2015; Mok et al., 2019; Nakaguchi, 2013; Park, Mok, et al., 2018; Parveen et al., 2008; Roque et al., 2009; Ryu, Mok, Lee,

TABLE 1 Example of studies on presence of *Vibrio parahaemolyticus* in oysters

Country	Prevalence (%)	Source of samples	Climate zone of sample source[a]	Reference
Malaysia	50.0	Markets in Kuala Lumpur and Selangor	Tropics	New et al. (2014)
India	93.9	Southwest coast of India	Tropics	Deepanjali et al. (2005)
	100.0	Markets in and around Cochin	Tropics	Sanjeev and Stephen (1993)
Brazil	77.0	Fisheries, restaurants and culturing environment in the coastal area of Sao Paulo	Tropics	Matté et al. (1994)
	99.2	Coastal area of Sao Paulo state	Tropics	Sobrinho et al. (2010)
	100.0	Markets in Sao Paulo state	Tropics	Sobrinho et al. (2011)
Taiwan	70.8	South-western coast of Taiwan	Tropics	Yu et al. (2013)
	12.5	Coastal areas of Thailand	Tropics	Nakaguchi (2013)
China	30.4	Markets in South China	Tropics	Yang et al. (2017)
	60.5	Markets in Shanghai	Subtropics	Yu et al. (2016)
	48.9	Coastal area of the South Yellow Sea and the East China Sea	Subtropics	Han et al. (2017)
Mexico	100.0	Mandinga Grande Lagoon	Subtropics	López-Hernández et al. (2015)
United States	100.0	Coastal area of Mississippi and Alabama	Subtropics	Zimmerman et al. (2007)
	100.0	Mobile Bay, Alabama	Subtropics	DePaola et al. (2003)
	51.5	Bayou LaBatre, Alabama	Subtropics	Ward and Bej (2006)
	87.0	Coastal area of Mississippi	Subtropics	Johnson et al. (2010)
	81.5	Coastal and Estuarine Waters of Louisiana, Maryland, Mississippi, and Washington	Subtropics and temperate	Johnson et al. (2012)
	72.9	Coastal and inland markets throughout the United States	Subtropics and temperate	Cook et al. (2002)
	33.0	Long Island coast, New York	Temperate	Tepedino (1982)
	71.3	Willapa Bay, Washington	Temperate	Kaysner, Abeyta, Stott, Lilja, et al. (1990)
	79.0	Chesapeake Bay, Maryland	Temperate	Parveen et al. (2008)
	100.0	Grays Harbor, Washington	Temperate	Kaysner, Abeyta, Stott, Krane, et al. (1990)
	100.0	East and West Oyster Bay Harbor and outer Cold Spring Harbor	Temperate	Jones et al. (2014)
	15.0	Oregon oyster-growing bays	Temperate	Duan & Su (2005b)
Canada	37.5	Canadian Atlantic area	Temperate	Thomson and Thacker (1972)
New Zealand	57.0	Whangaroe, Mahurangi, Coromandel, and Thames	Temperate	Fletcher (1985)
	94.8	North Island	Temperate	Kirs et al. (2011)
	81.0	North Island	Temperate	Cruz et al. (2015)
Spain	24.3	Ebro delta bay	Temperate	Roque et al. (2009)
	14.4	Ebro delta bay	Temperate	Lopez-Joven et al. (2015)
Poland	18.8	Polish markets	Temperate	Lopatek et al. (2015)
Korea	29.5	Coastal area of Gyeongnam	Temperate	Park, Mok, et al. (2018)
	52.8	Coastal area of Gyeongnam and Jeonnam	Temperate	Ryu et al. (2019)
	50.0	Jeju, Jeonnam, and Incheon coasts	Temperate	Mok et al. (2019)

[a]Climate zone was classified based on Meteoblue classification (https://content.meteoblue.com/nl/meteoscool/general-climate-zones, accessed on January 6, 2020).

Kwon, & Park, 2019; Tepedino, 1982; Thomson & Thacker, 1972). For example, concentrations of *V. parahaemolyticus* in oysters were 94% in India, between 77% and 100% in Brazil, 100% in Mexico, and 71% in Taiwan. However, several studies have reported that oyster samples collected from the temperate area exhibited high concentrations of *V. parahaemolyticus* as well. For example, Kirs et al. (2011) reported that nearly all (94.8%) the oyster samples collected from North Island, New Zealand, contained *V. parahaemolyticus*. Other studies have also reported that all samples collected from Long Island Sound and Grays Harbor in the United States contained this pathogen (Jones et al., 2014; Kaysner, Abeyta, Stott, Krane, et al., 1990). These findings indicated that contributing factors affecting the accumulation of *V. parahaemolyticus* in oysters are complex and not yet entirely understood.

These findings showed that numerous studies and growing body of the scientific literature have described dynamic variations in *V. parahaemolyticus* accumulation in oysters and their culturing environments over the past four decades. However, these studies were mostly performed in developed countries; consequently, limited information is available from developing countries, particularly those in Asia and Africa. The reason for availability of limited information is not known; the food safety of oysters in developing countries is probably not a priority in the food safety control measures of developing countries because of their limited financial and human resources. Alternatively, studies performed on the safety of oysters may have been published in these regions in their local languages; consequently, they were not included in this review. The behavior of *V. parahaemolyticus* in oysters and its culturing environment may differ among regions depending on regional climatic conditions (Alava et al., 2017; Watts et al., 2018). Understanding these variations will allow the development of region-specific policies, regulations, or guidelines to satisfy local needs.

Collectively, the aforementioned studies have shown that the accumulation of high concentrations of *V. parahaemolyticus* in oyster tissues indicated that oyster consumption may pose a potential health risk to susceptible consumers. The use of fast, highly accurate, and virulence-specific detection methods is critical for improving the detection of *V. parahaemolyticus* in oysters. Detection and quantification of *V. parahaemolyticus* carrying virulence factors (e.g., *tdh* and/or *trh* gene) may provide a highly reliable estimate of public health risk (Letchumanan et al., 2014). Accurate detection and quantification of this pathogen in oysters will allow an accurate risk estimation to support risk management practices. However, several challenges may arise to achieve this objective because it depends on the availability and adequacy of regulations governing monitoring approaches used for detecting *V. parahaemolyticus* in oysters as well as the adequacy of financial support and human resources.

4 | FACTORS AFFECTING THE ACCUMULATION OF *V. PARAHAEMOLYTICUS* IN OYSTERS

Table 2 presents a summary of contributing factors affecting the concentration of *V. parahaemolyticus* in oysters, including the culturing area and culturing method of oysters, climatic variations, extreme natural events, handling and processing of oysters, and time–temperature management in the cold chain of oysters. The accumulation of *V. parahaemolyticus* in oysters indicated the potential risk of infection by this pathogen following oyster consumption (Baker-Austin et al., 2018; Broberg et al., 2011; Qadri et al., 2003).

4.1 | Culturing area of oysters

Evidence suggests that culturing area affected the density of *V. parahaemolyticus* in oysters. For example, Yu et al. (2013) investigated the density of *V. parahaemolyticus* in oysters from five oyster-producing areas in Taiwan. Two sites were located near urban regions, near an industrial park and a river. The other three sites were located in agricultural regions, which were less populated. The density of this pathogen in samples of oysters and hard clams obtained from the culturing areas near the urban regions was significantly higher than that obtained from the site that was located in agricultural regions. The authors argued that the freshwater from the river and

TABLE 2 Factors affecting the risk of *V. parahaemolyticus* infection associated with oyster consumption

Category	Risk factors
Culturing area	– Human sewage – Effluent of fresh water – Water circulation
Culturing method	– On-bottom or off-bottom culture – Aquaculture practices
Climatic variations	– Seawater temperature – Salinity – Turbidity – Dissolved oxygen – pH – Water depth
Extreme natural events	– Hurricane – Floods
Handling and processing	– Cross-contamination – Cooking practices
Cold chain control	– Abuse temperature

effluent from populated urban areas could have altered environmental conditions (such as the salinity and concentration of dissolved oxygen), thus critically affecting the density of *V. parahaemolyticus* in samples. Another example is the study by Lopez-Joven et al. (2015) that investigated the presence of *V. parahaemolyticus* in mollusks (oysters, mussels, and clams) collected from the Ebro Delta Bays, Spanish Mediterranean Coast, and found that the source of samples was a significant factor affecting the density of this pathogen in samples. Based on logistic regression analysis, Lopez-Joven et al. (2015) further reported that the presence of *V. parahaemolyticus* in samples collected from the Fangar Bay was significantly higher than in the samples collected from the Alfacs Bay. The difference between these two bays probably related to differences in temperature and salinity (Lopez-Joven et al., 2015), which suggested that temperature and salinity variations were probably related to water circulation, evaporation, and freshwater inputs from nearby agriculture fields.

Several studies have shown that pathogenic strains (e.g., *tdh* and/or *trh*) are rarely found in isolates obtained from the environment; however, they are mostly found in clinical strains isolated from patients with gastroenteritis. However, other studies have shown that strains encoding virulence genes (*tdh* and/or *trh*) have been detected in environmental isolates (Gutierrez West, Klein, & Lovell, 2013; Kokashvili et al., 2015; Paranjpye et al., 2012; Velazquez-Roman, León-Sicairos, Flores-Villaseñor, Villafaña-Rauda, & Canizalez-Roman, 2012; Yu et al., 2013). There is a concern that pandemic strains from patients with gastroenteritis may enter the culturing area of oysters because of shedding of the pathogen in the feces of patients in adjacent urban areas. However, limited specific information is available about the transmission of pandemic strains from urban areas to the culturing areas of oysters (Hara-Kudo et al., 2003; Li et al., 2016).

4.2 | Culturing method of oysters

Production of oysters is of two types, namely, wild oyster fishery and aquaculture. The wild oyster fishery simply involves catching, processing, and selling oysters. By contrast, aquaculture involves the cultivation of oysters in natural or controlled environments. Because the supply of oysters from wild fisheries has not increased with time or has declined (Beck et al., 2011; FAO, 2019), the fishing community considers aquaculture an alternative method for increasing oyster production. Two methods are followed in oyster aquaculture, namely, the on-bottom and off-bottom methods. In the on-bottom method, oysters are simply grown on the ocean floor. By contrast, in the off-bottom method, oysters are grown above the tidal ground. The use of the off-bottom culture method has increased over the past four decades, and the method has undergone various modifications. Some off-bottom methods that are commonly used include rack culture, stake culture, raft culture, suspended baskets, floating baskets, and oyster cages (Matthiessen, 2001; Walton, Nelson, Hochman, & Schwarz, 2013; Walton, Rikard, et al., 2013). Aquaculture development has increased oyster production over the past decade, and it considerably exceeds the production by wild oyster fishery (See Figure 1a) because of technological advancement and increased government support through the development of relevant policies.

Concerns regarding food safety are increasing because of consumers' preference for variety and healthy food. Consequently, they may differ in their preference of consuming wild-caught or aquacultured oysters. However, studies on comparisons between the risk of *V. parahaemolyticus* infection resulting from the consumption of wild-caught oysters and aquacultured oysters are limited (Froelich, Phippen, Fowler, Noble, & Oliver, 2017). Nevertheless, studies have shown that the culturing method affects the concentration of *V. parahaemolyticus* in oysters (Cole, Supan, Ramirez, & Johnson, 2015; Feinman, Farah, Bauer, & Bowen, 2018). Cole et al. (2015) reported that the concentration of *V. parahaemolyticus* in oysters was generally lower in oysters cultured using the off-bottom method than in those cultured using the on-bottom method. In the off-bottom method, oysters are suspended above the sediment surface, and local currents create a buffer exchange between oysters and the underlying sediment (Feinman et al., 2018); consequently, lower concentrations of the pathogen are observed in oysters cultured using the off-bottom method. However, aquaculture practices, such as desiccation and/or dry storage, may allow *V. parahaemolyticus* to proliferate in closed oysters (Grodeska, Jones, Arias, & Walton, 2017; Grodeska, Jones, Walton, & Arias, 2019; Kinsey, Lydon, Bowers, & Jones, 2015). Grodeska et al. (2017) reported that desiccation practices can increase the concentrations of *V. parahaemolyticus* in oysters and that the concentrations of the pathogen in oyster samples after desiccation were significantly higher than those in oyster samples that remained continuously submerged in seawater without exposure to ambient temperature. Studies have recommended a minimum 7-day resubmersion treatment to enable the level of this pathogen to return to its original concentrations (Grodeska et al., 2017, 2019). This information indicated that the culturing method and aquaculture practices affect the concentrations of *V. parahaemolyticus* in oysters, thereby affecting the risk of *V. parahaemolyticus* infection.

4.3 | Climatic variations and extreme natural events

Considerable evidence suggests an association between climatic conditions and the concentration of *V. parahaemolyticus* in oysters. Multiple studies have shown that sea surface temperature (SST) was the most common factor determining the concentration of *V. parahaemolyticus* in

oysters and their culturing environment in regions where the temperature varied from 9.9 to 33 °C (Cruz et al., 2015; DePaola et al., 2003; Duan & Su, 2005b; Johnson et al., 2010; López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, & Uscanga-Serrano, 2015; López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, & Rendón-Castro, 2015; Parveen et al., 2008). Notably, other studies have also reported an association between the concentration of *V. parahaemolyticus* and other climatic variables. For example, Parveen et al. (2008) reported that the abundance of *V. parahaemolyticus* in oysters in the Chesapeake Bay was not only positively correlated with variations in water temperature but also with the turbidity of and concentration of dissolved oxygen in the water. Furthermore, López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, and Rendón-Castro (2015) reported that the seawater temperature, salinity, and pH considerably affected the abundance of *V. parahaemolyticus* in oysters harvested from Mexico's Gulf Coast. In a previous study (Konrad, Paduraru, Romero-Barrios, Henderson, & Galanis, 2017), relationships among climatic variables and the occurrence of *V. parahaemolyticus* in oysters collected from the west coast of Canada were investigated; the results showed that daily SST was associated with the concentration of this pathogen in oyster samples and that daily SST could be used to predict *V. parahaemolyticus* concentrations in seafood products. Williams et al. (2017) investigated the correlation between climatic conditions and the concentrations of *V. parahaemolyticus* in oysters collected from the North Carolina coast and found that SST and water depth significantly affected the concentrations of *V. parahaemolyticus* in oysters. Froelich et al. (2017) performed a study in the same location, North Carolina coast, and reported that SST was strongly correlated with the abundance of *V. parahaemolyticus* in oysters. A recent study by Hartwick et al. (2019) reported that seawater temperature and pH were predictors of *V. parahaemolyticus* concentrations in oysters in the Great Bay Estuary of New Hampshire.

Extreme events, such as hurricanes and floods, increase the accumulation of *V. parahaemolyticus* in oysters. Shaw, Jacobs, and Crump (2014) investigated the effect of hurricanes on concentrations of *V. parahaemolyticus* in oyster samples collected from the Chesapeake Bay estuary and found that the concentration of pathogen in the samples increased substantially in oyster samples after 1 day of stormy weather, and the pathogen concentration return to its prestorm level only after 4 days.

Moreover, the influence of environmental factors on the distribution of *V. parahaemolyticus* which carry virulence strains in oysters, however, has not been studied in detail. Nevertheless, a recent study showed that the presence of pathogenic *V. parahaemolyticus* (*trh*) in bivalves (oysters, mussels, and clams) was significantly influenced by seawater salinity (Lopez-Joven et al., 2015). However, the result of that study may be affected by the sampling location and bivalve species (Lopez-Joven et al., 2015). This is important because the concentration of *V. parahaemolyticus* can differ significantly between bivalve species, even if they are collected from the same location at the same period of time (Froelich et al., 2017). Understanding the influence of environmental condition on the concentration and distribution of *V. parahaemolyticus* that carry virulence strains in oysters will allow a better prediction of food safety risk associated with the consumption of oysters (Zimmerman et al., 2007).

Overall, information on the effects of climatic conditions and extreme events on the concentration of *V. parahaemolyticus* in oysters is crucial to food safety authorities and food managers in the oyster industry. For instance, oysters that are harvested during the warm season probably have higher concentrations of *V. parahaemolyticus* than those harvested in the cold season (Cruz et al., 2015; DePaola et al., 2003; DePaola, Hopkins, Peeler, Wentz, & McPhearson, 1990; Di, Lee, Jang, Han, & Hur, 2017; Duan & Su, 2005b; Mok et al., 2019; Parveen et al., 2008); consequently, oysters harvested in the warm season may not be safe for human consumption, particularly if oysters are intended to be consumed raw. This information can enable food managers to select appropriate interventions in controlling and/or reducing the number of this pathogen in oysters to an acceptable level. In addition, this information will also enable food safety authorities to inform the public about the potential threat of *V. parahaemolyticus* during the warm season and provide necessary guidelines to oyster producers and consumers for ensuring the safety of public health.

4.4 | Handling and processing

Handling and processing are essential to reduce the risk of *V. parahaemolyticus* infection because of consuming oysters. The steps involved in handling and processing of oysters are receiving, storing, washing, packaging, and distributing oysters to the customer (Baker, 2016). Incorrect handling and processing can allow initially low concentrations of *V. parahaemolyticus* to increase and become dangerously high in oysters. Therefore, the proper implementation of a food safety management system (FSMS) (such as Good Hygiene Practices, Good Manufacturing Practices, Hazard Analysis, and Critical Control Points) is necessary to prevent the growth and multiplication of *V. parahaemolyticus* in oysters, eliminate the pathogen, or at least reduce its concentrations to acceptable levels during handling and processing (Feng, Chen, Zhou, Rungsardthong, & Zhang, 2019; Garrido & Otwell, 2009; Tzouros & Arvanitoyannis, 2000).

Proper implementation of FSMSs are also expected to prevent cross-contamination of oysters during handling and processing or recontamination of oysters after processing. Preventing cross-contamination is critical because several reports on foodborne outbreaks have documented that *V. parahaemolyticus* infection occurs because of cross-contamination with seafood (Chen et al., 2017; Iwamoto et al., 2010; Jung, 2018; Liao et al., 2015; Wu et al., 2014). For example, Ma et al. (2014) reported that cross-contamination with salted food during food preparation was the main cause of *V. parahaemolyticus* infection in the Guangdong Province, China, between 2008 and 2010. Salinity concentration in salted oysters was reported to enable *V. parahaemolyticus* to survive and proliferate; thus, the pathogen concentration might have increased sufficiently to cause an infection (Yeung & Boor, 2004). Later, Chen et al. (2017) stated that cross-contamination, improper cooking, and improper storage were the main factors causing *V. parahaemolyticus* outbreaks in the Zhejiang Province, China between 2010 and 2014; furthermore, 31% of these outbreaks were related to cross-contamination with aquatic products (lobster, shrimp, yellow croakers, hair crabs, cuttlefish, salmon, squids, and fishcake). Jung (2018) investigated the source of and mode of contamination in vibriosis in a bazaar in Korea and found that cross-contamination between the squid and kimbap was the main cause of the outbreak. The author revealed that the kimbap and squid were prepared using the same cutlery and utensils (knife and cutting board) and thus caused the transmission of *V. parahaemolyticus* from squid to kimbap and other food products. These findings indicated that even completely cooked oysters can be recontaminated if cross-contaminated with other food products that carry *V. parahaemolyticus* or rinsed with seawater. Additionally, other seafood products carrying *V. parahaemolyticus* could also contaminate or cross-contaminate the oysters if they are prepared using the same utensils and cutlery (e.g., cutting boards and knives).

The effectiveness of implemented FSMSs to eliminate *V. parahaemolyticus* or reduce its concentration in oysters remains a challenge because of increasingly complex interactions among foodborne pathogens, food, vehicles, and environmental conditions (Froelich & Noble, 2016; Zannella et al., 2017). Challenges in the food safety management of oysters are also complicated by the dynamic operating environment as well as the increasing and changing consumer demands and expectations (Froelich & Noble, 2016). In this regard, oyster industries involved in handling and processing oysters are required to translate, implement, and tailor FSMSs to suit their specific circumstances. Management that relies only on audits and inspections to verify conformity of implemented FSMSs is inadequate (Kotsanopoulos & Arvanitoyannis, 2017; Powell et al., 2013). Audits and verifications commonly focus on comparing food safety output with specific requirements; consequently, they are not leveraged into corrective actions for mitigating risks (Kleboth, Luning, & Fogliano, 2016; Kotsanopoulos & Arvanitoyannis, 2017). Therefore, oyster industries should always evaluate the effectiveness and improve the implementation of FSMSs in their respective operations.

4.5 | Cold chain control

A series of actions and set of equipment applied to maintain a product within a specified low-temperature range is referred to as "cold chain" (Mercier, Villeneuve, Mondor, & Uysal, 2017; Ndraha, Hsiao, Vlajic, Yang, & Lin, 2018). Proper temperature control in the cold chain is critical for preventing the growth of foodborne pathogens. However, previous studies have shown that temperature abuse occurs in the cold chain of oysters (Love, Kuehl, et al., 2019; Love, Lane, et al., 2019; Madigan, 2007). Love, Lane, et al. (2019) investigated the performance of cold chains for the Chesapeake Bay farmed oysters in the United States and reported that 19% of shipments had temperatures higher than 10 °C (50 °F) for longer than 1 hr, which exceeded the recommendation of the National Shellfish Sanitation Program (NSSP) in the United States. In another study by Love, Kuehl, et al. (2019), 18% of the cold chain for the farmed oysters in the United States that were distributed nationally and internationally had temperatures exceeding 10 °C for at least 1 hr. A similar condition was reported by Madigan (2007) in the cold chain of shellfish in Australia; according to the report, 42% to 50% of shipments did not comply with Australian Shellfish Quality Assurance Programs because of nonconformity in terms of time–temperature control.

Climate change may adversely affect the performance of the cold chain of oysters. Love, Lane, et al. (2019) demonstrated that climatic variations affected the performance of the cold chain of oysters in the United States. Some parts of the cold chain in the study by Love, Lane, et al. (2019) could not maintain temperatures less than 7.28 °C, particularly during the warmer months when *Vibrio* control plans were in effect. Consequently, the internal temperature of oysters in the cold chain reached 12.5 °C, which is conducive for the multiplication of *V. parahaemolyticus* (Fernandez-Piquer et al., 2011; Parveen et al., 2013). Assuming that an increase in temperature due to climate change affects oyster cold chains, climate change is thus possibly contributing to the risk of *V. parahaemolyticus* infection because of eating oysters.

Collectively, these findings suggest that maintaining the temperature in the cold chain of oysters from harvest or production to consumption remains difficult (Love, Kuehl, et al., 2019; Love, Lane, et al., 2019; Madigan, 2007). Temperature abuse that may occur during processing, transportation, or storage can allow *V. parahaemolyticus* to grow to dangerously high concentrations in oysters. A previous study showed that this pathogen could increase as much as 790-fold when

live oysters were exposed to a temperature of 26 °C for 24 hr (Gooch et al., 2002). Mudoh, Parveen, Schwarz, Rippen, and Chaudhuri (2014) reported that *V. parahaemolyticus* concentrations increased by approximately three orders of magnitude from day 0 to day 10 at 20 °C. Thus, addressing the factors that affect cold chain performance is crucial. Many factors affect the performance of the food cold chain, including but not limited to, the adequacy of the cold chain infrastructure, the adequacy of cold chain personnel training, and climatic conditions (Accorsi, Gallo, & Manzini, 2017; Göransson, Nilsson, Jevinger, & Jevinger, 2018; Mercier et al., 2017; Ndraha et al., 2018). As an effort toward improving this situation, continuous data collection and data transparency in oyster cold chains are required to enhance the safety of oysters under the pressures of climate change (James & James, 2010; Ndraha et al., 2018). Therefore, time–temperature history in the cold chain of oysters should be recorded continuously by using temperature recorders and/or time–temperature indicators (Mercier et al., 2017; Ndraha et al., 2018). Continuous real-time collection of temperature data will alert and enable the personnel operating in oyster cold chains to take necessary and timely action when the temperature of oysters exceeds permissible levels. Furthermore, data transparency will help food safety authority to clarify responsibility for temperature management and develop necessary policies to ensure the safety of oysters. Realizing complete and accurate data collection and data transparency remain considerable challenges because they depend on the participation of oyster companies, enforcement of adequately comprehensive regulations, and availability of technology to facilitate the collection, sharing, and linking of data.

5 | EFFECTS OF PRESSURES OF CLIMATE CHANGE ON THE RISK OF *V. PARAHAEMOLYTICUS* INFECTION

5.1 | Climate change pathways affect the food safety of oysters

Changes in environmental conditions due to climate change can directly affect *V. parahaemolyticus* by affecting its survival, reproduction, and distribution. Climate change can also indirectly affect this pathogen by altering its physical environment and competitors (Adler et al., 2009; Brucet et al., 2012; Wu et al., 2016). Consequently, climate change not only affects the concentration of *V. parahaemolyticus* but also its geographical and seasonal distribution. Thus, this condition may affect the survival, growth, and proliferation of *V. parahaemolyticus* in oysters and their culturing environments (Fernandez-Piquer et al., 2011; Kim et al., 2012; Parveen et al., 2013; Yoon et al., 2008), which will affect the risk of infection because of consuming oysters. Previous studies have shown that the concentration of *V. parahaemolyticus* in oysters is associated with the concentration of this pathogen in the oyster culturing environment (i.e., seawater and sediment) (Givens et al., 2014; Parveen et al., 2008; Shaw et al., 2014; Yu et al., 2013).

Marine bacteria, such as *V. parahaemolyticus*, grow preferentially in warm areas with low salinity (>15 °C, <25 ppt). Hence, *V. parahaemolyticus* infection is generally expected to occur in tropical or subtropical regions such as Indonesia (Lesmana et al., 2002), Taiwan (Cheng et al., 2013; Lin et al., 2015), and Mozambique (Ansaruzzaman et al., 2005). However, *V. parahaemolyticus* infection has also been reported in temperate regions, such as Chile (González-Escalona et al., 2005; Harth et al., 2009), Peru (Martinez-Urtaza et al., 2008), the Pacific Northwest (USA) (U.S. CDC, 1998), and Northwest Spain (Baker-Austin, Stockley, Rangdale, & Martinez-Urtaza, 2010). This phenomenon might be related to climate change. The Intergovernmental Panel on Climate Change (IPCC) report noted that the global temperatures will possibly increase by up to 2.6 °C in the period 2046 to 2065 and by 4.8 °C in 2081 to 2100 because of climate change (IPCC, 2014). Increasing temperature, reduced salinity, and changes in other climatic conditions of coastal regions located at high latitudes may provide new areas for the pathogen to proliferate, thus increasing the risk of infection (Baker-Austin et al., 2013). A recent report of the Lancet Commission notes that the Baltic area and the Northeastern United States are among other areas that have become more suitable for *Vibrio* infections. More specifically, this report states that *Vibrio* infections have increased by 24% and 27%, respectively, from the 1980s to 2010s. The Lancet Commission report also notes a consistent association between SST anomalies and cases of vibriosis (Watts et al., 2018).

Climate change can also affect rainfall and evaporation, which may cause changes in seawater salinity. For example, heavy rainfall causes flooding that brings large volumes of freshwater to oceans, thus reducing the salinity of seawater. Salinity levels lower than 25 ppt favor the growth of *V. parahaemolyticus* (Konrad et al., 2017; Yu et al., 2013). Konrad et al. (2017) showed that a one-unit decrease in salinity increased the concentration of *V. parahaemolyticus* in oysters by up to 8%. Furthermore, changes in salinity could also affect the community composition of phytoplankton, zooplankton, and planktonic crustaceans (Esteves et al., 2015; Turner, Good, Cole, & Lipp, 2009). Consequently, these conditions may affect the abundance of *V. parahaemolyticus* in oysters culture environments because planktons could be vectors for *V. parahaemolyticus* (Frischkorn, Stojanovski, & Paranjpye, 2013; Hsieh, Fries, & Noble, 2007; Jahid, Mizan, Ha, & Ha, 2015; Shime-Hattori et al., 2006).

Climate change can also affect the dispersal of *V. parahaemolyticus* in oceanic areas. This effect is possible when

climate change interferes by causing episodes of anomalous weather conditions in the Pacific Ocean known as the El Nino Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO). Both ENSO and NAO have warm and cool phases that can cause significant changes in the structure and function of marine ecosystems (Barnard et al., 2015; Meehl, Hu, Santer, & Xie, 2016; Steinman, Mann, & Miller, 2015). Extended periods of hot weather due to climate change cause an increase in the average temperature of seawater bodies, particularly during warm ocean phases, and thus enhance the stratification and upwelling of nutrient-rich seawater. Increasing temperature and nutrient availability are the fundamental requirement for the reproductive cycles of marine microorganisms such as phytoplankton, zooplankton, and planktonic crustaceans (Martinez-Urtaza et al., 2012; Thomas, Kremer, Klausmeier, & Litchman, 2012; Vezzulli et al., 2016). Several studies have reported that these planktons represent nutrient-rich reservoirs and could be vectors and/or provide a medium for *V. parahaemolyticus* to grow and multiply on chitinaceous surfaces by forming biofilms (Frischkorn et al., 2013; Hsieh et al., 2007; Jahid et al., 2015; Shime-Hattori et al., 2006). This phenomenon has been demonstrated in a study by Martinez-Urtaza et al. (2012), which reported the occurrence of *V. parahaemolyticus* in offshore areas of the Ria of Vigo, the southernmost ria in Galicia, was almost exclusively associated with zooplankton. A study by Rehnstam-Holm, Atnur, and Godhe (2014) also reported that the occurrence of *V. parahaemolyticus* in offshore areas of the southwest coast of India in the Arabian Sea was positively correlated with the abundance of copepods. Evidence suggests that zooplankton and copepods facilitate the oceanic dispersal of *V. parahaemolyticus* populations (Martinez-Urtaza et al., 2012; Rehnstam-Holm et al., 2014), which facilitates the spread of *V. parahaemolyticus* infections (Raszl, Froelich, Vieira, Blackwood, & Noble, 2016; Yang et al., 2019). A study by Martinez-Urtaza et al. (2008) provided evidence suggesting an association between the El Nino episodes and the occurrence of *V. parahaemolyticus* infections along the coasts of Peru between 1994 and 2005. More specifically, they found that the isolates obtained in the period 1997 to 1998 belonged exclusively to the O3:K6 serotype, which was originally present in Asia. Furthermore, the study suggested that the El Nino episodes in 1997 were probably the cause of the *V. parahaemolyticus* migration from Asia to South America. A recent study by Raszl et al. (2016) revealed that *V. parahaemolyticus* outbreaks in the Pacific coast of South America were also associated with the El Nino episodes. The authors noted that the outbreaks were strongly related to the ingestion of shellfish (oysters, mussels, and clams) (Raszl et al., 2016).

Overall, these findings suggest that climate change possibly affects the concentration of *V. parahaemolyticus* in oysters, thus affecting the occurrence of *V. parahaemolyticus* infections. However, limited information is available on the effects of climate change on the risk of *V. parahaemolyticus* infection because of eating oysters. Furthermore, scant attention has been paid to determining how to manage oyster food safety in response to the effects of climate change (Jaykus, 2010; Marques et al., 2010). Moreover, the effects of climate change on the tolerance, growth variability, and toxicity of *V. parahaemolyticus* in oysters are not completely understood (Burge et al., 2014; Hasegawa et al., 2013; Whitaker et al., 2010). Different *V. parahaemolyticus* strains may respond to changes in the environment differently (Liu, Liu, Pan, Xie, & Zhao, 2016), and some strains of *V. parahaemolyticus* may pose greater health risks than others; hence, this information is necessary for risk assessment.

5.2 | Projection of future effects of climate change on the concentration of *V. parahaemolyticus* in oysters

Increasing global temperatures may accelerate the pathogen proliferation in food, which could subsequently increase the incidence of food poisoning (Muhling, Jacobs, Stock, Gaitan, & Saba, 2017; Ortiz-Jiménez, 2018). Therefore, the projection of the future effects of climate change on microbial food safety is necessary for informing risk management practices. Significant analysis and discussion on this subject are presented in a study by Muhling et al. (2017) that projected the future occurrence, distribution, and seasonality of *V. parahaemolyticus* in oysters in the Chesapeake Bay, by using a statistical downscaling and spatial disaggregation modeling framework. In their model, they used four general circulation models to represent the spanning range of future warming and precipitation, namely, the GFDL-CM3 and GFDL-ESM2G models developed by the Geophysical Fluid Dynamics Laboratory (Donner et al., 2011), the MRI-CGCM-3 model developed by the Meteorological Research Institute (Yukimoto et al., 2012), and the IPSL-CM5A-LR model developed by the Institut Pierre Simon Laplace (Dufresne et al., 2013). These models were then simulated under a high greenhouse gas emission scenarios combined with *V. parahaemolyticus* habitat models. The results of their simulation showed that the occurrence probability of *V. parahaemolyticus* in oysters in the Chesapeake Bay area could increase by 1.5 to 3.0 times higher than that in the late 20th century. Another significant study by Ortiz-Jiménez (2018) quantified the effects of climate change on the risk of consuming raw oysters in Tepic (Mexico) and predicted that the risk of consuming raw oysters in that area would increase as global climate worsens; the following time horizon was mentioned: the risk in 2100 could be 1.12-fold higher than that in 2010. These findings may serve as early warning information that can be used by the food safety authority and/or food managers to develop appropriate strategies to control the effects of climate change on seafood for ensuring the protection of public health.

Collectively, these findings highlighted the importance of projecting the future effects of climate change on oyster safety to serve as early warning information that could be useful in policy formulation or decision-making (Levy, 2018; Semenza et al., 2017). Understanding how and the degree to which climatic variations can affect *V. parahaemolyticus* in oysters and their role in the food chains, and the timescales at which changes might occur will allow the development of mitigation strategies for preventing *V. parahaemolyticus* infection because of eating oysters. However, extremely few tools are available to estimate or project the effects of climate change on oysters and evaluate the effects of mitigation measures on the future risk of *V. parahaemolyticus*. Scant information is available on how these tools are used to mitigate the risks of oyster consumption (Ortiz-Jiménez, 2018). In addition, the study by Muhling et al. (2017), which projected the future distribution of *V. parahaemolyticus* in oysters, or the study by Ortiz-Jiménez (2018), which predicted the future risk caused by this pathogen in oysters, only considered the factor of temperature changes. However, the presence, growth, and distribution of *V. parahaemolyticus* in oysters are affected by other climatic conditions, such as pH, dissolved oxygen, and salinity (Hartwick et al., 2019; López-Hernández, Pardío-Sedas, Lizárraga-Partida, Williams, Martínez-Herrera, Flores-Primo, Uscanga-Serrano, & Rendón-Castro, 2015; Parveen et al., 2008).

6 | INTERVENTION STRATEGIES FOR ELIMINATING *V. PARAHAEMOLYTICUS*, REDUCING *V. PARAHAEMOLYTICUS* CONCENTRATIONS, OR DECONTAMINATING OYSTERS

The U.S. FDA reported that an individual may become ill from consuming 4 log *V. parahaemolyticus* cells in a serving of oysters or approximately 50 cells/g of oysters. In some countries, oysters are frequently eaten raw (Mok et al., 2019; Taylor, Cheng, et al., 2018). Hence, eliminating or reducing *V. parahaemolyticus* in oysters to achieve acceptable concentrations of this pathogen is critical for reducing the risk involved in consuming oysters. Heating during cooking (also known as thermal processing) is one of the most effective methods for reducing the concentration of *V. parahaemolyticus* in oysters. Previous studies have demonstrated that *V. parahaemolyticus* is highly sensitive to heat (Beuchat, 1975; Vanderzant & Nickelson, 1972). Vanderzant and Nickelson (1972) reported that heating at 100 °C for only 1 min eliminated all *V. parahaemolyticus* cells in shrimp homogenates that were initially inoculated with 2.7 or 6.3 log/mL of *V. parahaemolyticus* cells. However, thermal processing adversely affects the sensory characteristics of oysters (Awuah, Ramaswamy, & Economides, 2007; Chai, Liang, Pace, & Schlimme, 1991), which limits its application in the oyster industry. To meet consumer demand for minimally processed oysters to preserve their nutritional and sensory value, the development of innovative intervention strategies for eliminating *V. parahaemolyticus*, reducing the concentration of *V. parahaemolyticus*, or decontaminating oysters is warranted.

Table 3 shows various types of intervention strategies that have been developed to reduce or decontaminate *V. parahaemolyticus* concentrations in raw oysters. Among others, these strategies include icing, immediate refrigeration, freezing, depuration, relaying and transplanting, mild thermal treatment, thermal shock, irradiation, high-pressure processing, and the use of natural antimicrobial agent. Other methods such as combination of several sublethal treatments could also effectively inactivate *V. parahaemolyticus* in oysters (Lai & Wong, 2013). Selection, implementation, and evaluation of the effectiveness of these intervention strategies are crucial for managing the risk of *V*. parahaemolyticus infection associated with consumption of oysters.

6.1 | Icing

The icing method involves simply placing oysters in crushed ice or an ice slurry. The main purpose of using ice is to chill the oysters as quickly as possible to lower their internal temperature, particularly after harvest, to prevent the growth of foodborne pathogens. Studies on the effects of icing on the growth of *V. parahaemolyticus* in oysters have shown that this method can retard the growth of this pathogen in oyster samples, but it is considered ineffective in reducing the concentration of *V. parahaemolyticus* in oysters after several days of icing. For example, Melody, Senevirathne, Janes, Jaykus, and Supan (2008) observed that the concentration of *V. parahaemolyticus* in oysters slightly increased by approximately 1 to 2 log CFU/g after 14 days of icing. The icing method may reduce the effects of *V. parahaemolyticus* concentration if oysters are placed in cold storage immediately after icing. This effect was reported by Gooch et al. (2002); the number of *V. parahaemolyticus* in oysters decreased by 0.8 log CFU/g after icing and placement in the cold storage at 3 °C for 14 hr. Although icing has proven useful to inhibit the growth of *V. parahaemolyticus* in oysters, a study by Lydon, Farrell-Evans, and Jones (2015) showed that this pathogen multiplied in the ice slurry water. Therefore, storing oysters in ice slurry for prolonged periods is not recommended.

6.2 | Refrigeration

The growth of *V. parahaemolyticus* is inhibited at refrigeration temperature (i.e., slightly higher than the freezing point). Jones et al. (2017) reported that oyster samples that were

TABLE 3 Intervention strategies for reducing *V. parahaemolyticus* concentrations in oysters

Intervention	Treatment	Reduction	Reference
Icing	15 min	No significant reduction	Jones et al. (2017)
	14 days	No significant reduction	Melody et al. (2008)
	4 days	No significant reduction	Phuvasate et al. (2012)
Refrigeration	14 hr at 3 °C	0.8 log CFU/g	Gooch et al. (2002)
Freezing	27 days at –18 °C	7 log CFU/g	Muntada-Garriga et al. (1995)
	28 days at –24 °C	7 log CFU/g	Muntada-Garriga et al. (1995)
	75 days at –30 °C	3.8 log MPN/g	Muntada-Garriga et al. (1995)
	1 month at –10 °C	2.45 log MPN/g	Liu et al. (2009)
	1 month at –20 °C	1.71 log MPN/g	Liu et al. (2009)
	1 month at –30 °C	1.45 log MPN/g	Liu et al. (2009)
	6 month at –10 °C	4.55 log MPN/g	Liu et al. (2009)
	6 month at –20 °C	4.13 log MPN/g	Liu et al. (2009)
	6 month at –30 °C	2.53 log MPN/g	Liu et al. (2009)
Depuration	48 hr at 22 °C	1.2 log MPN/g	Chae et al. (2009)
	48 hr at 15 °C	2.1 log MPN/g	Chae et al. (2009)
	96 hr at 15 °C	2.6 log MPN/g	Chae et al. (2009)
	96 hr at 5 °C	3.49 log MPN/g	Su et al. (2010)
	144 hr at 5 °C	3.22 log MPN/g	Su et al. (2010)
	5 days at 10 °C combined with LAB	3.4 log MPN/g	Xi et al. (2014)
	4 days at 12.5 °C	3.1 log MPN/g	Shen and Su (2017)
	5 days at 12.5 °C	3.7 log MPN/g	Shen and Su (2017)
	6 days at 12.5 °C	3.4 log MPN/g	Phuvasate et al. (2012)
	6 days at 15 °C	3.3 log MPN/g	Phuvasate et al. (2012)
	5 days at 12.5 °C	3.3 log MPN/g	Phuvasate and Su (2013)
	5 days at 12.5 °C at 10 ppt	2.1 log MPN/g	Phuvasate and Su (2013)
	5 days at 12.5 °C at 25 ppt	3.3 log MPN/g	Phuvasate and Su (2013)
	4 days at 12.5 °C with 2:1 L of ASW/oyster	3.6 log MPN/g	Shen et al. (2019)
	5 days at 12.5 °C with 2:1 L of ASW/oyster	3.9 log MPN/g	Shen et al. (2019)
	2 days at 12.5 °C combined with 1.0% of GSE	3.0 log MPN/g	Shen and Su (2017)
	2 days at 12.5 °C combined with 1.5% of GSE	4.2 log MPN/g	Shen and Su (2017)
	48 hr at 21.6 °C combined with UV light	2.4 log MPN/g	Ramos et al. (2012)
	48 hr at 22.4 °C combined with UV light plus chlorine	3.1 log MPN/g	Ramos et al. (2012)
Relaying	Relaying in clean water	Inconsistent results	Taylor, Yu, et al. (2018)
Transplanting	Transplanting in oyster growing environment for 14 days	Reduction was not linear over time	Walton, Nelson, et al. (2013)
High-pressure processing	200 MPa at 25 °C for 10 min	6 log CFU/mL	Berlin et al. (1999)
	293 MPa at 8 ± 1 °C for 2 min	4.0 to 4.7 log MPN/g	Ma and Su (2011)
	300 MPa at 28 °C for 3 min	5 log CFU/g	Cook (2003)
	300 MPa at 45 °C for 10 min	7 log MPN/g	Ye et al. (2012)
	345 MPa for 2 min at 21 °C	6.2 log CFU/ml	Calik et al. (2002)
	345 MPa at 21 °C for 7.7 min	4.5 log CFU/ml	Koo et al. (2006)
	350 MPa at 20 °C for 2 min	5.3 log CFU/g	Kural et al. (2008)
	350 MPa 1 °C for 2 min	5.4 log CFU/g	Kural et al. (2008)
	1.0 kGy to 1.5 kGy	6 log MPN/g	Andrews, Jahncke, et al. (2003)

(Continues)

TABLE 3 (Continued)

Intervention	Treatment	Reduction	Reference
Irradiation	3.0 kGy	6 log MPN/g	Jakabi et al. (2003)
	1 to 1.5 kGy	6 log MPN/g	Andrews, Jahncke, et al. (2003)
	1 kGy	2.0 log CFU/g	Mahmoud (2009)
	2 kGy	3.2 log CFU/g	Mahmoud (2009)
	3 kGy	3.7 log CFU/g	Mahmoud (2009)
	5 kGy	Up to 7 log CFU/g	Mahmoud (2009)
Electrolyzed oxidizing (EO) water	30 ppm of chlorine, pH 2.82, ORP of 1131 mV, 1%NaCl at room temperature for 4 to 6 hr	1.1 log MPN/g	Ren and Su (2006)
Mild thermal	10 min at 50 °C	4.8 log MPN/g	Cook and Ruple (1992)
	5 min at 50 °C	5 log MPN/g	Andrews et al. (2000)
Thermal shock	10 min at 52 °C and shocked in ice water	5 to 6 log MPN/g	Andrews, DeBlanc, et al. (2003)
	15 min	7 log MPN/g	Ye et al. (2012)
Natural antimicrobial agent	10% of green tea extract for 2 hr at room temperature	0.8 log MPN/g	Xi et al. (2012)
	10% of green tea extract for 2 hr at 5 °C	~1 log MPN/g	Xi et al. (2012)

Note. The salinity of ASW used in depuration process was 30 ppt unless otherwise stated.
Abbreviations: LAB, lactic acid bacteria; ASW, artificial seawater; GSE, grape seed extract; ORP, oxidation–reduction potential.

immediately refrigerated (at a temperature of <7 °C) had a lower concentration of *V. parahaemolyticus* than the samples that were not refrigerated. *Vibrio parahaemolyticus* could not grow, was injured, or at least inactivated at temperatures of <10 °C (Cook & Ruple, 1989; Gooch et al., 2002; Limthammahisorn, Brady, & Arias, 2009). Other studies have shown that immediate refrigeration of oysters reduced the concentration of this pathogen by approximately one order of magnitude (Cook & Ruple, 1989, 1992; Jones et al., 2017; Limthammahisorn et al., 2009). These results showed that refrigerating oysters as soon as possible after harvest is critical in preventing the rapid growth of *V. parahaemolyticus* in oysters.

6.3 | Freezing

The freezing method involves storing oysters at a temperature below freezing point. Muntada-Garriga, Rodriguez-Jerez, Lopez-Sabater, and Mora-Ventura (1995) revealed that inactivation of *V. parahaemolyticus* from 7 log CFU/g to an undetectable concentration at −18 and −24 °C required 27 and 28 days, respectively, in oyster homogenates. However, Liu, Lu, and Su (2009) showed that freezing only reduced the growth of *V. parahaemolyticus* in shell-stock oysters by 2.45, 1.71, and 1.45 log MPN/g after 1 month of storage at temperatures of −10, −20, and −30 °C, respectively. The study by Liu et al. (2009) showed that storage time affected a reduction in the concentration of *V. parahaemolyticus*. The authors observed that this microorganism was reduced by 4.55, 4.13, and 2.53 log MPN/g after 6 months of storage at temperatures −10, −20, and −30 °C, respectively (Liu et al., 2009). Probably because of the effect of ice crystallization, Liu et al. (2009) further reported that inactivation was more effective at −10 °C than storage at −20 or −30 °C.

Frozen storage has been largely used by the food industry to preserve product quality by inhibiting the growth of bacteria. Understanding the behavior of *V. parahaemolyticus* in oysters at temperatures below the freezing point will facilitate oyster processors in managing the safety of oysters. As indicated previously, the concentration of *V. parahaemolyticus* in oyster homogenates decreased considerably faster than in the shell-stock oysters in frozen storage; furthermore, the reduction of concentrations of this pathogen at −10 °C was greater than that at −20 or −30 °C. However, notably, studies by Muntada-Garriga et al. (1995) and Liu et al. (2009) were performed by using artificially contaminated oyster homogenates or live oysters, which may not reflect the diversity of the natural population of *V. parahaemolyticus* in live oysters (Kim et al., 2012; Parveen et al., 2013; U.S. FDA, 2005). The effects of frozen storage on naturally occurring *V. parahaemolyticus* in live oysters and the behavior of naturally occurring *V. parahaemolyticus* in different oyster species in frozen storage remain unclear.

6.4 | Depuration

Depuration of oysters is a process of holding the oysters in circulating clean seawater under controlled conditions over time (Chae, Cheney, & Su, 2009; Phuvasate & Su, 2013; Shen, Su, Liu, Oscar, & DePaola, 2019). The study by Eyles and Davey

(1984) showed that depuration was not effective in reducing *V. parahaemolyticus* concentrations in oysters at room temperature. Chae et al. (2009) reported that the concentration of *V. parahaemolyticus* in oysters decreased by 1.2 orders of magnitude after 48 hr of depuration in seawater at 22 °C. Furthermore, they revealed that the reduction could be as high as 2.1 and 2.6 orders of magnitude when the temperature was lowered to 15 °C for 48 and 96 hr, respectively. Su, Yang, and Häsk (2010) reported that the concentration of *V. parahaemolyticus* in oysters was reduced by 3.49 orders of magnitude after 4 days of depuration at 5 °C in the winter and by 3.22 orders of magnitude after 6 days of depuration at 5 °C in the summer. Ramos et al. (2012) found that a reduction by 2.4 and 3.1 orders of magnitude is obtained if the oysters were immersed in seawater at 21.6 °C with ultraviolet light and 22.4 °C with ultraviolet light and chlorine, respectively. Phuvasate, Chen, and Su (2012) reported that the concentration of this pathogen decreased from 4.83 to 1.39 log MPN/g and from 6.3 to 3.04 log MPN/g after depuration at 12.5 and 15 °C for 6 days, respectively. Phuvasate and Su (2013) further evaluated the effect of water salinity on the effectiveness of depuration in oysters at 12.5 °C for 5 days. The results showed that depuration could only reduce the concentration of this pathogen in oysters from 5.38 to 3.31 log MPN/g (2.1 log MPN/g) in water with salinity of 10 ppt, whereas a reduction of 3.26 and 3.28 log MPN/g was achieved in water with salinity of 25 and 30 ppt, respectively. Xi, Liu, and Su (2014) investigated the effect of using lactic acid bacteria (LAB) on the reduction of *V. parahaemolyticus* in oysters during depuration and found that LAB reduced the concentration of this pathogen from 4.7 to 1.9 log CFU/mL (3.4 log reductions) after 5 days of treatment at 10 °C. Shen and Su (2017) report that depuration of oyster samples at 12.5 °C for 4 and 5 days reduced the concentration of *V. parahaemolyticus* in samples by 3.1 and 3.7 orders of magnitude, respectively; they further reported that the concentration decreased by 3.0 and 4.2 orders of magnitude after 2 days of depuration at 12.5 °C in ASW with the addition of 1.0% and 1.5% grape seed extract (GSE), respectively (Shen & Su, 2017). Park and Ha (2018) evaluated a combination of sodium hypochlorite (NaClO) and gamma irradiation against *V. parahaemolyticus* in shucked oysters and found that 2 kGy of gamma irradiation combined with 60 ppm of NaClO reduced the concentration of *V. parahaemolyticus* by 3.6 orders of magnitude. Increasing the concentration of NaClO to 80 ppm combined with 2 kGy of gamma irradiation reduced the concentration of *V. parahaemolyticus* in shucked oysters by 2.2 orders of magnitude (Park & Ha, 2018). Shen et al. (2019) investigated the effects of seawater to oyster ratio on depuration for reducing the concentration of *V. parahaemolyticus* in raw oysters and found that the ratio of 2:1 of ASW/oyster could reduce the number of this pathogen by 3.6 and 3.9 orders of magnitude after 4 and 5 days of depuration, respectively.

Due to the potential efficacy of the depuration process in reducing the concentration of *V. parahaemolyticus* in oysters, this method is currently recognized by the Food and Agriculture Organization at an international level and suggested by the NSSP in the United States as one of the recommended methods for reducing the concentration of *V. parahaemolyticus* in oysters (Lee, Lovatelli, & Ababouch, 2008; U.S. FDA, 2017). However, notably, the efficacy of this method varied between 1.2 and 4.2 log MPN/g, depending on the time and temperature of processing, water salinity, the ratio of oyster to seawater, and the additional application of ultraviolet light, gamma irradiation, or use of NaClO, LAB, or a natural substance (e.g., GSE).

6.5 | Relaying and transplanting

Relaying is simply "translocating oysters from contaminated growing waters to less contaminated waters to reduce microbial contaminant levels" (Taylor, Yu, Howell, & Jones, 2018, p. 659). This method is recommended by the NSSP to reduce the concentration of *V. parahaemolyticus* in shellfish in the United States (U.S. FDA, 2017). Taylor, Yu, et al. (2018) reported that the concentration of *V. parahaemolyticus* in oysters that refrigerated within 1 hr of harvest was higher than that in oysters that were not refrigerated during harvest but refrigerated after an 8-hr trip. Taylor, Yu, et al. (2018) further investigated the effectiveness of transplanting in reducing the concentration of *V. parahaemolyticus* in oysters by determining the minimum time required and found that a reduction of 4.5 orders of magnitude was achieved after 14 days of relay.

The transplanting method involves placing the oysters back in the culturing environment to reduce microbial contaminant levels. This becomes necessary, particularly for oysters that might fail to meet microbial food safety levels recommended by food safety authorities. Walton, Nelson, et al. (2013) observed that the concentration of *V. parahaemolyticus* in oysters that were neither iced nor refrigerated during harvest but refrigerated after an 8-hr of trip (referred to as "green tag" shell-stock oysters) was higher than that in oysters that were immediately iced after harvest (referred to as "original harvest"). Walton, Nelson, et al. (2013) further investigated the effects of the transplanting method by determining the minimum required time of return of *V. parahaemolyticus* concentrations in green tag shell-stock oysters to those observed in the original harvest. They found that the concentration of *V. parahaemolyticus* returned to those observed on the original harvest after 14 days of transplanting.

Relaying and transplanting potentially reduced the concentration of *V. parahaemolyticus* in oysters but the application of these methods was highly dependent on the microbial community and environmental conditions at the relay or transplant sites. Walton, Nelson, et al. (2013) noted that the reduction effect of transplanting was not linear over the trial time,

whereas Taylor, Yu, et al. (2018) observed that the reduction effect of relaying was inconsistent. Investigation to identify key factors that affect the effectiveness of the relaying and transplanting in reducing the concentration of *V. parahaemolyticus* in oysters is thus warranted.

6.6 | High hydrostatic pressure

High hydrostatic pressure (HPP) involves the use of pressure to inactivate microorganisms in food. The use of high pressure in food processing can inhibit some enzyme activities and protein synthesis (Yamamoto, 2017). This method can also alter cell morphology and the cell membrane in some bacteria, which could result in disruption of transcription, translation, and cellular functions responsible for the survival and reproduction of a microorganism (Rendueles et al., 2011). The effectiveness of HPP on reducing the concentration of *V. parahaemolyticus* in oyster homogenates and whole oysters has been studied by multiple researchers (Berlin, Herson, Hicks, & Hoover, 1999; Calik, Morrissey, Reno, & An, 2002; Cook, 2003; Koo, Jahncke, Reno, Hu, & Mallikarjunan, 2006; Kural, Shearer, Kingsley, & Chen, 2008; Ma & Su, 2011; Ye, Huang, & Chen, 2012). These studies evaluated the effects of HPP at various levels of temperature and pressure at different times of exposure. Berlin et al. (1999) reported that a reduction of 6.0 orders of magnitude was obtained after oysters were treated with 200 MPa at 25 °C for 10 min. Ma and Su (2011) observed a reduction of *V. parahaemolyticus* in oyster samples between 4.0 and 4.7 orders of magnitude after treatment with 293 MPa at 8 ± 1 °C for 2 min. Cook (2003) investigated the effects of HPP in oyster samples and observed a reduction of 5.0 orders of magnitude after the samples were treated with 300 MPa at 28 °C for 3 min. Ye et al. (2012) reported that pressure of 300 MPa at 45 °C for 10 min reduced the concentration of *V. parahaemolyticus* in oyster samples by up to 7.0 orders of magnitude. Calik et al. (2002) reported a reduction in *V. parahaemolyticus* in oyster samples up to 6.2 orders of magnitude after the samples were treated with 345 MPa for 2 min at 21 °C. However, a study by Koo et al. (2006) only reported a reduction of 4.5 orders of magnitude after oyster samples underwent similar treatment (345 MPa at 21 °C) for 7.7 min. Kural et al. (2008) investigated the effects of HPP on the concentration of *V. parahaemolyticus* in oyster samples treated with 350 MPa for 2 min at two temperature levels (20 and 1 °C) and found that reduction by 5.3 and 5.4 orders of magnitude could be achieved using temperature and pressure treatments, respectively.

Although the effects of HPP in reducing the concentration of *V. parahaemolyticus* in oysters is not linear, this method effectively killed *V. parahaemolyticus* in oysters. The literature showed that the effectiveness of HPP in reducing the concentration of *V. parahaemolyticus* in oyster samples depended on the duration of the pressure and the temperature level used. Notably, the use of this method often kills the oysters and causes an immediate opening of the shells (Campus, 2010).

6.7 | Irradiation

Irradiation is a food processing technology that employs gamma rays, electron beams, or X-rays for reducing the concentration of microorganisms in food or eliminating them. The use of gamma irradiation with a dose of 3.0 kGy can reduce the concentration of *V. parahaemolyticus* in oysters by six orders of magnitude (Jakabi et al., 2003). Interestingly, Jakabi et al. (2003) observed that 3.0 kGy of gamma irradiation did not kill oysters or affect the sensory attributes of oysters. In another study, the concentration of this microorganism in oysters decreased from 6 log MPN/g to an undetectable concentration after being treated with 1.0 to 1.5 kGy dose Co-60 gamma irradiation (Andrews, Jahncke, & Mallikarjunan, 2003). Similar to the observations reported by Andrews, Jahncke, et al. (2003), Jakabi et al. (2003) observed that the treatment of gamma irradiation at the aforementioned dose did not affect the oyster's sensory attributes. Mahmoud and Burrage (2009) reported that 5 kGy of irradiation reduced the concentration of *V. parahaemolyticus* in whole oysters from 7 log MPN/g to a nondetectable (<1 log CFU/g) concentration. Although irradiation effectively reduced the number of *V. parahaemolyticus* in oysters, the application of this method may only be allowed in some countries with specific requirements (Baker, 2016). Furthermore, the widespread use of this method has been reported to be limited by the small number of irradiation facilities and low consumer acceptance of irradiated oysters (Baker, 2016; Ravindran & Jaiswal, 2019).

6.8 | Electrolyzed oxidizing water

The concentration of *V. parahaemolyticus* in oysters can also be reduced using electrolyzed oxidizing (EO) water. This type of water is produced by electrolysis of an extremely dilute salt (NaCl) solution (Huang et al., 2006; Quan, Choi, Chung, & Shin, 2010; Ren & Su, 2006). The application of EO water for decontaminating *V. parahaemolyticus* in oysters was studied by Ren and Su (2006); they used EO water (chlorine, 30 ppm; pH 2.82; oxidation–reduction potential of 1,131 mV) containing 1% NaCl at room temperature and found that the concentration of *V. parahaemolyticus* was reduced by 1.1 to 1.6 orders of magnitude after 4 to 6 hr of treatment. Although EO water and chlorine potentially reduced the concentration of *V. parahaemolyticus* in oysters, this method may only be applicable to oysters with low concentrations of *V. parahaemolyticus*. Furthermore, storing oysters in EO water containing chlorine for more than 6 hr can kill oysters (Ren & Su, 2006) probably because the use of this method creates an unfavorable growth environment for oysters.

6.9 | Mild thermal treatment and thermal shock

In mild thermal treatment, oysters are submerged in hot water at 50 °C for a specific processing time. This method was evaluated by Andrews, Park, and Chen (2000) who confirmed that submersion of oysters in hot water at 50 °C for 5 min reduced the concentration of *V. parahaemolyticus* from 5 log MPN/g to an undetectable concentration. In the study by Cook (as cited in the report of the U.S. FDA, 2005), the concentration of this pathogen in oyster was reduced by 4.5 to 6 log orders of magnitude after being heated to 50 °C for 5 min.

Thermal shock simply involves submerging oysters in water at a given temperature for a specific processing time followed by rapid cooling in ice water. This treatment reduced the concentration of *V. parahaemolyticus* in oysters from 5 to 6 log MPN/g to an undetectable concentration after being heated to 50 °C for 8 to 10 min (Andrews, DeBlanc, Veal, & Park, 2003). The authors noted that this treatment could affect pathogenic and nonpathogenic strains of *V. parahaemolyticus* in live oysters; the pathogenic strain was more heat resistant than the nonpathogenic strain (Andrews, DeBlanc, et al., 2003). They found that the concentration of the pathogen in oysters could be completely eliminated when the oysters were submerged in water at 52 °C for at least 22 min (including the time for temperature rise). Ye et al. (2012) reported that submerging live oysters in the water at 50 °C for 15 min reduced the concentration of this pathogen by 7 log MPN/g, but the temperature rise time was not included. Nevertheless, Ye et al. (2012) observed that *V. parahaemolyticus* was detected after enrichment even after exposure to 52 °C for 20 min.

In general, these finding suggest that mild thermal and thermal shock treatment can reduce the concentration of *V. parahaemolyticus* in oysters to an undetectable level. However, notably, the efficacy of these methods depended on the time–temperature control. Failure to control time and temperature (exposure of oysters to temperatures >53 °C) affected the sensory quality of oysters (Andrews, DeBlanc, et al., 2003; Chai et al., 1991). In addition, even with strict temperature control, Ye et al. (2012) observed slight changes in color and smell after mild thermal treatment of oysters at 50 °C for more than 5 min; these findings were contrary to previous observation of Cook and Ruple (1992) who reported that holding oysters at 50 °C for 10 min did not adversely affect the appearance or taste of oysters.

6.10 | Natural antimicrobial agent

The use of natural antimicrobial agents for reducing the concentration of *V. parahaemolyticus* in oysters was studied by Xi, Liu, and Su (2012). They reported that the concentration of *V. parahaemolyticus* in shucked oysters decreased from 4.7 to 3.9 log MPN/g after immersion of the samples in green tea extract (10%) for 2 hr at room temperature. The use of a natural antibacterial agent, such as green tea extract, potentially reduced the concentration of *V. parahaemolyticus* in oysters. However, it may be only applicable to oysters with low concentrations of *V. parahaemolyticus*, given the fact that the reduction effect of this method was lower than one order of magnitude (Xi et al., 2012). Nonetheless, natural antibacterial agents may be useful for inactivating *V. parahaemolyticus* in oysters at low-temperature storage. As reported by Xi et al. (2012), storing the shucked oysters that were immersed in 10% of green tea extract at 5 °C could enhanced the reduction of *V. parahaemolyticus* concentration by more than one order of magnitude.

Collectively, the literature review showed that many intervention strategies have been developed to control and/or reduce the concentration of *V. parahaemolyticus* in oysters, which provides many alternatives to the oyster industry to select appropriate strategies to ensure the safety of their product. Although these strategies are mainly focused on the control of *V. parahaemolyticus* concentrations downstream of the oyster supply chain (e.g., at postharvest, storage, and distribution), limited information is available on how to control concentrations of this pathogen upstream of the supply chain (e.g., in the culturing environment). Moreover, the efficacies of these intervention strategies vary, and the interventions may exhibit synergistic effects when combined. Some of these interventions reduce the concentrations of *V. parahaemolyticus* in fresh oysters to nondetectable concentrations. Notably, "nondetectable concentrations" of *V. parahaemolyticus* in oysters could differ among identification and detection methods. In some countries, the nondetectable concentrations of this pathogen in oysters was set at <30 MPN/g (Food Standards Australia New Zealand, 2018; U.K. Health Protection Agency, 2009; U.S. FDA, 2017). The main challenges with these intervention strategies are the regulations governing their implementation, validation, and verification of implemented intervention as well as access to the facility. In addition, the wide-scale commercial application of these intervention strategies may be challenged by consumer or market preferences as well as the cost of using these methods, which may not be easily passed on to the customer (Baker, 2016; Kecinski, Messer, Knapp, & Shirazi, 2017).

7 | POLICY, LEGAL REQUIREMENT, OR GUIDELINES REGARDING THE SAFETY OF OYSTERS

Vibrio parahaemolyticus infections associated with seafood products have drawn the attention of many stakeholders. Relevant food safety authorities have established and enforced relevant policies, legal requirements, and/or guidelines

regarding the safety of seafood, which also govern the safety of oysters. The code and guidelines governing the safety of oysters have been developed by the Codex at the international level under the "Code of Practice for Fish and Fishery Products and the Guidelines on the Application of General Principles of Food Hygiene to The Control of Pathogenic Vibrio Species in Seafood" (Codex, 2010, 2016), but this code and guideline do not recommend the use of microbial performance standards of *Vibrio* spp. in any shellfish products. The International Commission on Microbiological Specifications for Foods (ICMSF, 2011) recommend that the concentration of *V. parahaemolyticus* in live and raw seafood should not exceed 4 log CFU/g or MPN/g.

In the United States, the safety of oysters is controlled under the NSSP (U.S. FDA, 2017). Based on the NSSP guidelines, the concentration of *V. parahaemolyticus* in raw oysters also should not exceed 4 log CFU/g or MPN/g and should be undetectable in processed oysters (<30 MPN/g). Notably, the NSSP also provides guidelines governing the safety control of shellfish products, including oysters, during primary production, harvesting, processing, shipping, and/or handling. To control the growth of *V. parahaemolyticus* in oysters, the NSSP requires the internal temperature of this seafood to be <10 °C, and the environment temperature should be <7.2 °C during distribution and/or storage. To achieve nondetectable concentrations of *V. parahaemolyticus* in processed oysters, the NSSP requires the process to achieve a minimum reduction of 3.52 orders of magnitude.

The safety of oysters in Australia and New Zealand is controlled by the Compendium of Microbiological Criteria for Food (Food Standards Australia New Zealand, 2018). Ingestion of *V. parahaemolyticus* concentrations higher than 4 log CFU/g in shellfish products, such as oysters, is considered hazardous because it could cause infections. The number of *V. parahaemolyticus* should not be higher than 2 log CFU/g for oysters that are intended to be consumed raw and should be undetectable in processed oysters (<3 CFU/g). These microbial criteria in Australia and New Zealand required oysters to be chilled quickly at temperatures of <5 °C after harvest, and this seafood maintained at refrigeration temperatures to control the growth of *V. parahaemolyticus*.

In Japan, the maximum concentration of *V. parahaemolyticus* in fresh oysters should not exceed 2 log MPN/g and should not be undetectable in oysters intended to be consumed raw (Hara-Kudo et al., 2012). This limit is not only for oysters but also for all types of seafood. To prevent the growth of this pathogen, the Japanese Ministry of Health, Labour, and Welfare (MHLW) recommends that seafood handlers maintain oysters at temperatures <10 °C during distribution and storage (MHLW, 2010). Frozen oysters intended to be consumed raw should be stored at −15 °C or at lower temperatures.

In the United Kingdom, oysters with *V. parahaemolyticus* concentrations of more than 3 log CFU/g are considered high risk, potentially injurious to health, and unfit for human consumption (U.K. Health Protection Agency, 2009). *Vibrio parahaemolyticus* should not be detected <20 CFU/g in oysters intended for human consumption in the United Kingdom.

Because concerns regarding the safety of shellfish products such as oysters are increasing, the food safety authority in Canada is currently in the process of reviewing and establishing the microbiological criteria governing the safety of oysters to protect the health of Canadian citizens (Health Canada's Food Directorate, 2019). As part of this process, the Canadian food safety authority is collecting information regarding the factors that may increase the concentrations of *V. parahaemolyticus* in shellfish products. In addition, the authority is also collecting information about possible means of mitigation strategies for controlling the concentrations of this pathogen during cultivation, distribution, and consumption.

Although an increase in public concern related to seafood safety has encouraged the development of policies, legal requirements, and/or guidelines governing the safety of seafood, few of the policies consider the factor of climate change. In addition, this trend of development is observed in developed countries (Food Standards Australia New Zealand, 2018; Health Canada's Food Directorate, 2019; MHLW, 2010; U.K. Health Protection Agency, 2009; U.S. FDA, 2017); however, inadequate relevant information is available from developing countries. This is a crucial discrepancy because oysters are traded in international markets; hence, they cross countries or even continents depending on market demand (FAO, 2019). Ensuring the safety of oysters from primary production (that might be produced in developing countries) to consumption is critical to minimize the risk of infections is necessary. For achieving this end, harmonization of standards governing the safety of oysters between exporting and importing countries is necessary, including but not limited to food safety management during cultivation, harvesting, distribution, and storage.

8 | OVERALL CONCLUSIONS

This study reviewed the potential risk of *V. parahaemolyticus* infections associated with the consumption of oysters. Apparently, the management of the safety of oysters remains difficult, considering that cases of infections caused by the pathogen associated with eating oysters continue to be reported in many countries. This indicates that oyster safety management should be improved to ensure the protection of consumer health, given that oysters harbor high concentrations of *V. parahaemolyticus*. To improve the detection and the quantification of this pathogen in oysters, this review

highlighted the use of fast, highly accurate, and virulence-specific detection approaches. Furthermore, the development of predictive models describing the behavior of naturally occurring *V. parahaemolyticus* in different species of oysters is necessary for reducing the risk of infection by providing supportive management practices.

This review revealed that multiple factors affect the concentration of *V. parahaemolyticus* in oysters from upstream to downstream stages in the oyster supply chain (e.g., culturing area, culturing method, climatic variations, extreme natural events, handling and processing, and cold chain control), which consequently affect the risk of infection because of consuming oysters. In addition, this review also showed that climate change could possibly affect the safety of oysters, both directly and indirectly, thereby endangering public health. In an effort to minimize the risk, many intervention strategies have been developed to control and/or reduce the concentration of *V. parahaemolyticus* in oysters to acceptable levels. However, these strategies are mainly focused on the downstream steps of the oyster supply chain (e.g., at postharvest, storage, and distribution). There is limited information available on how to control *V. parahaemolyticus* in oysters in the upstream steps of the oysters supply chain (e.g., culturing environment).

Finally, this review highlighted the need for developing relevant policies, legal requirements, and/or guidelines regarding the safety of oysters, particularly in developing countries, by considering contributing factors affecting the risk involved in consuming oysters and potential effects of climate change and ensuring their implementation through inspection and monitoring. The implementation of the shellfish harvesting policy adopted in the United States and guidelines governing the safety of seafood products in Japan are examples of efforts to reduce the risk of vibriosis (Alvarez, Solís, & Hwang, 2019; Hara-Kudo & Kumagai, 2014). Additional efforts are required to encourage the harmonization of standards governing the safety of oysters between exporting and importing countries because oysters are traded in international markets.

AUTHOR CONTRIBUTIONS

Nodali Ndraha conceived the manuscript concept and design and has drafted, edited, and proofread the manuscript. Hsin-I Hsiao and Hin-chung Wong contributed substantially to the manuscript concept and design and aided in drafting and revising the manuscript. Hsin-I Hsiao provided final approval of the submission.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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REFERENCES

Accorsi, R., Gallo, A., & Manzini, R. (2017). A climate driven decision-support model for the distribution of perishable products. *Journal of Cleaner Production*, *165*, 917–929.

Adler, P. B., Leiker, J., & Levine, J. M. (2009). Direct and indirect effects of climate change on a prairie plant community. *PLoS ONE*, *4*, e6887.

Aik, J., Heywood, A. E., Newall, A. T., Ng, L. C., Kirk, M. D., & Turner, R. (2018). Climate variability and salmonellosis in Singapore—A time series analysis. *Science of the Total Environment*, *639*, 1261–1267.

Alava, J. J., Cheung, W. W. L., Ross, P. S., & Sumaila, U. R. (2017). Climate change—Contaminant interactions in marine food webs: Toward a conceptual framework. *Global Change Biology*, *23*, 3984–4001.

Alvarez, S., Solís, D., & Hwang, J. (2019). Modeling shellfish harvest policies for food safety: Wild oyster harvest restrictions to prevent foodborne *Vibrio vulnificus*. *Food Policy*, *83*, 219–230.

Andrews, L., Jahncke, M., & Mallikarjunan, K. (2003). Low dose gamma irradiation to reduce pathogenic *Vibrios* in live oysters (*Crassostrea virginica*). *Journal of Aquatic Food Product Technology*, *12*, 71–82.

Andrews, L. S., DeBlanc, S., Veal, C. D., & Park, D. L. (2003). Response of *Vibrio parahaemolyticus* 03:K6 to a hot water/cold shock pasteurization process. *Food Additives and Contaminants*, *20*, 331–334.

Andrews, L. S., Park, D. L., & Chen, Y.-P. (2000). Low temperature pasteurization to reduce the risk of vibrio infections from raw shell-stock oysters. *Food Additives and Contaminants*, *17*, 787–791.

Ansaruzzaman, M., Lucas, M., Deen, J. L., Bhuiyan, N. A., Wang, X.-Y., Safa, A., … Barreto, A. (2005). Pandemic serovars (O3:K6 and O4:K68) of *Vibrio parahaemolyticus* associated with diarrhea in Mozambique: Spread of the pandemic into the African continent. *Journal of Clinical Microbiology*, *43*, 2559–2562.

Anupama, K. P., Deeksha, K., Deeksha, A., Karunasagar, I. I., Karunasagar, I. I., & Maiti, B. (2019). Comparative performance of TCBS and TSA for the enumeration of trh+ *Vibrio parahaemolyticus* by direct colony hybridization. *Journal of Microbiological Methods*, *157*, 37–42.

Awuah, G. B., Ramaswamy, H. S., & Economides, A. (2007). Thermal processing and quality: Principles and overview. *Chemical Engineering and Processing: Process Intensification*, *46*, 584–602.

Baker-Austin, C., Oliver, J. D., Alam, M., Ali, A., Waldor, M. K., Qadri, F., & Martinez-Urtaza, J. (2018). *Vibrio* spp. infections. *Nature Reviews Disease Primers*, *4*, 8.

Baker-Austin, C., Stockley, L., Rangdale, R., & Martinez-Urtaza, J. (2010). Environmental occurrence and clinical impact of *Vibrio vulnificus* and *Vibrio parahaemolyticus*: A European perspective. *Environmental Microbiology Reports*, *2*, 7–18.

Baker-Austin, C., Trinanes, J. A., Taylor, N. G. H., Hartnell, R., Siitonen, A., & Martinez-Urtaza, J. (2013). Emerging *Vibrio* risk at high latitudes in response to ocean warming. *Nature Climate Change*, *3*, 73–77.

Baker, G. (2016). Food safety impacts from post-harvest processing procedures of molluscan shellfish. *Foods*, *5*, 29.

Barnard, P. L., Short, A. D., Harley, M. D., Splinter, K. D., Vitousek, S., Turner, I. L., … Heathfield, D. K. (2015). Coastal vulnerability across the Pacific dominated by El Niño/Southern oscillation. *Nature Geoscience*, *8*, 801–807.

Barrera-Escorcia, G., Wong-Chang, I., Fernández-Rendón, C. L., Botello, A. V., Gómez-Gil, B., & Lizárraga-Partida, M. L. (2016). Quantification of Vibrio species in oysters from the Gulf of Mexico with two procedures based on MPN and PCR. *Environmental Monitoring and Assessment*, *188*, 602.

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., … Guo, X. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience*, *61*, 107–116.

Bej, A. K., Patterson, D. P., Brasher, C. W., Vickery, M. C. L., Jones, D. D., & Kaysner, C. A. (1999). Detection of total and hemolysin-producing *Vibrio parahaemolyticus* in shellfish using multiplex PCR amplification of *tl*, *tdh* and *trh*. *Journal of Microbiological Methods*, *36*, 215–225.

Berlin, D. L., Herson, D. S., Hicks, D. T., & Hoover, D. G. (1999). Response of pathogenic *Vibrio* species to high hydrostatic pressure. *Applied and Environmental Microbiology*, *65*, 2776–2780.

Beuchat, L. R. (1975). Environmental factors affecting survival and growth of *Vibrio parahaemolyticus*. A review. *Journal of Milk and Food Technology*, *38*, 476–480.

Bisha, B., Simonson, J., Janes, M., Bauman, K., & Goodridge, L. D. (2012). A review of the current status of cultural and rapid detection of *Vibrio parahaemolyticus*. *International Journal of Food Science & Technology*, *47*, 885–899.

Blackstone, G. M., Nordstrom, J. L., Vickery, M. C., Bowen, M. D., Meyer, R. F., & DePaola, A. (2003). Detection of pathogenic *Vibrio parahaemolyticus* in oyster enrichments by real time PCR. *Journal of Microbiological Methods*, *53*, 149–155.

Broberg, C. A., Calder, T. J., & Orth, K. (2011). *Vibrio parahaemolyticus* cell biology and pathogenicity determinants. *Microbes and Infection*, *13*, 992–1001.

Brucet, S., Boix, D., Nathansen, L. W., Quintana, X. D., Jensen, E., Balayla, D., … Jeppesen, E. (2012). Effects of temperature, salinity and fish in structuring the macroinvertebrate community in Shallow lakes: Implications for effects of climate change. *PLoS ONE*, *7*, e30877.

Burdette, D. L., Yarbrough, M. L., Orvedahl, A., Gilpin, C. J., & Orth, K. (2008). *Vibrio parahaemolyticus* orchestrates a multifaceted host cell infection by induction of autophagy, cell rounding, and then cell lysis. *Proceedings of the National Academy of Sciences*, *105*, 12497–12502.

Burge, C. A., Mark Eakin, C., Friedman, C. S., Froelich, B., Hershberger, P. K., Hofmann, E. E., … Harvell, C. D. (2014). Climate change influences on marine infectious diseases: Implications for management and society. *Annual Review of Marine Science*, *6*, 249–277.

Butt, A. A., Aldridge, K. E., & Sanders, C. V. (2004). Infections related to the ingestion of seafood. Part I: Viral and bacterial infections. *Lancet Infectious Diseases*, *4*, 201–212.

Calik, H., Morrissey, M. T., Reno, P. W., & An, H. (2002). Effect of high-pressure processing on *Vibrio parahaemolyticus* strains in pure culture and Pacific oysters. *Journal of Food Science*, *67*, 1506–1510.

Campus, M. (2010). High pressure processing of meat, meat products and seafood. *Food Engineering Reviews*, *2*, 256–273.

Cao, X., Zhao, L., Zhang, J., Chen, X., Shi, L., Fang, X., … Wang, L. (2019). Detection of viable but nonculturable *Vibrio parahaemolyticus* in shrimp samples using improved real-time PCR and real-time LAMP methods. *Food Control*, *103*, 145–152.

Chae, M. J., Cheney, D., & Su, Y.-C. (2009). Temperature effects on the depuration of *Vibrio parahaemolyticus* and *Vibrio vulnificus* from the American oyster (*Crassostrea virginica*). *Journal of Food Science*, *74*, M62–M66.

Chai, T., Liang, K. T., Pace, J., & Schlimme, D. V. (1991). Effect of heat proacessing on quality of pasteurized oysters. *Journal of Food Science*, *56*, 1292–1294.

Chen, J., Zhang, R., Qi, X., Zhou, B., Wang, J., Chen, Y., & Zhang, H. (2017). Epidemiology of foodborne disease outbreaks caused by *Vibrio parahaemolyticus* during 2010–2014 in Zhejiang Province, China. *Food Control*, *77*, 110–115.

Chen, S., & Ge, B. (2010). Development of a toxR-based loop-mediated isothermal amplification assay for detecting *Vibrio parahaemolyticus*. *BMC Microbiology*, *10*, 41.

Cheng, W. C., Kuo, C. W., Chi, T. Y., Lin, L. C., Lee, C. H., Feng, R. L., & Tsai, S. J. (2013). Investigation on the trend of food-borne disease outbreaks in Taiwan (1991-2010). *Journal of Food and Drug Analysis*, *21*, 261–267.

Choi, C., Chun, H. S., Bahk, G. J., Kim, Y. S., Park, K. H., Chun, H. S., … Bahk, G. J. (2015). Correlations between climatic conditions and foodborne disease. *Food Research International*, *68*, 24–30.

Codex. (2010). Guidelines on the application of general principles of food hygiene to the control of pathogenic Vibrio species in seafood (GAC/GL 73–2010). Rome, Italy: World Health Organization/Food and Agriculture Organization.

Codex. (2016). Code of practice for fish and fishery products (CAC/RCP 52–2003). Rome, Italy: World Health Organization/Food and Agriculture Organization.

Cole, K. M., Supan, J., Ramirez, A., & Johnson, C. N. (2015). Suspension of oysters reduces the populations of *Vibrio parahaemolyticus* and *Vibrio vulnificus*. *Letters in Applied Microbiology*, *61*, 209–213.

Cook, D. W. (2003). Sensitivity of *Vibrio* species in phosphate-buffered saline and in oysters to high-pressure processing. *Journal of Food Protection*, *66*, 2276–2282.

Cook, D. W., O'Leary, P., Hunsucker, J. C., Sloan, E. M., Bowers, J. C., Blodgett, R. J., & Depaola, A. (2002). *Vibrio vulnificus* and *Vibrio parahaemolyticus* in U.S. Retail shell oysters: A national survey from June 1998 to July 1999. *Journal of Food Protection*, *65*, 79–87.

Cook, D. W., & Ruple, A. D. (1989). Indicator bacteria and Vibrionaceae multiplication in post-harvest shellstock oysters. *Journal of Food Protection*, *52*, 343–349.

Cook, D. W., & Ruple, A. D. (1992). Cold storage and mild heat treatment as processing aids to reduce the numbers of *Vibrio vulnificus* in raw oysters. *Journal of Food Protection*, *55*, 985–989.

Coutard, F., Crassous, P., Droguet, M., Gobin, E., Colwell, R. R., Pommepuy, M., & Hervio-Heath, D. (2007). Recovery in culture of viable but nonculturable *Vibrio parahaemolyticus*: Regrowth or resuscitation? *ISME Journal*, *1*, 111–120.

Cruz, C. D., Hedderley, D., & Fletcher, G. C. (2015). Long-term study of *Vibrio parahaemolyticus* prevalence and distribution in New Zealand shellfish. *Applied and Environmental Microbiology*, *81*, 2320–2327.

Davis, B. J. K., Jacobs, J. M., Davis, M. F., Schwab, K. J., DePaola, A., & Curriero, F. C. (2017). Environmental determinants of *Vibrio parahaemolyticus* in the Chesapeake Bay. *Applied and Environmental Microbiology*, *83*, 1–15.

Deepanjali, A., Kumar, H. S., Karunasagar, I., & Karunasagar, I. (2005). Seasonal variation in abundance of total and pathogenic *Vibrio para-*

haemolyticus bacteria in oysters along the southwest coast of India. *Applied and Environmental Microbiology*, *71*, 3575–3580.

DePaola, A., Hopkins, L. H., Peeler, J. T., Wentz, B., & McPhearson, R. M. (1990). Incidence of *Vibrio parahaemolyticus* in U.S. coastal waters and oysters. *Applied and Environmental Microbiology*, *56*, 2299–2302.

DePaola, A., Nordstrom, J. L., Bowers, J. C., Wells, J. G., & Cook, D. W. (2003). Seasonal abundance of total and pathogenic *Vibrio parahaemolyticus* in Alabama oysters. *Applied and Environmental Microbiology*, *69*, 1521–1526.

Di, D. Y. W., Lee, A., Jang, J., Han, D., & Hur, H.-G. (2017). Season-Specific occurrence of potentially pathogenic *Vibrio* spp. on the southern coast of South Korea. *Applied and Environmental Microbiology*, *83*, 1–13.

Donner, L. J., Wyman, B. L., Hemler, R. S., Horowitz, L. W., Ming, Y., Zhao, M., … Zeng, F. (2011). The dynamical core, physical parameterizations, and basic simulation characteristics of the atmospheric component AM3 of the GFDL global coupled model CM3. *Journal of Climate*, *24*, 3484–3519.

Drake, S. L., DePaola, A., & Jaykus, L.-A. (2007). An overview of *Vibrio vulnificus* and *Vibrio parahaemolyticus*. *Comprehensive Reviews in Food Science and Food Safety*, *6*, 120–144.

Duan, J., & Su, Y.-C. (2005a). Comparison of a chromogenic medium with thiosulfate-citrate-bile salts-sucrose agar for detecting *Vibrio parahaemolyticus*. *Journal of Food Science*, *70*, M125–M128.

Duan, J., & Su, Y.-C. (2005b). Occurrence of *vibrio parahaemolyticus* in two Oregon oyster-growing bays. *Journal of Food Science*, *70*, M58–M63.

Dufresne, J.-L., Foujols, M.-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., … Vuichard, N. (2013). Climate change projections using the IPSL-CM5 Earth System Model: From CMIP3 to CMIP5. *Climate Dynamics*, *40*, 2123–2165.

Esteves, K., Hervio-Heath, D., Mosser, T., Rodier, C., Tournoud, M.-G., Jumas-Bilak, E., … Monfort, P. (2015). Rapid proliferation of *Vibrio parahaemolyticus*, *Vibrio vulnificus*, and *Vibrio cholerae* during freshwater flash floods in French Mediterranean coastal lagoons. *Applied and Environmental Microbiology*, *81*, 7600–7609.

Eyles, M. J., & Davey, G. R. (1984). Microbiology of commercial depuration of the Sydney rock oyster, *Crassostrea commercialis*. *Journal of Food Protection*, *47*, 703–706.

FAO/WHO. (2011). *Risk assessment of Vibrio parahaemolyticus in seafood—Interpretative summary and technical report*. Microbial risk assessment series (Vol. *16*). Rome, Italy: Food and Agriculture Organization of the United Nations.

Food and Agriculture Organization (FAO) of The United Nation. (2019). *Fisheries and aquaculture information and statistics branch*. Retrieved from http://www.fao.org/fishery/statistics/global-production/en

Feinman, S. G., Farah, Y. R., Bauer, J. M., & Bowen, J. L. (2018). The Influence of oyster farming on sediment bacterial communities. *Estuaries and Coasts*, *41*, 800–814.

Feng, H., Chen, J., Zhou, W., Rungsardthong, V., & Zhang, X. (2019). Modeling and evaluation on WSN-enabled and knowledge-based HACCP quality control for frozen shellfish cold chain. *Food Control*, *98*, 348–358.

Fernandez-Piquer, J., Bowman, J. P., Ross, T., & Tamplin, M. L. (2011). Predictive models for the effect of storage temperature on *Vibrio parahaemolyticus* viability and counts of total viable bacteria in Pacific oysters (*Crassostrea gigas*). *Applied and Environmental Microbiology*, *77*, 8687–8695.

Fletcher, G. C. (1985). The potential food poisoning hazard of *Vibrio parahaemolyticus* in New Zealand Pacific oysters. *New Zealand Journal of Marine and Freshwater Research*, *19*, 495–505.

Food Standards Australia New Zealand. (2018). *Compendium of microbiological criteria for food*. Retrieved from http://www.foodstandards.gov.au/publications/pages/compendium-of-microbiological-criteria-for-food.aspx

Frischkorn, K. R., Stojanovski, A., & Paranjpye, R. (2013). *Vibrio parahaemolyticus* type IV pili mediate interactions with diatom-derived chitin and point to an unexplored mechanism of environmental persistence. *Environmental Microbiology*, *15*, 1416–1427.

Froelich, B. A., & Noble, R. T. (2016). Vibrio bacteria in raw oysters: Managing risks to human health. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150209.

Froelich, B. A., Phippen, B., Fowler, P., Noble, R. T., & Oliver, J. D. (2017). Differences in abundances of total *Vibrio* spp., *V. vulnificus*, and *V. parahaemolyticus* in clams and oysters in North Carolina. *Applied and Environmental Microbiology*, *83*, 1–11.

Garcia, K., Torres, R., Uribe, P., Hernandez, C., Rioseco, M. L., Romero, J., & Espejo, R. T. (2009). Dynamics of clinical and environmental *Vibrio parahaemolyticus* strains during seafood-related summer diarrhea outbreaks in southern Chile. *Applied and Environmental Microbiology*, *75*, 7482–7487.

Garrido, V., & Otwell, S. (2009). Hazard analysis and critical control point programs for raw oyster processing and handling. In S. E. Shumway, & G. E. Rodrick (Eds.), *Shellfish safety and quality* (pp. 295–316). Cambridge, UK: Woodhead Publishing.

Gil, A. I., Miranda, H., Lanata, C. F., Prada, A., Hall, E. R., Barreno, C. M., … Nair, G. B. (2007). O3:K6 Serotype of *Vibrio parahaemolyticus* identical to the global pandemic clone associated with diarrhea in Peru. *International Journal of Infectious Diseases*, *11*, 324–328.

Givens, C. E., Bowers, J. C., DePaola, A., Hollibaugh, J. T., & Jones, J. L. (2014). Occurrence and distribution of *Vibrio vulnificus* and *Vibrio parahaemolyticus*—Potential roles for fish, oyster, sediment and water. *Letters in Applied Microbiology*, *58*, 503–510.

González-Escalona, N., Cachicas, V., Acevedo, C., Rioseco, M. L., Vergara, J. A., Cabello, F., … Espejo, R. T. (2005). *Vibrio parahaemolyticus* diarrhea, Chile, 1998 and 2004. *Emerging Infectious Diseases*, *11*, 129–131.

Gooch, J. A., DePaola, A., Bowers, J., & Marshall, D. L. (2002). Growth and survival of *Vibrio parahaemolyticus* in postharvest American oysters. *Journal of Food Protection*, *65*, 970–974.

Göransson, M., Nilsson, F., Jevinger, Å., & Jevinger (2018). Temperature performance and food shelf-life accuracy in cold food supply chains—Insights from multiple field studies. *Food Control*, *86*, 332–341.

Grodeska, S. M., Jones, J. L., Arias, C. R., & Walton, W. C. (2017). Effects of desiccation practices of cultured atlantic oysters (*Crassostrea virginica*) on vibrio spp. in Portersville Bay, Alabama, USA. *Journal of Food Protection*, *80*, 1280–1287.

Grodeska, S. M., Jones, J. L., Walton, W. C., & Arias, C. R. (2019). Effects of desiccation practices and ploidy in cultured oysters, *Crassostrea virginica*, on Vibrio spp. abundances in Portersville Bay (Alabama, USA). *Aquaculture*, *507*, 164–171.

Gutierrez West, C. K., Klein, S. L., & Lovell, C. R. (2013). High frequency of virulence factor genes *tdh*, *trh*, and *tlh* in *Vibrio*

parahaemolyticus strains isolated from a pristine estuary. *Applied and Environmental Microbiology*, *79*, 2247–2252.

Guvener, Z. T., & McCarter, L. L. (2003). Multiple regulators control capsular polysaccharide production in *Vibrio parahaemolyticus*. *Journal of Bacteriology*, *185*, 5431–5441.

Han, F., Gu, R. R., Shen, X. S., Chen, Y. G., Tian, L. L., Zhou, W. F., & Cai, Y. Q. (2017). Detection of total and pathogenic *Vibrio parahaemolyticus* in shellfish growing along the south yellow sea and the East China sea. *Journal of Food Protection*, *17*, 1882–1889.

Hara-Kudo, Y., & Kumagai, S. (2014). Impact of seafood regulations for *Vibrio parahaemolyticus* infection and verification by analyses of seafood contamination and infection. *Epidemiology and Infection*, *142*, 2237–2247.

Hara-Kudo, Y., Saito, S., Ohtsuka, K., Yamasaki, S., Yahiro, S., Nishio, T., … Kumagai, S. (2012). Characteristics of a sharp decrease in *Vibrio parahaemolyticus* infections and seafood contamination in Japan. *International Journal of Food Microbiology*, *157*, 95–101.

Hara-Kudo, Y., Sugiyama, K., Nishibuchi, M., Chowdhury, A., Yatsuyanagi, J., Ohtomo, Y., … Kumagai, S. (2003). Prevalence of pandemic thermostable direct hemolysin-producing *Vibrio parahaemolyticus* O3:K6 in seafood and the coastal environment in Japan. *Applied and Environmental Microbiology*, *69*, 3883–3891.

Harth, E., Matsuda, L., Hernández, C., Rioseco, M. L., Romero, J., González-Escalona, N., … Espejo, R. T. (2009). Epidemiology of *Vibrio parahaemolyticus* outbreaks, Southern Chile. *Emerging Infectious Diseases*, *15*, 163–168.

Hartwick, M. A., Urquhart, E. A., Whistler, C. A., Cooper, V. S., Naumova, E. N., & Jones, S. H. (2019). Forecasting seasonal *Vibrio parahaemolyticus* concentrations in New England shellfish. *International Journal of Environmental Research and Public Health*, *16*, 4341.

Hasegawa, A., Hara-Kudo, Y., Ogata, K., Saito, S., Sugita-Konishi, Y., & Kumagai, S. (2013). Differences in the stress tolerances of *Vibrio parahaemolyticus* strains due to their source and harboring of virulence genes. *Journal of Food Protection*, *76*, 1456–1462.

Health Canada's Food Directorate. (2019). *Information document with request for input and scientific data: Vibrio parahaemolyticus in oyster shellstock intended for raw consumption*. Retrieved from https://www.canada.ca/en/health-canada/services/food-nutrition/public-involvement-partnerships/request-input-scientific-data-vibrio-parahaemolyticus-oyster-shellstock-intended-consumption/consultation.html

Heilandt, T., Mulholland, C., & Younes, M. (2014). Institutions involved in food safety: FAO/WHO Codex Alimentarius Commission (CAC). In Y. Motarjemi, G. Moy, & E. Todd (Ed.), *Encyclopedia of food safety* (pp. 345–353). Cambridge, MA: Academic Press.

Hiyoshi, H., Kodama, T., Iida, T., & Honda, T. (2010). Contribution of *Vibrio parahaemolyticus* virulence factors to cytotoxicity, enterotoxicity, and lethality in mice. *Infection and Immunity*,

Hiyoshi, H., Okada, R., Matsuda, S., Gotoh, K., Akeda, Y., Iida, T., & Kodama, T. (2015). Interaction between the Type III effector VopO and GEF-H1 activates the RhoA-ROCK pathway. *PLoS Pathogens*, *11*, 1–19.

Honda, T., Ni, Y., & Miwatani, T. (1988). Purification and characterization of a hemolysin produced by a clinical isolate of Kanagawa phenomenon-negative *Vibrio parahaemolyticus* and related to the thermostable direct hemolysin. *Infection and Immunity*, *56*, 961–965.

Hsiao, H. I., Jan, M. S., & Chi, H. J. (2016). Impacts of climatic variability on *Vibrio parahaemolyticus* outbreaks in Taiwan. *International Journal of Environmental Research and Public Health*, *13*, 188.

Hsieh, J. L., Fries, J. S., & Noble, R. T. (2007). Vibrio and phytoplankton dynamics during the summer of 2004 in a eutrophying estuary. *Ecological Applications*, *17*, S102–S109.

Huang, Y.-R., Hsieh, H.-S., Lin, S.-Y., Lin, S.-J., Hung, Y.-C., & Hwang, D.-F. (2006). Application of electrolyzed oxidizing water on the reduction of bacterial contamination for seafood. *Food Control*, *17*, 987–993.

Huang, Y.-S., Hwang, C.-A., Huang, L., Wu, V. C.-H., & Hsiao, H.-I. (2018). The risk of *Vibrio parahaemolyticus* infections associated with consumption of raw oysters as affected by processing and distribution conditions in Taiwan. *Food Control*, *86*, 101–109.

Humphries, R. M., & Linscott, A. J. (2015). Laboratory diagnosis of bacterial gastroenteritis. *Clinical Microbiology Reviews*, *28*, 3–31.

Hussain, M., & Dawson, C. (2013). Economic impact of food safety outbreaks on food businesses. *Foods*, *2*, 585–589.

Iida, T., Park, K.-S., Suthienkul, O., Kozawa, J., Yamaichi, Y., Yamamoto, K., & Honda, T. (1998). Close proximity of the *tdh*, *trh* and *ure* genes on the chromosome of *Vibrio parahaemolyticus*. *Microbiology*, *144*, 2517–2523.

ICMSF. (2011). *Microorganisms in foods 8 - use of data for assessing process control and product acceptance*. Boston, US: Springer.

Intergovernmental Panel on Climate Change (IPCC). (2014). Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: Author.

Iwamoto, M., Ayers, T., Mahon, B. E., & Swerdlow, D. L. (2010). Epidemiology of seafood-associated infections in the United States. *Clinical Microbiology Reviews*, *23*, 399–411.

Jahid, I. K., Mizan, M. F. R., Ha, A. J., & Ha, S.-D. (2015). Effect of salinity and incubation time of planktonic cells on biofilm formation, motility, exoprotease production, and quorum sensing of *Aeromonas hydrophila*. *Food Microbiology*, *49*, 142–151.

Jakabi, M., Gelli, D. S., Torre, J. C. M. D., Rodas, M. A. B., Franco, B. D. G. M., Destro, M. T., & Landgraf, M. (2003). Inactivation by ionizing radiation of *Salmonella Enteritidis*, *Salmonella infantis*, and *Vibrio parahaemolyticus* in oysters (*Crassostrea brasiliana*). *Journal of Food Protection*, *66*, 1025–1029.

James, S. J., & James, C. (2010). The food cold-chain and climate change. *Food Research International*, *43*, 1944–1956.

Jaykus, L.-A. (2010). Climate change: Implications for food safety. *Health San Francisco*, *1196*, 1–354.

Jiang, C., Shaw, K. S., Upperman, C. R., Blythe, D., Mitchell, C., Murtugudde, R., … Sapkota, A. (2015). Climate change, extreme events and increased risk of salmonellosis in Maryland, USA: Evidence for coastal vulnerability. *Environment International*, *83*, 58–62.

Jiang, W., Han, X., Wang, Q., Li, X., Yi, L., Liu, Y., & Ding, C. (2014). *Vibrio parahaemolyticus* enolase is an adhesion-related factor that binds plasminogen and functions as a protective antigen. *Applied Microbiology and Biotechnology*, *98*, 4937–4948.

Johnson, C. N., Bowers, J. C., Griffitt, K. J., Molina, V., Clostio, R. W., Pei, S., … Colwell, R. R. (2012). Ecology of *Vibrio parahaemolyticus* and *Vibrio vulnificus* in the Coastal and Estuarine Waters of Louisiana, Maryland, Mississippi, and Washington (United States). *Applied and Environmental Microbiology*, *78*, 7249–7257.

Johnson, C. N., Flowers, A. R., Noriea, N. F., Zimmerman, A. M., Bowers, J. C., DePaola, A., & Grimes, D. J. (2010). Relationships between environmental factors and pathogenic Vibrios in the Northern Gulf of Mexico. *Applied and Environmental Microbiology*, *76*, 7076–7084.

Jones, J. L., Lüdeke, C. H. M., Bowers, J. C., DeRosia-Banick, K., Carey, D. H., & Hastback, W. (2014). Abundance of *Vibrio cholerae*, *V. vulnificus*, and *V. parahaemolyticus* in oysters (*Crassostrea virginica*) and clams (*Mercenaria mercenaria*) from Long Island Sound. *Applied and Environmental Microbiology*, *80*, 7667–7672.

Jones, J. L., Lüdeke, C. H. M., Bowers, J. C., Garrett, N., Fischer, M., Parsons, M. B., … DePaola, A. (2012). Biochemical, serological, and virulence characterization of clinical and oyster *Vibrio parahaemolyticus* isolates. *Journal of Clinical Microbiology*, *50*, 2343–2352.

Jones, J. L., Lydon, K. A., Kinsey, T. P., Friedman, B., Curtis, M., Schuster, R., & Bowers, J. C. (2017). Effects of ambient exposure, refrigeration, and icing on *Vibrio vulnificus* and *Vibrio parahaemolyticus* abundances in oysters. *International Journal of Food Microbiology*, *253*, 54–58.

Jones, J. L., Noe, K. E., Byars, R., & Depaola, A. (2009). Evaluation of DNA colony hybridization and real-time PCR for detection of *Vibrio parahaemolyticus* and *Vibrio vulnificus* in postharvest-processed oysters. *Journal of Food Protection*, *72*, 2106–2109.

Jung, S. W. (2018). A foodborne outbreak of gastroenteritis caused by *Vibrio parahaemolyticus* associated with cross-contamination from squid in Korea. *Epidemiology and Health*, *40*, e2018056.

Kampeera, J., Pasakon, P., Karuwan, C., Arunrut, N., Sappat, A., Sirithammajak, S., … Kiatpathomchai, W. (2019). Point-of-care rapid detection of *Vibrio parahaemolyticus* in seafood using loop-mediated isothermal amplification and graphene-based screen-printed electrochemical sensor. *Biosensors and Bioelectronics*, *132*, 271–278.

Kaneko, T., & Colwell, R. R. (1975). Incidence of *Vibrio parahaemolyticus* in Chesapeake Bay. *Applied Microbiology*, *30*, 251–257.

Kaysner, C. A., Abeyta, C., Stott, R. F., Krane, M. H., & Wekell, M. M. (1990). Enumeration of *Vibrio* species, including V. Cholerae, from samples of an oyster growing area, Grays Harbor, Washington. *Journal of Food Protection*, *53*, 300–301.

Kaysner, C. A., Abeyta, C., Stott, R. F., Lilja, J. L., & Wekell, M. M. (1990). Incidence of urea-hydrolyzing *Vibrio parahaemolyticus* in Willapa Bay, Washington. *Applied and Environmental Microbiology*, *56*, 904–907.

Kecinski, M., Messer, K. D., Knapp, L., & Shirazi, Y. (2017). Consumer preferences for oyster attributes: Field experiments on brand, locality, and growing method. *Agricultural and Resource Economics Review*, *46*, 315–337.

Kim, J. S., Lee, G. G., Kim, J., Kwon, J. Y., & Kwon, S.-T. (2008). The development of rapid real-time PCR detection system for *Vibrio parahaemolyticus* in raw oyster. *Letters in Applied Microbiology*, *46*, 649–654.

Kim, Y., Lee, S., Hwang, I., & Yoon, K. (2012). Effect of temperature on growth of *Vibrio paraphemolyticus* and *Vibrio vulnificus* in flounder, salmon, sashimi, and oyster meat. *International Journal of Environmental Research and Public Health*, *9*, 4662–4675.

Kinsey, T. P., Lydon, K. A., Bowers, J. C., & Jones, J. L. (2015). Effects of dry storage and resubmersion of oysters on total *Vibrio vulnificus* and total and pathogenic (tdh/trh) *Vibrio parahaemolyticus* levels. *Journal of Food Protection*, *78*, 1574–1580.

Kirs, M., DePaola, A., Fyfe, R., Jones, J. L., Krantz, J., Van Laanen, A., … Castle, M. (2011). A survey of oysters (*Crassostrea gigas*) in New Zealand for *Vibrio parahaemolyticus* and *Vibrio vulnificus*. *International Journal of Food Microbiology*, *147*, 149–153.

Kleboth, J. A., Luning, P. A., & Fogliano, V. (2016). Risk-based integrity audits in the food chain—A framework for complex systems. *Trends in Food Science & Technology*, *56*, 167–174.

Kokashvili, T., Whitehouse, C. A., Tskhvediani, A., Grim, C. J., Elbakidze, T., Mitaishvili, N., … Tediashvili, M. (2015). Occurrence and diversity of clinically important *Vibrio* species in the aquatic environment of Georgia. *Frontiers in Public Health*, *3*, 232.

Konrad, S., Paduraru, P., Romero-Barrios, P., Henderson, S. B., & Galanis, E. (2017). Remote sensing measurements of sea surface temperature as an indicator of *Vibrio parahaemolyticus* in oyster meat and human illnesses. *Environmental Health*, *16*, 92.

Koo, J., Jahncke, M. L., Reno, P. W., Hu, X., & Mallikarjunan, P. (2006). Inactivation of *Vibrio parahaemolyticus* and *Vibrio vulnificus* in phosphate-buffered saline and in inoculated whole oysters by high-pressure processing. *Journal of Food Protection*, *69*, 596–601.

Kotsanopoulos, K. V., & Arvanitoyannis, I. S. (2017). The role of auditing, food safety, and food quality standards in the food industry: A review. *Comprehensive Reviews in Food Science and Food Safety*, *16*, 760–775.

Kural, A. G., Shearer, A. E. H., Kingsley, D. H., & Chen, H. (2008). Conditions for high pressure inactivation of *Vibrio parahaemolyticus* in oysters. *International Journal of Food Microbiology*, *127*, 1–5.

Lai, W. bin, & Wong, H. C. (2013). Influence of combinations of sublethal stresses on the control of *Vibrio parahaemolyticus* and its cellular oxidative response. *Food Control*, *33*, 186–192.

Lake, I. R. (2017). Food-borne disease and climate change in the United Kingdom. *Environmental Health*, *16*, 117.

Leal, N. C., da Silva, S. C., Cavalcanti, V. O., Figueiroa, Â. C. T. de A., Nunes, V. V. F., Miralles, I. S., & Hofer, E. (2008). *Vibrio parahaemolyticus* serovar O3:K6 gastroenteritis in northeast Brazil. *Journal of Applied Microbiology*, *105*, 691–697.

Lee, C. Y., Cheng, M. F., Yu, M. S., & Pan, M. J. (2002). Purification and characterization of a putative virulence factor, serine protease, from *Vibrio parahaemolyticus*. *FEMS Microbiology Letters*, *209*, 30–36.

Lee, R., Lovatelli, A., & Ababouch, L. (2008). *Bivalve depuration: Fundamental and practical aspects*. Rome, Italy: Food and Agriculture Organization of the United Nations.

León-Sicairos, N., Angulo-Zamudio, U. A., de la Garza, M., Velázquez-Román, J., Flores-Villaseñor, H. M., & Canizalez-Román, A. (2015). Strategies of *Vibrio parahaemolyticus* to acquire nutritional iron during host colonization. *Frontiers in Microbiology*, *6*, 1–14.

Lesmana, M., Subekti, D. S., Tjaniadi, P., Simanjuntak, C. H., Punjabi, N. H., Campbell, J. R., & Oyofo, B. A. (2002). Spectrum of vibrio species associated with acute diarrhea in North Jakarta, Indonesia. *Diagnostic Microbiology and Infectious Disease*, *43*, 91–97.

Letchumanan, V., Chan, K. G., & Lee, L. H. (2014). *Vibrio parahaemolyticus*: A review on the pathogenesis, prevalence, and advance molecular identification techniques. *Frontiers in Microbiology*, *5*, 705.

Levy, S. (2018). ECDC Vibrio map viewer: Tracking the whereabouts of pathogenic species. *Environmental Health Perspectives*, *126*, 8–9.

Li, H., Tang, R., Lou, Y., Cui, Z., Chen, W., Hong, Q., … Zhao, Y. (2017). A comprehensive epidemiological research for clinical *Vibrio parahaemolyticus* in Shanghai. *Frontiers in Microbiology*, *8*, 1–10.

Li, J., Xue, F., Yang, Z., Zhang, X., Zeng, D., Chao, G., … Li, B. (2016). *Vibrio parahaemolyticus* strains of pandemic serotypes identified from clinical and environmental samples from Jiangsu, China. *Frontiers in Microbiology*, *7*, 787.

Li, L., Meng, H., Gu, D., Li, Y., & Jia, M. (2019). Molecular mechanisms of *Vibrio parahaemolyticus* pathogenesis. *Microbiological Research*, *222*, 43–51.

Li, P., Kinch, L. N., Ray, A., Dalia, A. B., Cong, Q., Nunan, L. M., … Orth, K. (2017). Acute hepatopancreatic necrosis disease-causing *Vibrio parahaemolyticus* strains maintain an antibacterial Type VI Secretion System with versatile effector repertoires. *Applied and Environmental Microbiology*, *83*, 1–17.

Liao, Y., Li, Y., Wu, S., Mou, J., Xu, Z., Cui, R., … Cheng, J. (2015). Risk factors for *Vibrio parahaemolyticus* infection in a Southern Coastal Region of China. *Foodborne Pathogens and Disease*, *12*, 881–886.

Limthammahisorn, S., Brady, Y. J., & Arias, C. R. (2009). In vivo gene expression of cold shock and other stress-related genes in *Vibrio vulnificus* during shellstock temperature control conditions in oysters. *Journal of Applied Microbiology*, *106*, 642–650.

Lin, C.-C., Lin, P.-S., Kou, L.-L., Hong, Y.-P., & Wu, H.-S. (2015). Epidemiology of *Vibrio parahaemolyticus* in Southern Taiwan, 2004–2013. *Taiwan Epidemiology Bulletin*, *31*, 194–195.

Liu, B., Liu, H., Pan, Y., Xie, J., & Zhao, Y. (2016). Comparison of the effects of environmental parameters on the growth variability of *Vibrio parahaemolyticus* coupled with strain sources and genotypes analyses. *Frontiers in Microbiology*, *7*, 994.

Liu, C., Lu, J., & Su, Y.-C. (2009). Effects of flash freezing, followed by frozen storage, on reducing *Vibrio parahaemolyticus* in Pacific raw oysters (*Crassostrea gigas*). *Journal of Food Protection*, *72*, 174–177.

Liu, M., & Chen, S. (2015). A novel adhesive factor contributing to the virulence of *Vibrio parahaemolyticus*. *Scientific Reports*, *5*, 1–10.

Lopatek, M., Wieczorek, K., & Osek, J. (2015). Prevalence and antimicrobial resistance of *Vibrio parahaemolyticus* isolated from raw shellfish in Poland. *Journal of Food Protection*, *78*, 1029–1033.

López-Hernández, K. M., Pardío-Sedas, V., Lizárraga-Partida, L., Williams, J. de J., Martínez-Herrera, D., Flores-Primo, A., & Uscanga-Serrano, R. (2015). Seasonal abundance of Vibrio cholerae non O1/non O139 chxA+ in oysters harvested in a coastal lagoon of Mexico's Gulf coast: A seafood safety risk concern. *Food Control*, *53*, 46–54.

López-Hernández, K. M., Pardío-Sedas, V. T., Lizárraga-Partida, L., Williams, J. de J., Martínez-Herrera, D., Flores-Primo, A., … Rendón-Castro, K. (2015). Environmental parameters influence on the dynamics of total and pathogenic *Vibrio parahaemolyticus* densities in *Crassostrea virginica* harvested from Mexico's Gulf coast. *Marine Pollution Bulletin*, *91*, 317–329.

Lopez-Joven, C., de Blas, I., Furones, M. D., & Roque, A. (2015). Prevalences of pathogenic and non-pathogenic *Vibrio parahaemolyticus* in mollusks from the Spanish Mediterranean Coast. *Frontiers in Microbiology*, *6*, 736.

Love, D. C., Kuehl, L. M., Lane, R. M., Fry, J. P., Harding, J., Davis, B. J. K., … Hudson, B. (2019). Performance of cold chains and modeled growth of *Vibrio parahaemolyticus* for farmed oysters distributed in the United States and internationally. *International Journal of Food Microbiology*, *313*, 108378.

Love, D. C., Lane, R. M., Fry, J. P., Davis, B. J. K., Hudson, B., Clancy, K., & Harding, J. (2019). Performance of cold chains for Chesapeake Bay farmed oysters and modeled growth of *Vibrio parahaemolyticus*. *Journal of Food Protection*, *82*, 168–178.

Lozano-León, A., Torres, J., Osorio, C. R., & Martínez-Urtaza, J. (2003). Identification of tdh-positive *Vibrio parahaemolyticus* from an outbreak associated with raw oyster consumption in Spain. *FEMS Microbiology Letters*, *226*, 281–284.

Lydon, K. A., Farrell-Evans, M., & Jones, J. L. (2015). Evaluation of ice slurries as a control for postharvest growth of *Vibrio* spp. in oysters and potential for filth contamination. *Journal of Food Protection*, *78*, 1375–1379.

Ma, C., Deng, X., Ke, C., He, D., Liang, Z., Li, W., … Cui, Z. (2014). Epidemiology and etiology characteristics of foodborne outbreaks caused by *Vibrio parahaemolyticus* during 2008–2010 in Guangdong Province, China. *Foodborne Pathogens and Disease*, *11*, 21–29.

Ma, L., & Su, Y. C. (2011). Validation of high pressure processing for inactivating *Vibrio parahaemolyticus* in Pacific oysters (*Crassostrea gigas*). *International Journal of Food Microbiology*, *144*, 469–474.

Madigan, T. L. (2007). A critical evaluation of supply-chain temperature profiles to optimise food safety and quality of Australian oysters. Project No. 2007/700. Glenside, Australia: Australian Seafood Cooperative Research Center.

Mahmoud, B. S. M. (2009). Reduction of *Vibrio vulnificus* in pure culture, half shell and whole shell oysters (*Crassostrea virginica*) by X-ray. *International Journal of Food Microbiology*, *130*, 135–139.

Mahmoud, B. S. M., & Burrage, D. D. (2009). Inactivation of *Vibrio parahaemolyticus* in pure culture, whole live and half shell oysters (*Crassostrea virginica*) by X-ray. *Letters in Applied Microbiology*, *48*, 572–578.

Makino, K., Oshima, K., Kurokawa, K., Yokoyama, K., Uda, T., Tagomori, K., … Iida, T. (2003). Genome sequence of *Vibrio parahaemolyticus*: A pathogenic mechanism distinct from that of *V cholerae*. *The Lancet*, *361*, 743–749.

Malcolm, T. T. H., Cheah, Y. K., Radzi, C. W. J. W. M., Kasim, F. A., Kantilal, H. K., Huat John, T. Y., … Son, R. (2015). Detection and quantification of pathogenic *Vibrio parahaemolyticus* in shellfish by using multiplex PCR and loop-mediated isothermal amplification assay. *Food Control*, *47*, 664–671.

Marques, A., Nunes, M. L., Moore, S. K., & Strom, M. S. (2010). Climate change and seafood safety: Human health implications. *Food Research International*, *43*, 1766–1779.

Martinez-Urtaza, J., Blanco-Abad, V., Rodriguez-Castro, A., Ansede-Bermejo, J., Miranda, A., & Rodriguez-Alvarez, M. X. (2012). Ecological determinants of the occurrence and dynamics of *Vibrio parahaemolyticus* in offshore areas. *ISME Journal*, *6*, 994–1006.

Martinez-Urtaza, J., Huapaya, B., Gavilan, R. G., Blanco-Abad, V., Ansede-Bermejo, J., Cadarso-Suarez, C., … Trinanes, J. (2008). Emergence of Asiatic *Vibrio* diseases in South America in phase with El Niño. *Epidemiology*, *19*, 829–837.

Matsuda, S., Okada, R., Tandhavanant, S., Hiyoshi, H., Gotoh, K., Iida, T., & Kodama, T. (2019). Export of a *Vibrio parahaemolyticus* toxin by the Sec and type III secretion machineries in tandem. *Nature Microbiology*, *4*, 781–788.

Matté, G. R., Matté, M. H., Rivera, I. G., & Martins, M. T. (1994). Distribution of potentially pathogenic vibrios in oysters from a tropical region. *Journal of Food Protection*, *57*, 870–873.

Matthiessen, George C. (2001). *Oyster culture*. Oxford, UK: Fishing News Books.

McDonnell, S., Kirkland, K. B., Hlady, W. G., Aristeguieta, C., Hophins, R. S., Monroe, S. S., & Glass, R. I. (1997). Failure of cooking to prevent shellfish-associated viral gastroenteritis. *Archives of Internal Medicine*, *157*, 111–116.

McLaughlin, J. B., DePaola, A., Bopp, C. A., Martinek, K. A., Napolilli, N. P., Allison, C. G., … Middaugh, J. P. (2005). Outbreak of

Vibrio parahaemolyticus gastroenteritis associated with Alaskan oysters. *New England Journal of Medicine*, *353*, 1463–1470.

Meehl, G. A., Hu, A., Santer, B. D., & Xie, S. P. (2016). Contribution of the Interdecadal Pacific Oscillation to twentieth-century global surface temperature trends. *Nature Climate Change*, *6*, 1005–1008.

Melody, K., Senevirathne, R., Janes, M., Jaykus, L. A., & Supan, J. (2008). Effectiveness of icing as a postharvest treatment for control of *Vibrio vulnificus* and *Vibrio parahaemolyticus* in the eastern oyster (*Crassostrea virginica*). *Journal of Food Protection*, *71*, 1475–1480.

Mercier, S., Villeneuve, S., Mondor, M., & Uysal, I. (2017). Time-temperature management along the food cold chain: A review of recent developments. *Comprehensive Reviews in Food Science and Food Safety*, *16*, 647–667.

MHLW. (2010). *Specifications and standards for foods, food additives, etc. under the food sanitation act*. Retrieved from http://www.jetro.go.jp/en/reports/regulations/pdf/testing2009dec-e.pdf

Mok, J. S., Ryu, A., Kwon, J. Y., Kim, B., & Park, K. (2019). Distribution of Vibrio species isolated from bivalves and bivalve culture environments along the Gyeongnam coast in Korea: Virulence and antimicrobial resistance of *Vibrio parahaemolyticus* isolates. *Food Control*, *106*, 106697.

Mudoh, M. F., Parveen, S., Schwarz, J., Rippen, T., & Chaudhuri, A. (2014). The effects of storage temperature on the growth of *Vibrio parahaemolyticus* and organoleptic properties in oysters. *Frontiers in Public Health*, *2*, 45.

Muhling, B. A., Jacobs, J., Stock, C. A., Gaitan, C. F., & Saba, V. S. (2017). Projections of the future occurrence, distribution, and seasonality of three *Vibrio* species in the Chesapeake Bay under a high-emission climate change scenario. *GeoHealth*, *1*, 278–296.

Muntada-Garriga, J. M., Rodriguez-Jerez, J. J., Lopez-Sabater, E. I., & Mora-Ventura, M. T. (1995). Effect of chill and freezing temperatures on survival of *Vibrio parahaemolyticus* inoculated in homogenates of oyster meat. *Letters in Applied Microbiology*, *20*, 225–227.

Nair, G. B., Ramamurthy, T., Bhattacharya, S. K., Dutta, B., Takeda, Y., & Sack, D. A. (2007). Global dissemination of *Vibrio parahaemolyticus* serotype O3:K6 and its serovariants. *Clinical Microbiology Reviews*, *20*, 39–48.

Nakaguchi, Y. (2013). Contamination by *Vibrio parahaemolyticus* and its virulent strains in seafood marketed in Thailand, Vietnam, Malaysia, and Indonesia. *Tropical Medicine and Health*, *41*, 95–102.

Nauta, M. J. (2000). Separation of uncertainty and variability in quantitative microbial risk assessment models. *International Journal of Food Microbiology*, *57*, 9–18.

Ndraha, N., Hsiao, H. I., Vlajic, J., Yang, M. F., & Lin, H. T. V. (2018). Time-temperature abuse in the food cold chain: Review of issues, challenges, and recommendations. *Food Control*, *89*, 12–21.

New, C. Y., Kantilal, H. K., Tan, M. T. H., Nakaguchi, Y., Nishibuchi, M., & Son, R. (2014). Consumption of raw oysters: A risk factor for *Vibrio parahaemolyticus* infection. *International Food Research Journal*, *21*, 2459–2472.

Nishibuchi, M., & Kaper, J. B. (1995). Thermostable direct hemolysin gene of *Vibrio parahaemolyticus*: A virulence gene acquired by a marine bacterium. *Infection and Immunity*, *63*, 2093–2099.

Niu, B., Hong, B., Zhang, Z., Mu, L., Malakar, P. K., Liu, H., … Zhao, Y. (2018). A Novel qPCR method for simultaneous detection and quantification of viable pathogenic and non-pathogenic *Vibrio parahaemolyticus* (tlh+, tdh+, and ureR+). *Frontiers in Microbiology*, *9*, 1–10.

Nordstrom, J. L., & DePaola, A. (2003). Improved recovery of pathogenic *Vibrio parahaemolyticus* from oysters using colony hybridization following enrichment. *Journal of Microbiological Methods*, *52*, 273–277.

Nordstrom, J. L., Vickery, M. C. L., Blackstone, G. M., Murray, S. L., & DePaola, A. (2007). Development of a multiplex real-time PCR assay with an internal amplification control for the detection of total and pathogenic *Vibrio parahaemolyticus* bacteria in oysters. *Applied and Environmental Microbiology*, *73*, 5840–5847.

Odeyemi, O. A. (2016). Incidence and prevalence of *Vibrio parahaemolyticus* in seafood: A systematic review and meta-analysis. *SpringerPlus*, *5*, 464.

Ortiz-Jiménez, M. A. (2018). Quantitative evaluation of the risk of *Vibrio parahaemolyticus* through consumption of raw oysters (*Crassostrea corteziensis*) in Tepic, Mexico, under the RCP2.6 and RCP8.5 climate scenarios at different time horizons. *Food Research International*, *111*, 111–119.

Osei-Adjei, G., Gao, H., Zhang, Y., Zhang, L., Yang, W., Yang, H., … Zhou, D. (2017). Regulatory actions of ToxR and CalR on their own genes and type III secretion system 1 in *Vibrio parahaemolyticus*. *Oncotarget*, *8*, 65809–65822.

Ottaviani, D., Leoni, F., Rocchegiani, E., Santarelli, S., Canonico, C., Masini, L., … Carraturo, A. (2008). First clinical report of pandemic *Vibrio parahaemolyticus* O3:K6 infection in Italy. *Journal of Clinical Microbiology*, *46*, 2144–2145.

Panicker, G., Call, D. R., Krug, M. J., & Bej, A. K. (2004). Detection of pathogenic *Vibrio* spp. in shellfish by using multiplex PCR and DNA microarrays. *Applied and Environmental Microbiology*, *70*, 7436–7444.

Paranjpye, R., Hamel, O. S., Stojanovski, A., & Liermann, M. (2012). Genetic diversity of clinical and environmental *Vibrio parahaemolyticus* strains from the pacific Northwest. *Applied and Environmental Microbiology*, *78*, 8631–8638.

Paranjpye, R. N., Nilsson, W. B., Liermann, M., Hilborn, E. D., George, B. J., Li, Q., … Sandifer, P. A. (2015). Environmental influences on the seasonal distribution of *Vibrio parahaemolyticus* in the Pacific Northwest of the USA. *FEMS Microbiology Ecology*, *91*, 1–12.

Park, K.-S., Ono, T., Rokuda, M., Jang, M.-H., Okada, K., Iida, T., & Honda, T. (2004). Functional characterization of two type III secretion systems of *Vibrio parahaemolyticus*. *Infection and Immunity*, *72*, 6659–6665.

Park, K., Mok, J. S., Ryu, A. R., Kwon, J. Y., Ham, I. T., Shim, K. B., … Ryu, A. R. (2018). Occurrence and virulence of *Vibrio parahaemolyticus* isolated from seawater and bivalve shellfish of the Gyeongnam coast, Korea, in 2004–2016. *Marine Pollution Bulletin*, *137*, 382–387.

Park, K. S., Ono, T., Rokuda, M., Jang, M. H., Iida, T., & Honda, T. (2004). Cytotoxicity and enterotoxicity of the thermostable direct hemolysin-deletion mutants of *Vibrio parahaemolyticus*. *Microbiology and Immunology*, *48*, 313–318.

Park, M. S., Park, K. H., & Bahk, G. J. (2018). Combined influence of multiple climatic factors on the incidence of bacterial foodborne diseases. *Science of the Total Environment*, *610–611*, 10–16.

Park, S. Y., & Ha, S. D. (2018). Inactivation of *Vibrio parahaemolyticus* in shucked raw oyster (*Grassostrea gigas*) and clam (*Venerupis phillippinarum*) by using a combination of NaClO and gamma irradiation. *Food Science and Technology International*, *24*, 43–52.

Parveen, S., DaSilva, L., DePaola, A., Bowers, J., White, C., Munasinghe, K. A., … Tamplin, M. (2013). Development and validation

of a predictive model for the growth of *Vibrio parahaemolyticus* in post-harvest shellstock oysters. *International Journal of Food Microbiology*, *161*, 1–6.

Parveen, S., Hettiarachchi, K. A., Bowers, J. C., Jones, J. L., Tamplin, M. L., McKay, R., … DePaola, A. (2008). Seasonal distribution of total and pathogenic *Vibrio parahaemolyticus* in Chesapeake Bay oysters and waters. *International Journal of Food Microbiology*, *128*, 354–361.

Phuvasate, S., Chen, M. H., & Su, Y. C. (2012). Reductions of *Vibrio parahaemolyticus* in Pacific oysters (*Crassostrea gigas*) by depuration at various temperatures. *Food Microbiology*, *31*, 51–56.

Phuvasate, S., & Su, Y. C. (2013). Impact of water salinity and types of oysters on depuration for reducing *Vibrio parahaemolyticus* in Pacific oysters (*Crassostrea gigas*). *Food Control*, *32*, 569–573.

Pinto, A. Di, Terio, V., Novello, L., & Tantillo, G. (2011). Comparison between thiosulphate-citrate-bile salt sucrose (TCBS) agar and CHROMagar *Vibrio* for isolating *Vibrio parahaemolyticus*. *Food Control*, *22*, 124–127.

Powell, D. A., Erdozain, S., Dodd, C., Costa, R., Morley, K., & Chapman, B. J. (2013). Audits and inspections are never enough: A critique to enhance food safety. *Food Control*, *30*, 686–691.

Qadri, F., Shamsul Alam, M., Nishibuchi, M., Rahman, T., Alam, N. H., Chisti, J., … Nair, G. B. (2003). Adaptive and inflammatory immune responses in patients infected with strains of *Vibrio parahaemolyticus*. *The Journal of Infectious Diseases*, *187*, 1085–1096.

Quan, Y., Choi, K.-D., Chung, D., & Shin, I.-S. (2010). Evaluation of bactericidal activity of weakly acidic electrolyzed water (WAEW) against *Vibrio vulnificus* and *Vibrio parahaemolyticus*. *International Journal of Food Microbiology*, *136*, 255–260.

Racicot, M., Zanabria, R., Paradis, M.-È., Gaucher, M.-L., Arsenault, J., Leroux, A., … Quessy, S. (2019). Identification of risk factors to be considered for food establishments' risk assessment models. *Microbial Risk Analysis*, *11*, 1–10.

Ramos, R. J., Miotto, M., Squella, F. J. L., Cirolini, A., Ferreira, J. F., & Vieira, C. R. W. (2012). Depuration of oysters (*Crassostrea gigas*) contaminated with *Vibrio parahaemolyticus* and *Vibrio vulnificus* with UV Light and Chlorinated Seawater. *Journal of Food Protection*, *75*, 1501–1506.

Raszl, S. M., Froelich, B. A., Vieira, C. R. W., Blackwood, A. D., & Noble, R. T. (2016). *Vibrio parahaemolyticus* and *Vibrio vulnificus* in South America: Water, seafood and human infections. *Journal of Applied Microbiology*, *121*, 1201–1222.

Ravindran, R., & Jaiswal, A. K. (2019). Wholesomeness and safety aspects of irradiated foods. *Food Chemistry*, *285*, 363–368.

Reardon, T. (2001). The rise of private food quality and safety standards: Illustrations from Brazil. *The International Food and Agribusiness Management Review*, *4*, 413–421.

Rehnstam-Holm, A. S., Atnur, V., & Godhe, A. (2014). Defining the niche of *Vibrio parahaemolyticus* during pre- and post-monsoon seasons in the Coastal Arabian Sea. *Microbial Ecology*, *67*, 57–65.

Ren, T., & Su, Y. C. (2006). Effects of electrolyzed oxidizing water treatment on reducing *Vibrio parahaemolyticus* and *Vibrio vulnificus* in raw oysters. *Journal of Food Protection*, *69*, 1829–1834.

Rendueles, E., Omer, M. K., Alvseike, O., Alonso-Calleja, C., Capita, R., & Prieto, M. (2011). Microbiological food safety assessment of high hydrostatic pressure processing: A review. *LWT—Food Science and Technology*, *44*, 1251–1260.

Roque, A., Lopez-Joven, C., Lacuesta, B., Elandaloussi, L., Wagley, S., Furones, M. D., … Gomez-Gil, B. (2009). Detection and identification of tdh- and trh-positive *Vibrio parahaemolyticus* strains from four species of cultured bivalve molluscs on the Spanish Mediterranean Coast. *Applied and Environmental Microbiology*, *75*, 7574–7577.

Ryu, A. R., Mok, J. S., Lee, D. E., Kwon, J. Y., & Park, K. (2019). Occurrence, virulence, and antimicrobial resistance of *Vibrio parahaemolyticus* isolated from bivalve shellfish farms along the southern coast of Korea. *Environmental Science and Pollution Research*, *26*, 21034–21043.

Saito, S., Iwade, Y., Tokuoka, E., Nishio, T., Otomo, Y., Araki, E., … Hara-Kudo, Y. (2015). Epidemiological evidence of lesser role of thermostable direct hemolysin (TDH)—Related hemolysin (TRH) than TDH on *Vibrio parahaemolyticus* pathogenicity. *Foodborne Pathogens and Disease*, *12*, 131–138.

Sakazaki, R., Tamura, K., Kato, T., Obara, Y., Yamai, S., & Hobo, K. (1968). Studies on the enteropathogenic, facultatively halophilic bacteria, *Vibrio parahaemolyticus*. *Japanese Journal of Medical Science and Biology*, *21*, 325–331.

Sanjeev, S., & Stephen, J. (1993). Incidence of *Vibrio parahaemolyticus* in fish and shellfish marketed in Cochin. *Indian Journal of Marine Sciences*, *22*, 70–71.

Semenza, J. C., Trinanes, J., Lohr, W., Sudre, B., Löfdahl, M., Martinez-Urtaza, J., … Rocklöv, J. (2017). Environmental suitability of *Vibrio* infections in a warming climate: An early warning system. *Environmental Health Perspectives*, *125*, 107004.

Shaw, K. S., Jacobs, J. M., & Crump, B. C. (2014). Impact of hurricane irene on *Vibrio vulnificus* and *Vibrio parahaemolyticus* concentrations in surface water, sediment, and cultured oysters in the Chesapeake Bay, MD, USA. *Frontiers in Microbiology*, *5*, 1–10.

Shen, X., Cai, Y., Liu, C., Liu, W., Hui, Y., & Su, Y.-C. C. (2009). Effect of temperature on uptake and survival of *Vibrio parahaemolyticus* in oysters (*Crassostrea plicatula*). *International Journal of Food Microbiology*, *136*, 129–132.

Shen, X., & Su, Y. C. (2017). Application of grape seed extract in depuration for decontaminating *Vibrio parahaemolyticus* in Pacific oysters (*Crassostrea gigas*). *Food Control*, *73*, 601–605.

Shen, X., Su, Y. C., Liu, C., Oscar, T., & DePaola, A. (2019). Efficacy of *Vibrio parahaemolyticus* depuration in oysters (*Crassostrea gigas*). *Food Microbiology*, *79*, 35–40.

Shime-Hattori, A., Iida, T., Arita, M., Park, K., Kodama, T., & Honda, T. (2006). Two type IV pili of *Vibrio parahaemolyticus* play different roles in biofilm formation. *FEMS Microbiology Letters*, *264*, 89–97.

Shimohata, T., & Takahashi, A. (2010). Diarrhea induced by infection of *Vibrio parahaemolyticus*. *The Journal of Medical Investigation*, *57*, 179–182.

Smith, B. (2018). *Doing a literature review: Releasing the research imagination*. London, UK: SAGE Publications.

Smith, B. A., Ruthman, T., Sparling, E., Auld, H., Comer, N., Young, I., … Fazil, A. (2015). A risk modeling framework to evaluate the impacts of climate change and adaptation on food and water safety. *Food Research International*, *68*, 78–85.

Sobrinho, D. S. C. P., Destro, M. T., Franco, B. D. G. M., & Landgraf, M. (2014). A quantitative risk assessment model for *Vibrio parahaemolyticus* in raw oysters in Sao Paulo State, Brazil. *International Journal of Food Microbiology*, *180*, 69–77.

Sobrinho, P. D. S. C., Destro, M. T., Franco, B. D. G. M., & Landgraf, M. (2010). Correlation between environmental factors and prevalence of

Vibrio parahaemolyticus in oysters harvested in the Southern Coastal area of Sao Paulo State, Brazil. *Applied and Environmental Microbiology*, *76*, 1290–1293.

Sobrinho, P. de S. C., Destro, M. T., Franco, B. D. G. M., & Landgraf, M. (2011). Occurrence and distribution of *Vibrio parahaemolyticus* in retail oysters in Sao Paulo State, Brazil. *Food Microbiology*, *28*, 137–140.

Steinman, B. A., Mann, M. E., & Miller, S. K. (2015). Atlantic and Pacific multidecadal oscillations and Northern Hemisphere temperatures. *Science*, *347*, 988–991.

Su, Y. C., Yang, Q., & Häsk, C. (2010). Refrigerated seawater depuration for reducing *Vibrio parahaemolyticus* contamination in pacific oyster: (*Crassostrea gigas*). *Journal of Food Protection*, *73*, 1111–1115.

Suffredini, E., Mioni, R., Mazzette, R., Bordin, P., Serratore, P., Fois, F., … Croci, L. (2014). Detection and quantification of *Vibrio parahaemolyticus* in shellfish from Italian production areas. *International Journal of Food Microbiology*, *184*, 14–20.

Taiwo, M., Baker-Austin, C., Powell, A., Hodgson, E., Natås, O. B., & Walker, D. I. (2017). Comparison of toxR and tlh based PCR assays for *Vibrio parahaemolyticus*. *Food Control*, *77*, 116–120.

Takahashi, H., Iwade, Y., Konuma, H., & Hara-Kudo, Y. (2005). Development of a quantitative real-time PCR method for estimation of the total number of *Vibrio parahaemolyticus* in contaminated shellfish and seawater. *Journal of Food Protection*, *68*, 1083–1088.

Tang, X., Zhao, Y., Sun, X., Xie, J., Pan, Y., & Malakar, P. K. (2015). Predictive model of *Vibrio parahaemolyticus* O3:K6 growth on cooked *Litopenaeus vannamei*. *Annals of Microbiology*, *65*, 487–493.

Taylor, M. A., Yu, J. W., Howell, T. L., & Jones, S. H. (2018). Varying success of relaying to reduce *Vibrio parahaemolyticus* levels in oysters (*Crassostrea virginica*). *Journal of Food Protection*, *81*, 659–669.

Taylor, M., Cheng, J., Sharma, D., Bitzikos, O., Gustafson, R., Fyfe, M., … Galanis, E. (2018). Outbreak of *Vibrio parahaemolyticus* associated with consumption of raw oysters in Canada, 2015. *Foodborne Pathogens and Disease*, *15*, 554–559.

Tepedino, A. A. (1982). *Vibrio parahaemolyticus* in Long Island oysters. *Journal of Food Protection*, *45*, 150–151.

Theethakaew, C., Feil, E. J., Castillo-Ramírez, S., Aanensen, D. M., Suthienkul, O., Neil, D. M., & Davies, R. L. (2013). Genetic relationships of *Vibrio parahaemolyticus* isolates from clinical, human carrier, and environmental sources in Thailand, determined by multilocus sequence analysis. *Applied and Environmental Microbiology*, *79*, 2358–2370.

Thomas, M. K., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2012). A global pattern of thermal adaptation in marine phytoplankton. *Science*, *338*, 1085–1088.

Thomson, W. K., & Thacker, C. L. (1972). Incidence of *Vibrio parahaemolyticus* in shellfish from eight Canadian Atlantic sampling areas. *Journal of the Fisheries Research Board of Canada*, *29*, 1633–1635.

Thomson, W. K., & Thacker, C. L. (1973). Effect of temperature on *Vibrio parahaemolyticus* in oysters at refrigerator and deep freeze temperatures. *Canadian Institute of Food Science and Technology Journal*, *6*, 156–158.

Torraco, R. J. (2016). Writing integrative literature reviews: Using the past and present to explore the future. *Human Resource Development Review*, *15*, 404–428.

Turner, J. W., Good, B., Cole, D., & Lipp, E. K. (2009). Plankton composition and environmental factors contribute to *Vibrio* seasonality. *ISME Journal*, *3*, 1082–1092.

Tzouros, N. E., & Arvanitoyannis, I. S. (2000). Implementation of Hazard Analysis Critical Control Point (HACCP) system to the fish/seafood industry: A review. *Food Reviews International*, *16*, 273–325.

U.K. Health Protection Agency. (2009). *Guidelines for assessing the microbiological safety of ready-to-eat foods placed on the market*. London, UK: Health Protection Agency.

U.S. CDC. (1998). Outbreak of *Vibrio parahaemolyticus* infections associated with eating raw oysters—Pacific Northwest, 1997. *Morbidity and Mortality Weekly Report*, *47*, 457–462. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9639367

U.S. CDC. (2019). *Multistate outbreak of gastrointestinal illnesses linked to oysters imported from Mexico*. Retrieved from https://www.cdc.gov/vibrio/investigations/rawoysters-05-19/index.html

U.S. Food and Drug Administration (U.S. FDA). (2005). *Quantitative risk assessment on the public health impact of pathogenic* Vibrio parahaemolyticus *in raw oysters*. Retrieved from https://www.fda.gov/Food/FoodScienceResearch/RiskSafetyAssessment/ucm050421.htm

U.S. Food and Drug Administration (U.S. FDA). (2017). *National Shellfish Sanitation Program (NSSP)*. Retrieved from https://www.fda.gov/food/federalstate-food-programs/national-shellfish-sanitation-program-nssp

Vanderzant, C., & Nickelson, R. (1972). Survival of *Vibrio parahaemolyticus* in shrimp tissue under various environmental conditions. *Applied Microbiology*, *23*, 34–37.

Velazquez-Roman, J., León-Sicairos, N., Flores-Villaseñor, H., Villafaña-Rauda, S., & Canizalez-Roman, A. (2012). Association of pandemic *Vibrio parahaemolyticus* O3:K6 present in the coastal environment of Northwest Mexico with cases of recurrent diarrhea between 2004 and 2010. *Applied and Environmental Microbiology*, *78*, 1794–1803.

Vezzulli, L., Grande, C., Reid, P. C., Hélaouët, P., Edwards, M., Höfle, M. G., … Pruzzo, C. (2016). Climate influence on *Vibrio* and associated human diseases during the past half-century in the coastal North Atlantic. *Proceedings of the National Academy of Sciences*, *113*, E5062–E5071.

Walton, W. C., Nelson, C., Hochman, M., & Schwarz, J. (2013). Preliminary study of transplanting as a process for reducing levels of *Vibrio vulnificus* and *vibrio parahaemolyticus* in shellstock oysters. *Journal of Food Protection*, *76*, 119–123.

Walton, W. C., Rikard, F. S., Chaplin, G. I., Davis, J. E., Arias, C. R., & Supan, J. E. (2013). Effects of ploidy and gear on the performance of cultured oysters, *Crassostrea virginica*: Survival, growth, shape, condition index and Vibrio abundances. *Aquaculture*, *414–415*, 260–266.

Ward, L. N., & Bej, A. K. (2006). Detection of *Vibrio parahaemolyticus* in shellfish by use of multiplexed real-time PCR with TaqMan fluorescent probes. *Applied and Environmental Microbiology*, *72*, 2031–2042.

Watts, N., Amann, M., Arnell, N., Ayeb-Karlsson, S., Belesova, K., Berry, H., … Costello, A. (2018). The 2018 report of the Lancet Countdown on health and climate change: Shaping the health of nations for centuries to come. *The Lancet*, *392*, 2479–2514.

Whistler, C. A., Hall, J. A., Xu, F., Ilyas, S., Siwakoti, P., Cooper, V. S., & Jones, S. H. (2015). Use of whole-genome phylogeny and comparisons for development of a multiplex PCR assay to identify sequence type 36 *Vibrio parahaemolyticus*. *Journal of Clinical Microbiology*, *53*, 1864–1872.

Whitaker, W. B., Parent, M. A., Naughton, L. M., Richards, G. P., Blumerman, S. L., & Boyd, E. F. (2010). Modulation of responses of *Vibrio parahaemolyticus* O3:K6 to pH and temperature stresses by growth at different salt concentrations. *Applied and Environmental Microbiology*, *76*, 4720–4729.

World Health Organization (WHO). (2019). *Food safety—Climate change and the role of WHO*. Retrieved from https://www.who.int/foodsafety/publications/all/climate_change/en/

Williams, T. C., Froelich, B. A., Phippen, B., Fowler, P., Noble, R. T., & Oliver, J. D. (2017). Different abundance and correlational patterns exist between total and presumed pathogenic *Vibrio vulnificus* and *V. parahaemolyticus* in shellfish and waters along the North Carolina coast. *FEMS Microbiology Ecology*, *93*, 1–11.

Winchester, C. L., & Salji, M. (2016). Writing a literature review. *Journal of Clinical Urology*, *9*, 308–312.

Wong, H. C., & Wang, P. (2004). Induction of viable but nonculturable state in *Vibrio parahaemolyticus* and its susceptibility to environmental stresses. *Journal of Applied Microbiology*, *96*, 359–366.

Wu, X., Lu, Y., Zhou, S., Chen, L., & Xu, B. (2016). Impact of climate change on human infectious diseases: Empirical evidence and human adaptation. *Environment International*, *86*, 14–23.

Wu, Y., Wen, J., Ma, Y., Ma, X., & Chen, Y. (2014). Epidemiology of foodborne disease outbreaks caused by *Vibrio parahaemolyticus*, China, 2003–2008. *Food Control*, *46*, 197–202.

Xi, D., Liu, C., & Su, Y. C. (2012). Effects of green tea extract on reducing *Vibrio parahaemolyticus* and increasing shelf life of oyster meats. *Food Control*, *25*, 368–373.

Xi, D., Liu, C., & Su, Y. C. (2014). Impacts of *Lactobacillus plantarum* in depuration for reducing *Vibrio parahaemolyticus* in Pacific oysters (*Crassostrea gigas*). *Journal of Aquatic Food Product Technology*, *23*, 165–174.

Xu, D., Ji, L., Wu, X., Yan, W., & Chen, L. (2018). Detection and differentiation of *Vibrio parahaemolyticus* by multiplexed real-time PCR. *Canadian Journal of Microbiology*, *64*, 809–815.

Yamamoto, K. (2017). Food processing by high hydrostatic pressure. *Bioscience, Biotechnology, and Biochemistry*, *81*, 672–679.

Yang, C., Pei, X., Wu, Y., Yan, L., Yan, Y., Song, Y., … Cui, Y. (2019). Recent mixing of *Vibrio parahaemolyticus* populations. *The ISME Journal*, *13*, 2578–2588.

Yang, Y., Xie, J., Li, H., Tan, S., Chen, Y., & Yu, H. (2017). Prevalence, antibiotic susceptibility and diversity of *Vibrio parahaemolyticus* isolates in seafood from South China. *Frontiers in Microbiology*, *8*, 2566.

Yang, Z., Jiao, X., Li, P., Pan, Z., Huang, J., Gu, R., … Chao, G. (2009). Predictive model of *Vibrio parahaemolyticus* growth and survival on salmon meat as a function of temperature. *Food Microbiology*, *26*, 606–614.

Ye, M., Huang, Y., & Chen, H. (2012). Inactivation of *Vibrio parahaemolyticus* and *Vibrio vulnificus* in oysters by high-hydrostatic pressure and mild heat. *Food Microbiology*, *32*, 179–184.

Yeung, P. S. M., & Boor, K. J. (2004). Epidemiology, pathogenesis, and prevention of foodborne *Vibrio parahaemolyticus* infections. *Foodborne Pathogens and Disease*, *1*, 74–88.

Yoon, K. S., Min, K. J., Jung, Y. J., Kwon, K. Y., Lee, J. K., & Oh, S. W. (2008). A model of the effect of temperature on the growth of pathogenic and nonpathogenic *Vibrio parahaemolyticus* isolated from oysters in Korea. *Food Microbiology*, *25*, 635–641.

Yu, Q., Niu, M., Yu, M., Liu, Y., Wang, D., & Shi, X. (2016). Prevalence and antimicrobial susceptibility of *Vibrio parahaemolyticus* isolated from retail shellfish in Shanghai. *Food Control*, *60*, 263–268.

Yu, W. T., Jong, K. J., Lin, Y. R., Tsai, S. E., Tey, Y. H., & Wong, H. C. (2013). Prevalence of *Vibrio parahaemolyticus* in oyster and clam culturing environments in Taiwan. *International Journal of Food Microbiology*, *160*, 185–192.

Yukimoto, S., Adachi, Y., Hosaka, M., Sakami, T., Yoshimura, H., Hirabara, M., … Kitoh, A. (2012). A new global climate model of the Meteorological Research Institute: MRI-CGCM3—Model description and basic performance. *Journal of the Meteorological Society of Japan*, *90A*, 23–64.

Zanabria, R., Racicot, M., Cormier, M., Arsenault, J., Ferrouillet, C., Letellier, A., … Quessy, S. (2018). Selection of risk factors to be included in the Canadian Food Inspection Agency risk assessment inspection model for food establishments. *Food Microbiology*, *75*, 72–81.

Zannella, C., Mosca, F., Mariani, F., Franci, G., Folliero, V., Galdiero, M., … Galdiero, M. (2017). Microbial diseases of bivalve mollusks: Infections, immunology and antimicrobial defense. *Marine Drugs*, *15*, 182.

Zha, Z., Li, C., Li, W., Ye, Z., & Pan, J. (2016). LptD is a promising vaccine antigen and potential immunotherapeutic target for protection against Vibrio species infection. *Scientific Reports*, *6*, 38577.

Zhang, L., Osei-Adjei, G., Zhang, Y., Gao, H., Yang, W., Zhou, D., … Zhang, Y. (2017). CalR is required for the expression of T6SS2 and the adhesion of *Vibrio parahaemolyticus* to HeLa cells. *Archives of Microbiology*, *199*, 931–938.

Zhang, L., Weng, Y., Wu, Y., Wang, X., Yin, Z., Yang, H., … Zhang, Y. (2018). H-NS is an activator of exopolysaccharide biosynthesis genes transcription in *Vibrio parahaemolyticus*. *Microbial Pathogenesis*, *116*, 164–167.

Zhang, Y., Gao, H., Osei-Adjei, G., Zhang, Y., Yang, W., Yang, H., … Zhou, D. (2017). Transcriptional regulation of the type VI secretion system 1 genes by quorum sensing and ToxR in *Vibrio parahaemolyticus*. *Frontiers in Microbiology*, *8*, 2005.

Zimmerman, A. M., DePaola, A., Bowers, J. C., Krantz, J. A., Nordstrom, J. L., Johnson, C. N., & Grimes, D. J. (2007). Variability of total and pathogenic *Vibrio parahaemolyticus* densities in Northern Gulf of Mexico water and oysters. *Applied and Environmental Microbiology*, *73*, 7589–7596.

Zulkifli, Y., Alitheen, N. B., Son, R., Yeap, S. K., Lesley, M. B., & Raha, A. R. (2009). Identification of *Vibrio parahaemolyticus* isolates by PCR targeted to the toxR gene and detection of virulence genes. *International Food Research Journal*, *16*, 289–296.

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