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► To cite this version:

Thomas Brauge, Julia Mougin, Timothy Ells, Graziella Midelet. Sources and contamination routes of seafood with human pathogenic *Vibrio* spp.: A Farm-to-Fork approach. *Comprehensive Reviews in Food Science and Food Safety*, 2023, 23 (1), pp.1-25. 10.1111/1541-4337.13283 . hal-04353943

HAL Id: hal-04353943

<https://hal.science/hal-04353943>

Submitted on 3 Jan 2024

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COMPREHENSIVE REVIEW

Sources and contamination routes of seafood with human pathogenic *Vibrio* spp.: A *Farm-to-Fork* approach

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Funding information

Haut de France region; OECD Co-operative Research Programme: Sustainable Agricultural and Food Systems, Grant/Award Number: TAD/CRP PO 500120218; The Structure Fédérative de Recherche; Campus de la Mer; Embassy of France in Canada

Abstract

Vibrio spp., known human foodborne pathogens, thrive in freshwater, estuaries, and marine settings, causing vibriosis upon ingestion. The rising global vibriosis cases due to climate change necessitate a deeper understanding of *Vibrio* epidemiology and human transmission. This review delves into *Vibrio* contamination in seafood, scrutinizing its sources and pathways. We comprehensively assess the contamination of human-pathogenic *Vibrio* in the seafood chain, covering raw materials to processed products. A “*Farm-to-Fork*” approach, aligned with the *One Health* concept, is essential for grasping the complex nature of *Vibrio* contamination. *Vibrio*’s widespread presence in natural and farmed aquatic environments establishes them as potential entry points into the seafood chain. Environmental factors, including climate, human activities, and wildlife, influence contamination sources and routes, underscoring the need to understand the origin and transmission of pathogens in raw seafood. Once within the seafood chain, the formation of protective biofilms on various surfaces in production and processing poses significant food safety risks, necessitating proper cleaning and disinfection to prevent microbial residue. In addition, inadequate seafood handling, from inappropriate processing procedures to cross-contamination via pests or seafood handlers, significantly contributes to *Vibrio* food contamination, thus warranting attention to reduce risks. Information presented here support the imperative for proactive measures, robust research, and interdisciplinary collaboration in order to effectively mitigate the risks posed by human pathogenic *Vibrio* contamination, safeguarding public health and global food security. This review serves as a crucial resource for researchers, industrials, and policymakers, equipping them with the knowledge to develop biosecurity measures associated with *Vibrio*-contaminated seafood.

KEYWORDS

foodborne pathogens, One Health, seafood safety, *Vibrio*

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1 | INTRODUCTION

Vibrio spp. are highly human pathogenic bacteria that naturally inhabit freshwater, estuaries, and marine environments. Consumption of contaminated water or seafood can lead to severe human outbreaks, causing diseases collectively referred to as vibriosis. Although strains of *Vibrio cholerae* O1 or O139 are responsible for cholera, a severe diarrheal illness that can rapidly progress to dehydration and death without timely intervention, there are three main non-cholera pathogenic *Vibrio* species. These include strains of *V. cholerae* non-O1/non-O139, as well as *Vibrio parahaemolyticus*, which carries the gene for at least one of the two hemolysins: TDH (thermostable direct hemolysin) or TRH (TDH-related hemolysin). Another significant pathogen is *Vibrio vulnificus*. Although the specific major pathogenic factors of *V. vulnificus* have not been definitively identified, all strains are considered pathogenic. Infections with non-cholera *Vibrio* spp. result in vibriosis, characterized by gastrointestinal symptoms such as nausea, vomiting, abdominal pain, and diarrhea. In addition, *V. vulnificus* can also cause cutaneous infections that rapidly progress to necrotic ulcers (Bonnin-Jusserand et al., 2019; Robert-Pillot et al., 2014; Sampaio et al., 2022). It is important to exercise caution with the term “pathogenic *Vibrio* spp.,” which should primarily refer to *Vibrio* species or strains isolated after clinical cases of human illness. Although the characterization and prediction of pathogenicity and virulence are commonly based on the detection of a few virulence associated genes, such as *tdh* and *trh* for *V. parahaemolyticus*, other evidences propose a more complex mechanism, bringing difficulties in the characterization of pathogenicity based on few genetic traits. Indeed, several authors have found that *V. parahaemolyticus* lacking *tdh* and *trh* genes remained pathogenic, suggesting the existence of different virulence factors at play (Ottaviani et al., 2012; Xu et al., 1994). Recently, a novel hemolysin (α -hemolysin) was discovered in a pathogenic strain of *V. parahaemolyticus* lacking both *tdh* and *trh* genes (Zha et al., 2023). Given this discovery, it would be appropriate to include *tdh*-, *trh*-, and α -hemolysin+ *V. parahaemolyticus* strains in the category of potentially pathogenic strains, even if their pathogenicity might be lower than that of strains carrying these genes. Furthermore, the pathogenicity of *Vibrio* spp. can vary depending on various factors, including the host's susceptibility and the specific strain involved, bringing further complexity to the characterization of pathogenicity and virulence (Baker-Austin et al., 2018; Igbinsosa & Okoh, 2008).

Incidences of such bacterial pathogens are particularly alarming in regions of the globes with high water temperatures, in particular in the Southern Hemisphere. However,

today occurrence rates in several countries in the Northern Hemisphere are increasing due to climate changes and its related consequences, including acidification, increasing temperature, and salinity (Le Roux et al., 2015; Trinanes & Martinez-Urtaza, 2021; Vezzulli et al., 2015). In the United States, the annual incidence of reported vibriosis per 100,000 population has increased significantly, from 0.09 in 1996 to 0.28 in 2010 under COVIS (cholera and other *Vibrio* illness surveillance), and from 0.15 in 1996 to 0.42 in 2010 under foodborne diseases active surveillance network (Newton et al., 2012). In France, since 2016, an increase in the number of clinical cases of infections with human pathogenic *Vibrio* spp. has been observed, with a total of 26 cases in 2017, 60 in 2018, and 69 in 2019, mainly represented by the species *V. cholerae* and *V. parahaemolyticus* (Centre National de Référence des Vibrions et du Choléra [CNRVC], 2021). It is important to note that the average number of reported infection cases was only 10 between 1995 and 2015. Recently, a study conducted by Amato et al. (2022) provided an overview of the epidemiology of vibriosis cases in the countries bordering the North and Baltic Seas during the exceptionally warm year of 2018. This study showed that since 2014, vibriosis rates had significantly increased to reach 445 cases in 2018, including 100 cases related to *V. cholerae*, 89 cases related to *V. parahaemolyticus*, and 45 cases related to *V. vulnificus*. These results highlight the urgent need to develop effective prevention strategies to control the spread of human pathogenic *Vibrio* spp. in seafood products and minimize the risks of food contamination for consumers.

When *Vibrio* outbreaks occur, epidemiological investigations are conducted to confirm the diagnosis, determine the epidemiological characteristics and possible sources of the outbreak, in order to provide appropriate control measures. During a *Vibrio* spp. outbreak that occurred in the United States in 2018, epidemiological investigations conducted by federal, state, and local partners in public health and regulation, identified 35 cases of food poisoning, including nine hospitalizations, linked to the consumption of crab meat. The investigations were able to identify the source of contamination to Venezuelan processors that supplied various brands of crab meat. However, limitations such as in the investigation prevented precise identification of the contamination source (Seelman et al., 2023). In the same year, following a lull of over 20 years, a significant cholera epidemic broke out in northern Algeria, with 291 suspected cases of cholera, out of which 270 required hospitalization. Phylogenetic investigation revealed the involvement of an O1 isolate of *V. cholerae* from the El Tor pandemic sublineage, AFR14, newly introduced to Africa from South Asia. Despite the identification of numerous strains of *V. cholerae* in both wild and farmed seafood along the Algerian Mediterranean coast, the

precise attribution of the sources of this pandemic could not be determined (Arab et al., 2020, 2021; Benamrouche et al., 2022). Despite efforts, sources of *Vibrio* spp. contamination are sometimes not found or the contamination scenario is not understood (Okada et al., 2023). One reason is often a lack of knowledge pertaining to the sources and contamination routes with *Vibrio* spp., which limits investigations. However, precise attribution of contamination scenarios during a human pathogenic *Vibrio* spp. outbreak is crucial to develop corrective measures to prevent the recurrence of the event. Such work is essential for public health authorities and food industry professionals, who would be able to quickly take actions to guaranty microbiological safety, prevent the spread of contamination to other foods, and spread of the disease among consumers (Greig & Ravel, 2009). Therefore, it is essential to have a good understanding of the sources and contamination routes to ensure public safety.

Human pathogenic *Vibrio* spp. contamination in seafood is a complex and multifactorial phenomenon that can be initiated or amplified by several processes. Due to the ubiquitous nature of this pathogen, evaluating sources and pathways of contamination is a significant challenge. The multiple pathways for contamination by these bacteria, both in their natural environment and in the processing and handling environments, require the consideration of the entire seafood processing chain, within a “Farm-to-Fork” framework.

Current literature reviews have primarily focused on the incidence of pathogenic *Vibrio* in various contexts, including wildlife (Ma et al., 2023), humans (Ghenem et al., 2017; Letchumanan et al., 2014), or water environment (Ibangha et al., 2023; Lovell, 2017). Meanwhile, other authors have centered their work on *Vibrio* ecology (Brumfield et al., 2021) and strategies for mitigation (Ndraha et al., 2020; Spaur et al., 2020; Wang et al., 2015). However, there has been no comprehensive effort to encompass this knowledge from these different perspectives. This holistic understanding would be invaluable in unraveling the intricate and complex interplay between animal and human contamination, as well as the ecological behaviors and virulence factors that can elevate the prevalence of these zoonoses in humans.

The objective of this review is therefore to investigate and assess a better understanding of the sources and routes of human pathogenic *Vibrio* spp. contamination throughout the seafood chain, from sea to fork. This review discussed the sources and contamination routes of (i) raw seafood material contamination by *Vibrio* spp., as well as (ii) cross-contamination of processed seafood products during seafood processing and in food-handling scenarios. By understanding these sources and pathways of contamination, this work benefit researchers and experts, who will

gain the necessary knowledge to develop effective biosecurity control methods to reduce microbiological hazard and public health risks associated with the consumption of *Vibrio* spp.-contaminated seafood.

2 | SOURCES AND CONTAMINATION ROUTES OF RAW SEAFOOD

As human pathogenic *Vibrio* spp. are ubiquitous in aquatic habitats, the natural and farm marine environments represent a possible entry point into the seafood chain for human pathogenic *Vibrio* spp. that are of significance to human health (Figure 1). Sources and routes of contamination vary widely for distinct fishery and aquaculture areas, harboring different combinations of environmental risk factors including climate, anthropogenic activities, or wildlife (Ndraha et al., 2020; Noorian et al., 2023). A thorough understanding of the possible origin and transmission process of key target organisms into raw seafood products, from both natural and farm marine environment, is of paramount importance to settle effective surveillance and control strategies. Although reviews conducted by Brumfield et al. (2021) and Noorian et al. (2023) have partially addressed this subject by focusing on environmental reservoirs of human pathogenic *Vibrio* spp., a comprehensive perspective integrating the challenges related to food safety and additional information is necessary to provide a comprehensive and in-depth understanding of the issue.

2.1 | The marine environment as a natural habitat of human pathogenic *Vibrio* spp

Members of the Vibrionaceae family are natural inhabitants of the aquatic environment, especially marine, existing in both free-living states in the water column and within biofilms attached to biotic or abiotic surfaces, including sediments and suspended particulates. The ability of human pathogenic *Vibrio* spp. to survive outside the host is crucial for their successful transmission to a host (Kirn et al., 2005). The prevalence and occurrence of these pathogens in seafood are influenced by environmental conditions that favor their survival and proliferation in the surrounding environment (water column, sediments, etc.), leading to an increased presence of human pathogenic *Vibrio* spp. (Brumfield et al., 2021).

Previous research has demonstrated the significant roles of water temperature and salinity in the occurrence and abundance of human pathogenic *Vibrio* spp., as confirmed by a comprehensive meta-analysis conducted by

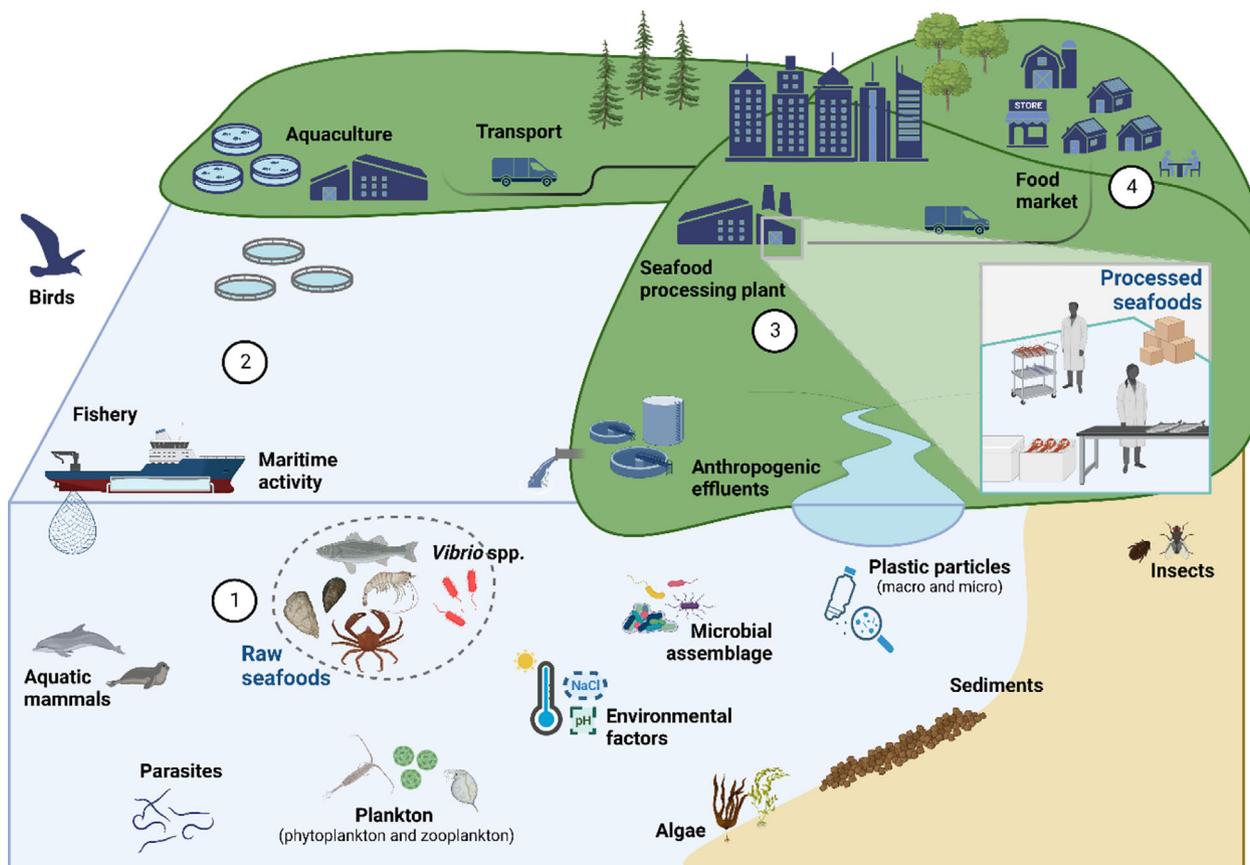


FIGURE 1 Sources and contamination routes of seafood with human pathogenic *Vibrio* spp. ① The contamination of raw seafood with human pathogenic *Vibrio* spp. arises from their ubiquity in aquatic environments. This contamination is influenced by various environmental factors such as climate (temperature, salinity, and pH), anthropogenic activities (maritime activity, effluents, plastic particles, and aquaculture), and wildlife interactions (birds, aquatic mammals, parasites, plankton, microbial assemblage, algae, and insects). ② Both wild-caught and farmed seafood may serve as potential entry points of pathogenic *Vibrio* spp. into the seafood supply chain. The initial contamination of raw seafood occurs through two primary processes: direct contact with contaminated water and internalization via ingestion, filtration, or skin abrasions. Additionally, *Vibrio* adhesion to biotic elements, like the chitinous surfaces of aquatic organisms, can promote their survival in animals by forming robust and resilient biofilms. ③ Once upon the seafood chain, pathogenic *Vibrio* can survive by adhering to surfaces and forming protective biofilms, thus becoming resilient to cleaning procedures which pose a significant public health risk. Cross-contamination in seafood processing occurs through several pathways: contact with contaminated processing equipment including surface, cutting boards and knives, food packaging, wash water; or contact with carrier organisms such as insects/pest or food handlers. ④ Without effective control procedures, these contaminated seafoods will reach the food market, potentially posing significant health risks to consumers. It is imperative for the seafood industry to implement rigorous measures to minimize the chances of contamination. This could include regular monitoring of both wild and farmed seafoods, stringent hygiene practices, or thorough cleaning of processing equipment. By taking these proactive steps, we can help safeguard public health and maintain the integrity of the seafood supply chain.

Takemura et al. (2014). This correlation between human pathogenic *Vibrio* spp. and temperature has been globally observed across various sample types, including water and sediment. Numerous longitudinal studies carried out in Europe (Böer et al., 2013; Høi et al., 1998; Julie et al., 2010; Martinez-Urtaza et al., 2008; Vezzulli et al., 2016), USA (Blackwell & Oliver, 2008; Davis et al., 2017; Duan & Su, 2005; Johnson et al., 2012; Wetz et al., 2014), Middle and South America (Bacian et al., 2021), and Asian countries (Fukushima & Seki, 2004) have provided robust evidence to support this phenomenon. Although other environmental factors such as turbidity, dissolved oxygen,

chlorophyll a, inorganic nutrients, and dissolved organic carbons have been identified as additional influencers for the human pathogenic occurrence and abundance of human pathogenic *Vibrio* spp. in marine environments, the findings across studies have yielded inconsistent results (Blackwell & Oliver, 2008; Johnson et al., 2012; Takemura et al., 2014).

Several studies have demonstrated that changes in water temperature have a significant impact on the prevalence of human pathogenic *Vibrio* spp. in seafood, thereby posing a potential threat to seafood safety. Longitudinal investigations have revealed a consistent association between

elevated temperatures and contamination with *V. parahaemolyticus* in various fish species (*Sebastes schlegelii*; *Pagrus major*), shrimp (*Litopenaeus vannamei*) (Mok et al., 2021), and oysters (Duan & Su, 2005; Johnson et al., 2012; King et al., 2021; Sobrinho et al., 2010). The occurrence of *V. vulnificus* in oysters has also been linked to higher surface seawater temperatures (Johnson et al., 2012; King et al., 2021). Similarly, *V. cholerae*, *V. parahaemolyticus*, and *V. vulnificus* were exclusively detected in blue mussels (*Mytilus edulis*) during warmer months of the year (Collin & Rehnstam-Holm, 2011). Experimental immersion of oysters (*Crassostrea plicatula*) with *V. parahaemolyticus* at different temperatures demonstrated that higher temperatures led to increased pathogen accumulation in oysters (Shen et al., 2009). However, findings vary between studies, as Jones et al. (2014) found no correlation between temperature and the abundance of *V. parahaemolyticus* in clams (*Mercenaria mercenaria*) and oysters (*Crassostrea virginica*). These discrepancies may arise from differences in geographical locations and the range of temperature and salinity encountered during the sampling period. Importantly, fish intestines have been identified as significant sources of *V. parahaemolyticus* and *V. vulnificus*, as high abundances of these pathogens have been detected throughout both warmer and colder months of the year, with no correlation to bacterial abundance in the surrounding environment (Givens et al., 2014). Thus, it can be postulated that seafood may serve as specific reservoirs and ecological niches for human pathogenic *Vibrio* spp., potentially contributing to the seasonal reemergence of pathogens in the natural environment.

The strong correlations observed between high temperatures and human pathogenic *Vibrio* spp. from water, sediments, and seafood highlight the challenges posed by global warming, emphasizing the concept of One Health. It is anticipated that as temperatures rise, the occurrence of human pathogenic *Vibrio* spp. contamination may increase, affecting both human health and the environment (Deeb et al., 2018; Trinanes & Martinez-Urtaza, 2021; Vezzulli et al., 2015). In fact, alarming increases in human pathogenic *Vibrio* spp. contamination risk indices have been observed in regions of the globe where the presence of these pathogens was previously negligible, emphasizing the interconnectedness of human, animal, and environmental health (Baker-Austin et al., 2016; Brehm et al., 2021). These findings collectively emphasize the urgent need for effective and preventive control strategies to mitigate the potential impact of global warming and its associated effects on the occurrence of human pathogenic *Vibrio* spp. in different parts of the world, promoting a holistic One Health approach.

2.2 | Contamination mechanism of raw seafood

Most Vibrionaceae bacteria, including human pathogenic *Vibrio* spp., demonstrate opportunistic pathogenic behavior and naturally exist as part of the normal microflora in aquatic animals. This inherent association enables their persistence and survival within seafood products (Destoumieux-Garzón et al., 2020). The colonization and proliferation of human pathogenic *Vibrio* spp. in aquaculture organisms intended for human consumption are influenced by several crucial factors. These factors encompass the specific type of infected aquatic animal, the virulence and pathogenicity characteristics of the bacteria, the physiological condition of the infected organism, and the prevailing environmental conditions.

The initial stage of contamination in raw seafood primarily occurs through two key processes. First, bacterial attachment takes place through direct contact with contaminated water. The ability to attach to external surfaces of marine organisms, including their skin, gills, or shells, is vital for the colonization and subsequent transmission of these bacterial pathogens. Extensive studies have demonstrated the adhesive and biofilm-forming capabilities of human pathogenic *Vibrio* spp. on biotic surfaces of marine organisms. Bacteria residing in biofilms are encased in a self-produced matrix of extracellular polymeric substances (EPS), composed primarily of various macromolecules such as polysaccharides, proteins, lipids, nucleic acids, and other constituents. The composition of this matrix is influenced by the specific microflora involved and the environmental conditions during biofilm development (Carrascosa et al., 2021). Particularly, the adherence and biofilm production capacities of *V. parahaemolyticus* and *V. vulnificus*, facilitated by the presence of pili or flagella on the bacterial surface, have been identified as crucial for their successful colonization and persistence in oysters (Aagesen et al., 2013; Paranjpye et al., 2007). Chitinous surfaces of crabs and shrimps have also been reported as optimal substrates for *V. parahaemolyticus* (Han et al., 2016; Roy et al., 2021), and *V. cholerae* (Castro-Rosas & Escartin, 2002) adhesion and biofilm formation. Once human pathogenic *Vibrio* spp. attach to a chitinous surface, they may produce several chitinases, which degrade chitin to *N*-acetyl glucosamine, providing essential carbon and nitrogen sources. Therefore, the degradation of chitin generates nutrients that are vital for the multiplication of human pathogenic *Vibrio* spp. and creates openings for colonizing the host, leading to internal contamination (Pruzzo et al., 2008). Interestingly, *V. parahaemolyticus* and *V. cholerae* are also capable of adhering to phytoplankton

and zooplankton, such as copepods or diatoms, which constitute the foundation of the marine food web and may be ingested as feed sources by various aquatic organisms (Frischkorn et al., 2013; Huq et al., 1983; Tamplin et al., 1990). The adherence of such pathogens to these living prey and phytoplankton, often used as aquaculture feeds, may facilitate the contamination and internalization of potential human pathogenic *Vibrio* spp. in raw seafood.

Second, *Vibrio* spp. can enter seafood organisms through ingestion, filtration, or skin aberrations. Hence, another plausible route of *Vibrio* spp. contamination is internationalization via the mouth, gills, or skin aberrations. Filter-feeding organisms, such as mollusks and crustaceans, can capture and concentrate various nutrients, pollutants, and bacteria, including human pathogenic *Vibrio* spp., from the surrounding water. Indeed, the presence of *V. parahaemolyticus* in the surrounding environment of oysters has been correlated with its presence and accumulation in the gills and digestive glands (Wang et al., 2010). In fish, immersion exposure of eels (*Anguilla anguilla*) to *V. vulnificus* demonstrated that this pathogen can attach to gills and subsequently reach internal organs by entering the capillaries and circulating through the bloodstream (Valiente et al., 2008). Skin lesions or microtraumas have also been identified as potential routes of entry for *V. parahaemolyticus* in fish (Liu et al., 2016). In fact, the increased infection rate of human pathogenic *Vibrio* spp. in large yellow croaker (*Pseudosciaena crocea*) raised in sea cages was associated with the development of skin cuts.

The retention of human pathogenic *Vibrio* spp. through attachment and biofilm formation on biotic surfaces and their internationalization into aquatic organisms contributes to the bioaccumulation of these bacteria in seafood intended for human consumption. As part of developing control strategies, the aforementioned tissues and organs should be further investigated as potential key samples for monitoring the contamination of human pathogenic *Vibrio* spp. in different organisms intended for human consumption.

2.3 | Anthropogenic vectors

Although human pathogenic *Vibrio* spp. benefit from different reservoirs in the natural aquatic environment, anthropogenic activities, and related pollution from hospital, urban and industrial effluents may impact aquatic ecosystems, altering the ecology of microbial communities, and subsequently affect the prevalence and abundance of pathogens in raw seafood (Nogales et al., 2011). A close relationship with anthropogenic areas, reservoirs of antimicrobial resistance (AMR) genes, will naturally lead to increased prevalence of AMR with related therapeutic

failure threatening animal and human safety (Bourdonnais et al., 2022). Consequences and risk factors of the propagation of AMR within human pathogenic *Vibrio* spp. have already been assessed by Loo et al. (2020) and will not be discussed in this review.

2.3.1 | Maritime sources

Previous studies identified the significance of the role of ballast water in the spread of human pathogenic *Vibrio* spp. Water held in the ballast tanks of ships, used to maintain stability, can carry a wide range of microorganisms, including potential pathogens. Their discharge from ports to ports had been identified as a significant risk factor for pathogen transmission. Most studies have focused on the detection of *V. cholerae* in ballast water due to its pandemic potential (Cohen et al., 2012; Dobbs et al., 2013; McCarthy & Khambaty, 1994; Meena et al., 2022; Rivera et al., 2013; Ruiz et al., 2000). Several authors confirmed the presence of *V. cholerae* in ballast water of ships in North America (Dobbs et al., 2013; McCarthy & Khambaty, 1994; Ruiz et al., 2000), middle America (Cohen et al., 2012), South America (Rivera et al., 2013), and India (Meena et al., 2022). Importantly, the causative role of ballast water for pathogen transfer was postulated, when the toxigenic strain of *V. cholerae* O1, serotype Inaba, and biotype El Tor, originally detected in Latin America, was isolated in the ballast water of ships within the coastal waters of the United States in the Gulf of Mexico (Centers for Disease Control and Prevention [CDC], 1993; McCarthy & Khambaty, 1994). Similarly, the spread of *V. parahaemolyticus* O3:K6, from India to the Gulf of Mexico, was hypothetically associated with ballast water (Myers et al., 2003). More recently, along with *V. cholerae*, both *V. parahaemolyticus* and *V. vulnificus* were also detected in the ballast water of ships in Asia (Ng et al., 2018). As a result, today, the International Maritime Organization (IMO) has provided regulations to manage the impact of ballast water-mediated transfer of microorganisms and especially to regulate the spread of toxigenic *V. cholerae*. Another risk factor associated with the maritime transfer is the presence of pathogenic bacteria on the surface of vessels and harbor structures (Georgiades et al., 2021). Indeed, biofouling from vessels have been identified as potential reservoirs of *V. parahaemolyticus* (Revilla-Castellanos et al., 2015) or *V. cholerae* (Shikuma & Hadfield, 2010), which can promote their dissemination.

Despite a solid body of evidence regarding the role of maritime activities as reservoirs and vectors of human pathogenic *Vibrio* spp., these pathways have been largely neglected, and no study has formally implicated these factors as responsible for the contamination of marine

organisms intended for human consumption. These transmission routes deserve particular attention to prevent the spread of human pathogenic *Vibrio* spp. through the science-based application of appropriate regulations and guidelines.

2.3.2 | Urban and industrial impact

As discussed earlier, the microbiological status of the surrounding environment naturally affects the proliferation and contamination of raw seafood. Urban and industrial effluents are usually poor in microbiological quality, harboring an array of different enteric bacteria, as well as an overabundance of nutrients, heavy metals, AMR genes and bacteria, or pharmaceutical products, responsible for eutrophication. Their discharge into the aquatic environment represents a determinant risk of seafood contamination. Indeed, in different regions of the globe, it has been shown that pollution through discharge of untreated wastewater effluents was associated with increased occurrence of *V. cholerae* (Chávez et al., 2005) and *V. parahaemolyticus* (Watkins & Cabelli, 1985) within the surrounding environment and/or aquatic animals. For example, during an epidemic in Algeria, the presence of *V. cholerae* in both wild and farmed mussels was correlated with untreated urban wastewater (Arab et al., 2020). Similarly, an experiment performed by Conrad and Harwood (2022) demonstrated that the addition of only 1% sewage to estuarine water resulted in a significant increase in *V. vulnificus* densities in seawater. Due to the water eutrophication, areas subject to urban and industrial effluents are more vulnerable to phytoplankton blooms (Heisler et al., 2008; Michael Beman et al., 2005), which indirectly affect the proliferation of human pathogenic *Vibrio* spp. Indeed, *V. parahaemolyticus* was associated with an enrichment of seawater with phytoplankton-derived dissolved organic matter related to increased surface runoff (Thickman & Gobler, 2017). This correlation is particularly observed after rainfalls or storms which not only lead to release of sediment-bound bacteria in the aquatic environment but also nutrients, with subsequent eutrophication (Thickman & Gobler, 2017; Wetz et al., 2008).

Monitoring the biological contamination of anthropogenic areas is of concern to ensure human safety. Most regulatory agencies use the fecal indicator bacteria, including fecal coliforms, enterococci, or *Escherichia coli*, which fail in evaluating human pathogenic *Vibrio* spp. pollution, such as *V. parahaemolyticus* (Chahouri et al., 2022). Therefore, the developments of standard and effective human pathogenic *Vibrio* spp. contamination indices are urgently needed for efficient surveillance and control strategies.

2.3.3 | Aquaculture

Aquaculture farming generates complex ecosystems where the ecology and evolution of pathogens contrast with nature, affecting pathogen life cycles as well as their transmission. Dynamics of bacteria, which originate from the natural environment, animals, and also humans via farm workers, are regularly perturbed through the feeding of animals, harvesting, disinfection procedures, vaccination, and so on.

Pathogen transmission is a density-dependent phenomenon and, consequently, is impacted by the stocking rates in aquaculture farms (Owens, 2019). Host densities in rearing conditions are overall higher than in the natural environment. By reducing the distance between aquatic animals, as well as the total space available, the probability of bacterial transmission from water, animal, or biofilm is significantly increased. Importantly, biofilm from sediments or walls of aquaculture tanks may be a reservoir for human pathogenic *Vibrio* spp. (Arunkumar et al., 2020). These bacterial complexes could further bring tolerance against antibiotics and disinfectants and may result in a persistence of pathogens at farm sites. For instance, Mougin et al. (2021) identified one isolate of *V. parahaemolyticus* from biofilm associated with sea bass rearing tanks (*Dicentrarchus labrax*), whereas the bacteria were not isolated from rearing water, or water sources supplying the farm. Intensive aquaculture practices thus create favorable conditions for the propagation and persistence of pathogens. Furthermore, densely populated farmed marine organisms are subjected to constant stress due handling and competition for food, space, and resources (Ciji & Akhtar, 2021). This chronic stress weakens their immune systems, increasing their susceptibility for human pathogenic *Vibrio* spp. transmission. In addition, by comparing the impact of shrimp stocking densities on human pathogenic *Vibrio* spp. dynamics, Alfiansah et al. (2018) demonstrated that higher densities correlate with higher human pathogenic *Vibrio* spp. densities in aquaculture ponds. Higher bacterial densities may also favor the exchange of bacterial genetic elements, which will increase the risk for the emergence of new virulent bacterial strains and those with increased AMR. A multisite study on antibiotic resistance involving 150 strains of *Vibrio* spp. isolated from farmed European sea bass in Italian mariculture revealed that 96% of the strains exhibited multiple resistance to 15 tested antibiotics. Notably, four strains of *V. parahaemolyticus* displayed resistance to amoxicillin, cephalothin, erythromycin, and streptomycin, whereas one remaining strain of *V. vulnificus* exhibited resistance to oxolinic acid, flumequine, and sulfadiazine (Scarano et al., 2014). It has also been demonstrated that

the transport of shellfish from one farm to another had been proven to favor the transmission and microevolution of *V. parahaemolyticus* populations due to genomic exchanges (Fu et al., 2021a). However, the stocking density is a critical point in industry, in which balance between productivity and operational costs is essential to ensure both animals health and welfare, as well as the economic well-being of the company. Although significant efforts have been made to characterize the dynamics of human pathogenic *Vibrio* spp. in aquaculture farming in order to propose better management practices, the complex and specific interplay among environment, animal, and bacteria, as well as the multifactorial nature of the transmission, make the task more challenging (Mougin et al., 2021; Prescott & Barkovskii, 2022).

Discharge of aquaculture wastewater carrying distinct communities of human pathogenic *Vibrio* spp., as well as an enriched concentration of chemical and organic elements, may affect the ecology of the surrounding environment. Xu et al. (2020) identified a distance-decay pattern in the abundance of human pathogenic *Vibrio* spp. from farms to the natural environment, indicating potential adverse effects and spread of human pathogenic *Vibrio* spp. to wildlife and humans. Similarly, Dowle et al. (2015) recorded different bacterial diversities with distance away from salmon farms, mostly associated with a gradient of organic matters. However, in the study of Zeng et al. (2019), only weak differences in human pathogenic bacterial communities were deciphered between areas with distinct aquaculture intensities. These results vary across studies, as a metagenomic analysis of the wastewater of an aquaculture farm and its surrounding environment demonstrated no clear evidence of alteration or increase of the surrounding human pathogenic *Vibrio* spp. community in China (Möller et al., 2020).

Nevertheless, caution should be made when drawing conclusions on the effect of aquaculture farms, as such impact seems to be dependent on individual on-farm management practices and systems. For example, a comparison of *V. parahaemolyticus* populations associated with two different types of shellfish farms (i.e., traditional farms with water exchange vs. recirculating aquaculture system [RAS] farming) indicated different dynamics (Yang et al., 2022). In particular, populations from RAS farming appeared more stable than the traditional system, which favors the introduction and renewal of *V. parahaemolyticus*, with an increased risk for seafood safety.

2.3.4 | Plastic particles

It is now well established that plastics and microplastics can play a significant role in the contamination of

seafood by bacteria such as human pathogenic *Vibrio* spp., both in fishing waters and aquaculture environments. These plastic particles serve as vectors for the contamination of seafood and contribute to the contamination of the aquatic environment by facilitating the transport, dissemination, accumulation, and persistence of human pathogenic *Vibrio* spp. and other pathogenic bacteria. Plastic particles affords surfaces for which human pathogenic *Vibrio* spp. can attach, thereby creating an environment that human pathogenic facilitates biofilm formation and provides nutrients for their proliferation (Bowley et al., 2021). A study conducted by Kirstein et al. (2016) revealed the presence of *V. parahaemolyticus* on different types of microplastics, such as polyethylene, polypropylene, and polystyrene, originating from the North Sea and the Baltic Sea. Similarly, plastic samples collected from the surrounding waters of Guanabara Bay in Brazil showed the presence of *V. cholerae* and *V. vulnificus*, whereas the respective water samples exhibited low concentrations of human pathogenic *Vibrio* spp. (Silva et al., 2019). These studies clearly highlight that plastics and microplastics can serve as a vector of environmental contamination for *Vibrio* in marine and aquaculture environments. Therefore, it is essential to maintain clean aquatic environments free from plastic debris.

In addition to promoting the presence of human pathogenic *Vibrio* spp. in the environment, plastic particles, particularly microplastics, can be ingested by fish and shellfish species harvested for human consumption. A study conducted in China showed that 84% of oyster samples collected from 17 distinct cities contained microplastics, with an average concentration of 2.93 particles per individual (Teng et al., 2019). When animals consume microplastics carrying human pathogenic *Vibrio* spp., bacterial cells can be internalized, human pathogenic leading to the contamination of the tissues of the seafood itself, thereby increasing the risk of infection for human consumers. Few studies have investigated the ability of plastic particles to serve as vectors of human pathogenic *Vibrio* spp. for the contamination of seafood. However, a study by Sun et al. (2023) demonstrated the capacity of *V. parahaemolyticus*-carrying microplastics to contaminate *Mytilus galloprovincialis* mussels. In other research, the impact of microplastics on the proliferation of human pathogenic *Vibrio* spp. in the stomach of *Clarias gariepinus* catfish was studied. It was shown that the use of biodegradable polylactic acid-based microplastics led to a significant increase in the number of *Vibrio* sp. in the stomach of these fish, potentially due to dysbiosis caused by the release of chemical components from the microplastics (Jang et al., 2022). Despite the growing body of evidence implicating microplastics as vectors for *V. parahaemolyticus* contamination, no specific study has investigated the impact of

microplastics as a source of contamination for *V. cholerae* or *V. vulnificus*. Furthermore, the existing studies have primarily focused on assessing the contamination levels in the stomach contents of raw seafood. It would be of interest to expand these investigations to include the evaluation of contamination levels not only in the stomach contents but also within the tissues intended for human consumption.

2.4 | Wildlife sources and contamination routes

Human pathogenic *Vibrio* spp. are integral components of the natural aquatic food web. As such, their growth, survival, and ability to cause contamination are influenced by trophic regulations, including the dynamics of various organisms and predation within aquatic ecosystems (Vezzulli et al., 2013; Worden et al., 2006). These bacteria interact with a diverse range of wildlife species, including marine mammals, birds, fish, and invertebrates, serving as potential reservoirs or hosts. Therefore, various wildlife species can play a crucial role in the transmission and dissemination of human pathogenic *Vibrio* spp. within the marine environment. For example, marine mammals, such as seals or sea lions, have been identified as carriers of human pathogenic *Vibrio* spp., and their excretions can contribute to the contamination of aquaculture and fishery areas. Furthermore, predation within aquatic ecosystems can influence the prevalence and distribution of *Vibrio* bacteria. The selective pressures exerted by higher trophic levels, such as predatory fish or crustaceans, can shape *Vibrio* populations by favoring certain strains or reducing their abundance. The ecological dynamics of human pathogenic *Vibrio* spp. in relation to predation interactions are not only relevant for understanding their natural distribution but also for comprehending the potential risks they pose to human health when contaminated seafood is consumed. The interplay among human pathogenic *Vibrio* spp., various wildlife species, and the wider food web is further influenced by environmental factors and interactions with other organisms. Nutrient availability, temperature fluctuations, and other environmental stressors can impact the growth and persistence of human pathogenic *Vibrio* spp. populations. Additionally, the interactions between *Vibrio* bacteria and other microorganisms, such as bacteriophages or competing bacterial species, can shape their ecological niche and influence their potential to cause contamination. Understanding the wildlife sources and routes of contamination by human pathogenic *Vibrio* spp. in the marine environment is essential for assessing and managing the risks of raw seafood contamination associated with these bacteria.

2.4.1 | Parasites

The contribution of parasites to human pathogenic *Vibrio* spp. contamination of seafood is a critical topic that warrants attention, as it has been overlooked thus far. Parasites can act as both vectors for human pathogenic *Vibrio* spp. and as factors that facilitate bacterial invasion in seafood. Previous studies have reported cases of co-contamination of human pathogenic *Vibrio* spp. with various parasites in marine organisms intended for human consumption (Bienlien et al., 2022; Dhakal et al., 2006; Elgendy et al., 2016; Amalisa et al., 2021; Ravichandran et al., 2001). Despite the recognition of these co-occurrences, no research has yet been conducted to understand the underlying mechanisms driving the proliferation of human pathogenic *Vibrio* spp. within parasitized marine species. For instance, a study conducted by Elgendy et al. (2016) examined the co-occurrence of the parasite *Gyrodactylus anguillae* and *V. vulnificus* in cultured eels (*A. anguilla*). The authors hypothesized that parasite infection weakens the host's immune defenses, thereby creating vulnerability to *V. vulnificus* contamination. It is also worth noting that many marine parasites, such as *Anisakis*, possess a chitin-rich surface, a structural polysaccharide (Chen & Peng, 2019). The presence of chitin on parasites may play a role in the adherence of human pathogenic *Vibrio* spp. bacteria to their surface, potentially leading to cross-contamination of seafood during parasitic infection through bacterial transfer. This hypothesis raises questions regarding the presence of human pathogenic *Vibrio* spp. on the parasites themselves and their potential for contaminating marine organisms intended for human consumption.

This knowledge gap makes it challenging to accurately assess the risk of seafood contamination through this potential pathway.

2.4.2 | Plankton and algae

The plankton, composed of phytoplankton and zooplankton, along with algae (including macroalgae and microalgae), plays a crucial role in marine ecosystems. However, it is important to recognize that they can also act as reservoirs and vectors for human pathogenic *Vibrio* spp., which poses potential risks to seafood safety. Numerous studies have demonstrated that these organisms harbor human pathogenic *Vibrio* spp. and facilitate their adhesion or association with their tissues, thus promoting the formation of aggregates or biofilms that provide protected niches for *Vibrio* survival and proliferation (Noorian et al., 2023). These associations have been closely correlated with

excessive proliferation of human pathogenic *Vibrio* spp. during plankton and algal blooms (Epstein, 1993; Xu et al., 2022). In the context of aquaculture and fisheries systems, it is crucial to consider that plankton and algae can represent a potential source of human pathogenic *Vibrio* spp. contamination for marine organisms intended for human consumption. When plankton or algae are contaminated with *Vibrio*, they can be ingested or come into contact with marine organisms. This process can lead to the transfer of *Vibrio* to higher trophic levels of the food chain, including marine organisms consumed by humans. A study conducted by Sathiyamurthy et al. (2013) evaluated the prevalence of human pathogenic *Vibrio* spp. in various environmental samples and seafood products in the Tamil Nadu region, India. The results revealed the exclusive presence of *V. cholerae* and *V. parahaemolyticus* in phytoplankton and seafood samples, whereas these pathogens were absent from samples obtained from freshwater sources and coastal water bodies. Similarly, research conducted by Wright et al. (1996) provided compelling evidence of co-contamination of plankton and oysters, which are commonly consumed, by *V. vulnificus* originating from the Chesapeake Bay. However, to our knowledge, no study has yet established a link between the contamination of zooplankton and algae and the contamination of marine organisms intended for human consumption by *Vibrio*. Additionally, it is worth noting that the study by Worden et al. (2006) revealed that populations of *V. cholerae* can experience mortality due to predation by protozoan grazers. This grazing-induced mortality helps balance the growth of *V. cholerae* populations, thus keeping their levels under control. Net population gains have been observed under particularly intense bloom conditions, where *V. cholerae* has managed to overcome grazing pressure through rapid growth (more than 4 days for doubling time). Therefore, it is crucial to understand the role of plankton and algae in the spread of human pathogenic *Vibrio* spp. in marine ecosystems, as well as within the human food chain.

2.4.3 | Aquatic birds and mammals

Birds and marine mammals play a significant role in coastal and marine ecosystems as predators and scavengers. However, these organisms can also contribute to the dissemination of human pathogenic *Vibrio* spp. in fishing and aquaculture areas. Studies conducted in the United States (Ogg et al., 1989) and England (Lee et al., 1982) have revealed the presence of *V. cholerae* in fecal samples and cloacal swabs taken from wild aquatic birds. Similarly, a subsequent study conducted in Japan by Miyasaka et al. (2006) demonstrated that wild aquatic

birds carried *V. parahaemolyticus* and *V. vulnificus* during the winter season. Research on marine mammals has also clearly demonstrated their ability to carry *V. parahaemolyticus* (Goertz et al., 2013) and *V. vulnificus* (Li et al., 2018), as well as *V. cholerae* (Buck & McCarthy, 1994). Although it is evident that these bacteria may be present in the intestines of birds and marine mammals, it is also reasonable to assume that they may be present on their external surfaces. Thus, when these organisms move within fishing or aquaculture areas, they can contaminate these zones with bacteria present on their surface or excreted in their feces. Seafood located near these contaminated areas can come into contact with these bacteria and become contaminated. Despite tangible evidence of the transportation of human pathogenic *Vibrio* spp. by seabirds and marine mammals, few studies have evaluated the impact of these vectors on seafood contamination in the marine environment. In 2004, an epidemiological study was conducted in Alaska following an outbreak of *V. parahaemolyticus* associated with the consumption of oysters cultivated in farms located in Prince William Sound and southeast Alaska. Restriction fragment length polymorphism-electrophoresis profiles of the implicated *V. parahaemolyticus* strains revealed genetic similarities with strains previously isolated in Puget Sound, located 2100 km away from the contaminated farms in Alaska. Although hypotheses were put forth by the coauthors, the possibility of these strains being spread through avenues such as seabirds was suggested (McLaughlin et al., 2005). Therefore, it is essential to deepen our understanding of the role of seabirds and marine mammals as sources and vectors of contamination by human pathogenic *Vibrio* spp.

2.4.4 | Insects

The contamination of seafood by human pathogenic *Vibrio* spp. through insects represents a significant concern in terms of food safety and public health. These insects play a significant role in the transmission of pathogenic bacteria to marine organisms. Several insects have been identified as potential reservoirs of *V. cholerae* or *V. parahaemolyticus*, including marine and terrestrial insects such as chironomids (Halpern et al., 2004), house flies (Yap et al., 2008), mosquito larvae (Fukuda et al., 1997), cockroaches, and ants (Barber, 1914; Cao et al., 2010). These insects can feed on food waste and/or fecal matter contaminated with human pathogenic *Vibrio* spp. or land on surfaces already contaminated with these bacteria, subsequently moving into marine environments such as fishing or aquaculture areas. Consequently, they can transmit these bacteria to marine organisms when they alight or come into direct contact with them, notably through feeding.

Regrettably, despite evidence of human pathogenic *Vibrio* spp. carriage by several insects, no study has assessed the cross-contamination of marine organisms intended for human consumption. It is therefore crucial to conduct comprehensive studies to better understand the extent of this risk and to implement appropriate preventive measures.

3 | CONTAMINATION ROUTES OF PROCESSED SEAFOOD

3.1 | Inappropriate handling scenarios in seafood industry

Poor handling of seafood plays a crucial role in *Vibrio* food contamination. A 2007 examination found that improper food handling may have been a factor in 97% of all foodborne illnesses associated with the food service industry (Egan et al., 2007). In fact, according to World Health Organization (WHO), global epidemiological studies show that, in most cases, outbreaks of foodborne disease can be attributed to improper food handling by food handlers (WHO, 2008). The role of food workers in human pathogenic *Vibrio* spp. foodborne outbreaks has been clearly demonstrated by several authors (Jung, 2018; Liu et al., 2015; Merson et al., 1976; Taha & Mohamed, 2020).

3.1.1 | Slicing scenarios: equipment usage

Cross-contamination scenarios involving the use of equipment and utensils, such as cutting boards, knives, and slicers, are likely to occur when good hygiene practices are not applied by personnel and are probably underreported. Slicing food such as ready-to-eat (RTE) seafood can increase the risk of cross-contamination by contact with contaminated surfaces. Not only slicing, but also cutting, handling, or packaging operations contribute to increasing the risk of cross-contamination. For example, investigations carried out during a vibriosis outbreak in September 2017 in Korea strongly suggested that the infection vehicle was a knife and a cutting board (Jung, 2018). It was determined that contaminated squid was sliced using a knife and a cutting board, which were then used to slice egg sheets, spreading the contamination to *V. parahaemolyticus*. The potential risk for the transfer of human pathogenic *Vibrio* spp. in slicing scenarios has not been well evaluated so far. However, the study of such situations would provide empirical data to develop guidelines for the industry and retailers on good slicing practices and clean-

ing and disinfection procedures to prevent transfer and survival of these enteric pathogens. In a survey conducted by Asmawi et al. (2018) in Malaysia (the eighth largest shrimp producer in 2010; Chowdhury et al., 2012), on food handlers' knowledge, attitudes, and practices regarding food hygiene, 5.5% of respondents were reported to be uncertain or not at all agreeable to changing gloves after handling raw food and before handling RTE food.

3.1.2 | Hygiene and glove usage

Direct handling of food with contaminated gloves represents a critical source of cross-contamination and dissemination of human pathogenic *Vibrio* spp. A study conducted by Xiao et al. (2018) aimed to quantify the transfer of *V. parahaemolyticus* during the shrimp peeling process via gloves in three different scenarios. The first two scenarios provided quantitative information on the probability distribution of bacterial transfer rates, from (i) contaminated shrimp (6 log CFU/g) to non-contaminated gloves (scenario 1) and from (ii) contaminated gloves (6 log CFU/pair) to non-contaminated shrimp (scenario 2). In scenario 3, bacterial transfer from contaminated shrimp to non-contaminated shrimp during the peeling process via gloves was studied to develop a predictive model to describe successive bacterial transfer. The results showed that *V. parahaemolyticus* could not only be transferred from shrimp to gloves and from gloves to shrimp, but also that successive shrimp contamination could also occur easily without changing gloves. On the other hand, it was shown that 18% of seafood warehouse workers cleaned seafood with seawater after unloading in the warehouse (Zanin et al., 2015).

3.1.3 | Contaminated seawater

Seawater is a major source of human pathogenic *Vibrio* spp. contamination and therefore represents a significant risk for the cross-contamination of surfaces in contact with food, especially RTE products (Collin & Rehnstam-Holm, 2011; Tey et al., 2015). Between December 1974 and February 1975, two outbreaks of *V. parahaemolyticus* linked to the consumption of seafood cocktails, shrimp, and lobster led to 697 cases of vibriosis on two cruise ships. The investigation revealed the use of seawater in the kitchen from the ships' fire system, which was contaminated with *V. parahaemolyticus* (Merson et al., 1976). A study on the use of *V. parahaemolyticus* contaminated seawater for washing naturally contaminated fish clearly showed that contaminated wash water significantly increased the *V. parahaemolyticus* load on the fish (Hara-Kudo et al., 2013).

3.1.4 | Food packaging

The contribution of food containers and transport bags to food contamination is an important topic to address. Reusable bags, when not properly washed between uses, pose a risk for cross-contamination of food. For example, when raw seafood and RTE foods are transported together in the same bag, or among different uses of the bag, this increases the opportunity for cross-contamination. In a study conducted by Barbosa et al. (2019), the cultivable bacterial flora of 30 reusable plastic bags was analyzed. Results showed the presence of numerous Enterobacteriaceae and staphylococci in all bags, as well as one bag contaminated with the foodborne pathogen *Listeria monocytogenes*. The study suggested that raw seafood or other uncooked food products had contaminated the bags. Although human pathogenic *Vibrio* spp. were not isolated, the presence of other enteric bacteria demonstrates that food containers and reusable bags can be contaminated by enteric microorganisms, posing a potential danger, especially if leaked food residues on the internal surfaces permit the growth of pathogens. It is also important to note that once contaminated, bags are often used for purposes other than transporting seafood, which increases the risk of cross-contamination. The aforementioned study by Barbosa et al. (2019) also revealed that consumers rarely wash reusable bags, which allows bacteria to grow when stored under appropriate conditions. This highlights the need for targeted recommendations to consumers and professionals to reduce the risk of cross-contamination when using reusable shopping bags.

3.2 | Carrier organisms

3.2.1 | Food handlers

Aside from poor handling practices, seafood handlers themselves can represent a source of contamination due to their health status and asymptomatic carriage of human pathogenic *Vibrio* spp. (Chonsin et al., 2021). In May 2013, 99 employees of a company in Guangdong, China, contracted a co-infection with *V. parahaemolyticus* and norovirus after consuming roast duck, an uncommon vector for these two pathogens. Epidemiological and laboratory investigations, including similarity analyses of serotypes, sequence types, and PFGE results, indicated that a single asymptomatic food handler was the source of the infection (Liu et al., 2015). It is difficult to assess the percentage of asymptomatic carriers of human pathogenic *Vibrio* spp., as this is poorly investigated and varies depending on regions, populations, and environmental conditions. In Japan, the prevalence of *V. parahaemolyticus* in

food handlers was reported to be 0.3% (17/450), with three isolates being Kanagawa phenomenon positive (Nishlo et al., 1969). In 2002–2003, the presence of pathogenic strains of *V. parahaemolyticus* among asymptomatic workers in shrimp processing plants in Thailand was nearly 35% (25.8% *tdh+* *trh-*; 4.8% *tdh-* *trh+*; 4.8% *tdh+* *trh+*) (Chonsin et al., 2021). Additionally, a phylogenetic study using multilocus sequencing typing analyzed strains of *V. parahaemolyticus* from Thailand recovered from various sources associated with the seafood industry, including clinical samples, healthy workers, fresh seafood, frozen shrimp, farmed shrimp tissues, and pond water for shrimp culture. It showed that human carrier isolates carrying virulence factors were closely related to clinical isolates, but not to those of environmental origin (Theethakaew et al., 2013). Recently, Chonsin et al. (2021) aimed to evaluate the potential role of fish handlers in seafood processing plants as probable sources of *V. parahaemolyticus* contamination. They found 12 *V. parahaemolyticus* isolates from asymptomatic workers to be toxigenic strains (*tdh+* or *trh+* genotype) along with 49 other non-toxigenic isolates (*tdh-* *trh-* genotype), confirming the major danger posed by fish handlers as a source of foodborne *Vibrio* contamination. The involvement of seafood handlers as carriers of *V. cholerae* has also been demonstrated in foodborne outbreaks implicating this pathogen (Lalitha et al., 2008), but the same has not been shown in outbreaks involving *V. vulnificus*.

3.2.2 | Pests

Attention must also be given to pests that can be responsible for cross-contamination by human pathogenic *Vibrio* spp. As previously mentioned (Section 2.4.4), insects can act as potential reservoirs of human pathogenic *Vibrio* spp. (Barber, 1914; Cao et al., 2010; Echeverria et al., 1983; Halpern et al., 2004; Lee et al., 1982; Miyasaka et al., 2006; Ogg et al., 1989). They can come into contact with *Vibrio*-contaminated food human pathogenic and then move to other food preparation or storage areas, thereby facilitating the spread of these bacteria to food contact surfaces and/or directly to food items that were previously free of pathogens. The potential for such transfer of *Vibrio* was demonstrated in experiments carried out by Yap et al. (2008), where domestic flies were placed in a room containing *V. cholerae*-contaminated liquid bait. After 2 h, 10 flies were sequentially removed and cultured for the presence of *V. cholerae*. The results revealed that the pathogen was isolated from four domestic flies; specifically, two were obtained from the legs of the flies and two from the bodies with the legs or wings removed. These observations underscore the potential role of insects in the dissemination of

human pathogenic *Vibrio* spp. and cross-contamination to food. To mitigate these risks, it is imperative to implement effective pest control measures in food handling and storage areas. Additionally, gaining a better understanding of the role of insects and birds in the cross-contamination of processed seafood is crucial for implementing targeted prevention strategies. Further studies are necessary to assess the extent of their impact and develop appropriate preventive measures.

3.3 | Biofilms: catalyzing contamination pathways

3.3.1 | A catalyzer of cross-contamination in seafood industry

The colonization and persistence of enteric pathogens, such as human pathogenic *Vibrio* spp., on food processing and preparation surfaces represent a major risk to food safety. Cross-contamination can occur among food handlers, food products, and surfaces in contact with raw and/or processed foods when these pathogens adhere to surfaces (Mungai et al., 2002). Once attached to surfaces, *Vibrio* cells have the ability to form protective biofilms. Biofilms are of high importance across the entire food industry as they can form on food products or on any abiotic surface associated with food production/processing chains (Figure 1). Human pathogenic *Vibrio* spp. are able to form biofilms on biotic surfaces such as crustacean shells, fish opercula, or mollusk shells (Wang et al., 2022; Yu & Rhee, 2023), and this may enhance their survival through the processing chain and represent a significant risk of cross-contamination, especially during the processing of seafood products. In addition, numerous studies have shown that these pathogens are capable of adhering to and/or forming biofilms on several types of materials commonly found in food processing plants, such as plastic or glass (Drescher et al., 2016; Gallego-Hernandez et al., 2020; Leighton et al., 2022; Rosa et al., 2018). In the food industry, the most widely used material for the fabrication of processing equipment, pipelines, and work surfaces is stainless steel. This material is traditionally chosen in seafood processing plants for food preparation due to its mechanical strength, corrosion resistance, and longevity (Awad et al., 2018). Biofilms also form at liquid-air interfaces as would be the case of pellicles formed at a liquid surface (McLandsborough et al., 2006). More recently, the definition has expanded to include aggregates or flocs of cells, a phenomenon relevant to *V. cholerae* survival in aquatic environments and virulence (Yildiz & Visick, 2009). Regardless of the substratum used for attachment, this preferred sessile mode of life offers many advan-

tages for resident bacteria and enables them to grow and survive under stressful environmental conditions, such as food and environmental surface cleaning and drying procedures. Consequently, pathogenic cells can persist in biofilms on food contact surfaces for extended periods, thereby increasing the risk of cross-contamination (Ashrafudoulla et al., 2021; Han et al., 2016). There is very little research on the occurrence of *V. vulnificus*, *V. cholerae*, and *V. parahaemolyticus* on surfaces in seafood production, processing, or distribution environments. Some authors have reported the natural presence of *V. cholerae* on different pipes made of stainless steel in a metropolitan drinking water distribution system (Fu et al., 2021b). An unpublished study by Hossain et al. (2016, 2018) also investigated household contamination of *V. cholerae* in Bangladesh. In this survey, 39.6% of samples among a collection of 660 hot spot swabs from various surfaces (door knobs, cutting knives, drinking water pots, food plates, and leftover foods) tested positive for *V. cholerae*. To our knowledge, the only published study is that of Ngan et al. (2020), who analyzed the microbial profiles of biofilms on wooden cutting boards from 11 wet markets in Hong Kong and found natural surface presence of *V. parahaemolyticus* and *V. vulnificus*, which was later confirmed by Rao et al. (2021). Cutting boards represent hotspots for cross-contamination ranging from food processing plants to the kitchens of consumers. These surfaces have porous surfaces that provide a favorable environment for the proliferation and persistence of human pathogenic *Vibrio* spp. In addition, the nicks and cracks that form on the surface of cutting boards over time can provide growth niches for bacteria, making them difficult to eliminate even with thorough cleaning. To our knowledge, only Chiu et al. (2006) have evaluated the colonization ability of human pathogenic *Vibrio* spp. on cutting boards. They showed that *V. parahaemolyticus* could adhere in just 10 min to bamboo, wood, and plastic cutting boards, as well as to other surfaces in contact with food (stainless steel and glazed ceramic tiles). If cutting boards are used for the preparation of different types of food, such as raw and cooked seafood, this can lead to cross-contamination of RTE foods, thus increasing the risk of foodborne *Vibrio* infections. Malcolm et al. (2018) showed that *V. parahaemolyticus* could be transferred to lettuce when it came into contact with cutting boards and stainless steel knives used previously on contaminated bloody clams (*Anadara granosa*). To do this, they evaluated the potential for transfer and cross-contamination of *V. parahaemolyticus* from bloody clams to RTE foods (lettuce) according to three scenarios: (i) direct cross-contamination of *V. parahaemolyticus* from bloody clams to surfaces that do not come into contact with lettuce; (ii) effectiveness of superficial cleaning with water or wiping with a paper towel; and (iii) secondary

cross-contamination by the transfer of *Vibrio* from cleaning residues to lettuce. These studies demonstrated significant direct and indirect transfer of *V. parahaemolyticus* to lettuce and inefficiency of superficial cleaning in combating cross-contamination.

3.3.2 | Factors enhancing biofilm formation and contamination

In addition to the nature of the surfaces, other extrinsic and intrinsic factors influence the attachment capacities and the biofilm development of human pathogenic *Vibrio* spp. on processing equipment. Several authors have reviewed these factors, including Wang et al. (2022) who suggest the need to understand the mechanisms of *V. parahaemolyticus* biofilm formation, such as the role of mobility and flagella in adhesion and biofilm structuring, as well as the identification of polysaccharides and protein components of the extracellular matrix at different stages of biofilm development. Although intrinsic molecular factors favoring the formation of biofilms by human pathogenic *Vibrio* spp. are beyond the reach of food industry professionals, they can easily influence extrinsic factors. Two widely recognized extrinsic factors in the formation of human pathogenic *Vibrio* spp. biofilms are temperature and the composition of the growth/attachment medium. Recent studies have primarily focused on these two factors. Due to multiple experimental conditions, it is difficult to reach a consensus on the effect of temperature on the formation of *V. parahaemolyticus* biofilms. Castro-Rosas and Escartin (2002) and Han et al. (2016) agreed that the formation of *V. parahaemolyticus* biofilms on abiotic (stainless steel) and biotic surfaces (crustaceans and shrimp) is favored by temperatures above 30°C. However, Leighton et al. (2022) showed a greater biomass of *V. parahaemolyticus* biofilms cultured on glass and plastic at 25°C compared to those cultured at 30 and 35°C. Using the crystal violet microplate assay, Song et al. (2017) also noted greater biofilm formation at 25°C relative to 15 or 37°C for a collection of both pathogenic and nonpathogenic *V. parahaemolyticus* strains. They also reported that, as a group, the pathogenic strains produced more biofilm at all temperatures. Mougín et al. (2019) did not observe any difference in biofilm production of *V. parahaemolyticus* on stainless steel between 8 and 37°C in three different media, but highlighted that *V. cholerae* exhibited greater survival at 8°C rather than 37°C, when cultivated in brine. Regarding *V. vulnificus*, it has been demonstrated that biofilm production by *V. vulnificus* cultured on glass and plastic is more significant at low temperatures (24–25°C) than at high temperatures (35 and 37°C) (Çam & Brinkmeyer, 2020; Leighton et al., 2022; Velez et al., 2023). In contrast, in their study of biofilms

formed in glass tubes, Hernández-Cabanyero et al. (2020) showed no significant difference in biofilm production at temperatures ranging from 20 to 37°C, although a slight increase in biofilm quantity with increasing temperature was observed. Studies on biofilm-formation by non-O1/non-O139 serotype strains of *V. cholerae* are rare. To our knowledge, the only recent study conducted is that of Mougín et al. (2019) which showed that *V. cholerae* biofilms cultured on stainless steel in three different media have higher viable populations at 8°C than at 37°C. However, the biofilm capacities of serotype O1 and O139 strains are well documented (Yildiz & Visick, 2009) and much is known regarding the mechanisms involved as detailed by Teschler et al. (2022). In another earlier study, Castro-Rosas and Escartin (2002) also showed that temperature impacted the attachment of *V. cholerae* O1 to fresh crabs (*Callinectes sapidus*) and shrimp (*Penaeus duorarum*) surfaces, whereby the adherence was found to be less than 2% at 3°C but greater than 20% at 37°C.

The composition of the fixation medium, such as seafood exudates on contaminated surfaces, also influences the adhesion and biofilm formation of *V. parahaemolyticus*. Recent studies have shown that a low salt concentration promotes the formation of biofilms of this pathogen. For example, maximal biofilm formation by *V. parahaemolyticus* was observed on black tiger shrimp (*Penaeus monodon*) surfaces at a NaCl concentration of 2% compared to 5% NaCl. In combination with 2% NaCl and varying concentrations of glucose, the greatest biofilm production was observed at a low glucose concentration of 0.015% compared to a concentration of 0.05%. The addition of salt and glucose, at concentrations higher than 2% and 0.015%, respectively, inhibited the formation of *V. parahaemolyticus* biofilms (Mizan et al., 2018). More recently, Li et al. (2022) showed better biofilm formation for *V. parahaemolyticus* on polystyrene at a salinity of 0.5% NaCl than at a salinity of 4%. Regarding *V. cholerae*, a study conducted by Castro-Rosas and Escartin (2002) showed that attachment and colonization on shrimp exoskeletons were optimal at a salinity range of 1.0%–1.5% NaCl, a pH range of 6.0–7.0, and a temperature of 37°C. Even at 3% NaCl, some bacterial attachment was observed. To our knowledge, no recent studies have evaluated the impact of salt on the adhesion and formation of biofilms by *V. vulnificus*. On the other hand, the study by Velez et al. (2023) showed higher biofilm production by several clinical and environmental strains of *V. vulnificus* and *V. parahaemolyticus* at acidic pH values. Çam and Brinkmeyer (2020) confirmed these observations and also demonstrated a strong correlation between the concentration of iron in the growth medium and the production of biofilms by *V. vulnificus*. Similar observations were also made for *V. cholerae* O1 where its attachment to and subsequent colonization of

shrimp exoskeletons was found to be optimal in the pH range of 6.0–7.0 (Castro-Rosas & Escartin, 2002).

3.3.3 | An increase resistance/tolerance

In order to control the spread of human pathogenic *Vibrio* spp. biofilms, professionals use cleaning and sanitizing procedures, relying on a range of disinfectants. A study by Wang et al. (2023) revealed that *V. parahaemolyticus* biofilms required sodium hypochlorite concentrations 75 times higher than those needed for planktonic cells, highlighting the importance of developing effective biofilm control strategies. The results of various studies referenced by Wang et al. (2022) have shown that although cleaning products and disinfectants remove impurities and inactivate *V. parahaemolyticus* cells within the biofilm, the use of disinfectants alone at recommended concentrations makes effective biofilm control difficult as the presence of organic matter can neutralize the effectiveness of common sanitizing agents such as quaternary ammonium compounds and sodium hypochlorite (Bridier et al., 2011; Gelinas & Goulet, 1983). Moreover, it is possible that pathogenic communities of *V. parahaemolyticus* with acquired resistance may persist on surfaces (Rosa et al., 2018). Furthermore, it has been observed that human pathogenic *Vibrio* spp. can enter a state known as viable but non-culturable (VBNC), wherein *Vibrio* cells are not detectable through standard culture methods (Mougin et al., 2019; Rice et al., 2000; Yoon & Lee, 2022). Nevertheless, they remain viable and capable of regrowth when environmental conditions become favorable. Disinfectants can trigger this VBNC state by altering physicochemical factors in the surrounding environment, such as ion concentrations, pH, and temperature. This phenomenon has been documented, notably in *L. monocytogenes* (Brauge et al., 2020). However, the induction of the VBNC state in human pathogenic *Vibrio* spp. by disinfectants has not yet undergone comprehensive investigation.

3.3.4 | Single-species versus consortium

The vast majority of research on biofilms of foodborne pathogenic bacteria has been carried out using pure cultures. However, in the “real world,” biofilms do not exist as monocultures but instead they comprise a consortium of microbial species. The intimate interactions/associations between these microorganisms, whether be synergistic, antagonistic, or seemingly neutral, determine the overall development, structure, and function of the biofilm (Flemming et al., 2016). For example, relative to monoculture biofilms, a much greater diversity of constituents

is expected to be present in the EPS of polymicrobial biofilms. Furthermore, the amounts and combinations of these components not only depend on specific interactions between denizen microorganisms, but they also depend on when these interactions occur as well as their location within the biofilm during its development. Therefore, both the EPS matrix and composition of the community are dynamic in constant transition (Flemming et al., 2023). As such, the general architectures of multispecies biofilms are substantially different from those harboring a single species and consequently, the increased complexity can contribute to enhanced protection for the biofilm residents against external stressors. Numerous published works involving various foodborne pathogens have reported improved resistance to inimical challenges in mixed-species biofilms. For example, when cocultured with *Pseudomonas* spp. in biofilms formed on stainless-steel or plastics, the intracellular pathogen *L. monocytogenes* displays greater resistance to benzalkonium chloride (Haddad et al., 2021; Ibusquiza et al., 2012). Compared to their monoculture biofilms on stainless-steel, dual-species biofilms of Shiga-toxin producing *E. coli* paired with *Salmonella typhimurium* were shown to have increased bio-volume and biomass. Upon exposure to a NaClO solution (100 µg/mL) for 1 min, a significant decrease in the inactivation of cells was observed for those dwelling in the mixed-species biofilm versus their pure culture counterparts (Lin et al., 2022). Regarding human pathogenic *Vibrio* spp., Tan et al. (2021) showed that, relative to their monoculture counterparts, dual-culture biofilms formed by *V. parahaemolyticus* and the spoilage bacterium, *Shewanella putrefaciens*, displayed an altered spatial distribution of cells within the biofilm, resulting in greater EPS production and overall biomass. Ultimately, this rendered pathogen cells residing within this biofilm significantly less sensitive to photodynamic inactivation as compared to monoculture biofilm cells. In contrast, when Chen et al. (2019) examined dual-species biofilms formed by two foodborne pathogenic bacteria, *V. parahaemolyticus* and *L. monocytogenes*, they noted the overall biomass, bio-volume, and thickness of the monoculture biofilms of each bacterium was significantly greater than their biofilm in the combined culture. This modified architecture impacted the general susceptibility of these pathogens to the antibiotics ciprofloxacin and cefotaxime, whereby the minimum biofilm inhibitory concentrations were significantly reduced.

Although these dual-species biofilm studies provide useful baseline insight to help expand our understanding the interspecies interactions between these bacteria within sessile multispecies communities, they still represent very simplistic models compared to the natural world. The lack of realistic multispecies models that accurately mimic

real food industry biofilms remains a major hurdle for advancing our knowledge in this area. Some researchers have carried out biofilm studies with other foodborne pathogens in tri-species (Almeida et al., 2011; Haddad et al., 2021), or quadruple-species (Iñiguez-Moreno et al., 2019) biofilms, but to our knowledge, no studies to date research have investigated *Vibrio* spp. biofilms cocultured with more than one other species. Going forward there is a need for research examining the behavior of human pathogenic *Vibrio* spp. in multispecies biofilms of greater complexity. Such work is warranted as it could provide useful information to help gain a better understanding of its persistence in seafood processing environments, thus enabling science-based strategies aimed at mitigating the risk of contamination involving these important pathogens.

4 | CONCLUSION AND FUTURE PERSPECTIVES

To culminate the holistic approach outlined in this review, which addresses *Vibrio* contamination from both seafood production and processing, we were able to discern and pinpoint diverse sources and routes of contamination throughout the entire seafood supply chain. Human pathogenic *Vibrio* spp. are ubiquitous in aquatic environments, leading to the contamination of raw seafood. As a result, both wild-caught and farmed seafood can act as potential entry points for pathogenic *Vibrio* spp. into the seafood supply chain. The initial contamination of raw seafood occurs through two main processes: direct contact with contaminated water and internalization via ingestion, filtration, or skin abrasions. Additionally, *Vibrio* can adhere to biotic elements, like the chitinous surfaces of aquatic organisms, promoting their survival by forming robust and resilient biofilms. Within the environment, we have identified various factors which can influence the contamination of raw seafood, such as climate conditions (temperature, salinity, and pH), human activities (maritime operations, effluents, plastic particles, and aquaculture), and interactions with wildlife (birds, aquatic mammals, parasites, plankton, microbial communities, algae, and insects). Once within the seafood chain, contaminations mainly occur via cross-contamination through various pathways, including contact with contaminated processing equipment like surfaces, cutting boards, and knives, as well as food packaging and wash water. It can also occur through contact with carrier organisms such as insects/pests or food handlers. Moreover, the development of robust and tolerant/resistant biofilms by pathogenic *Vibrio* may impede their eradication through disinfection procedures, consequently accelerating con-

tamination pathways and heightening the likelihood of disinfection failure. In the end, without effective control measures, these contaminated seafood products may reach the food market, potentially posing significant health risks to consumers.

Today, significant issues persist in monitoring and reporting foodborne and human infections caused by *Vibrio*, greatly hindering our understanding of the attribution of sources of contamination by pathogenic *Vibrio* for humans. These gaps could be addressed by establishing an international surveillance network dedicated to pathogenic *Vibrio* for humans, following the model of the COVIS (cholera and other *Vibrio* illness surveillance) network established in the United States (Newton et al., 2012). At the European level, such infrastructure is lacking. Human vibriosis is not subject to mandatory reporting, and there are no formal regulatory microbiological criteria for *Vibrio* (European Food Safety Authority [EFSA], 2012; Food and Drug Administration [FDA], 2021; Hartnell et al., 2019). Therefore, microbiological surveillance of pathogenic *Vibrio* entailing pathogens remains voluntary and nonobligatory for each European country. It would be beneficial for Europe to establish European criteria for contamination by pathogenic *Vibrio* for humans, as well as a common methodology and surveillance network. This initiative would help gather crucial epidemiological data on *Vibrio* and conduct larger-scale investigations.

In this review, we have identified several knowledge gaps that warrant attention for future research. First, no study has been undertaken to understand the genetic evolution of *Vibrio* populations resulting from primary marine contamination throughout the seafood chain. It would be particularly interesting to investigate the impact of environmental factors encountered throughout this chain, such as temperature or surrounding microorganisms, on the growth of *Vibrio* pathogens for humans in food matrices and on the surfaces of processing facilities. This approach would help us better understand the actual health risks associated with RTE seafood products. Second, we should consider populations of VBNC flora, as demonstrated in the study by Mougín et al. (2019). VBNC flora present a significant health risk, as they are not detected by conventional microbiology methods, while remaining potentially pathogenic under favorable conditions (Oliver & Bockian, 1995). This approach would allow us to identify the environmental factors that influence the viability and growth of clinically important *Vibrio* in humans, thus paving the way for treatment strategies. Third, we could seek to identify potential indicators of the presence of pathogenic *Vibrio* in humans, such as a particular bacterial species or a specific gene. For example, the presence of *Listeria* sp. has been identified as an indicator of the zoonotic pathogen *L. monocytogenes* (Malley

et al., 2015). In addition, much like the study by Mougin and Joyce (2023), which delves into the potential of microbial dysbiosis-associated biomarkers as a means to prevent fish diseases in aquaculture, it would be intriguing to investigate biomarkers indicating an elevated risk of contamination due to the complex interplay between the microbiome and pathogen proliferation along the seafood supply chain. This approach could be useful in enhancing surveillance and early detection of pathogenic *Vibrio* in seafood, thereby contributing to improved food safety and public health protection. Fourth, we have highlighted studies that have genetically characterized strains of *Vibrio* pathogenic to humans isolated throughout the seafood supply chain. It would also be interesting to track the genetic evolution of a specific clone of pathogenic *Vibrio* throughout the seafood chain to better understand the acquisition or loss of resistance and/or virulence genes (such as *tdh*, *trh*, or *ctx*). Special attention could be given to biofilm sampling, as several studies have reported facilitated horizontal genetic exchanges within these structures (Madsen et al., 2012).

Finally, the impact of climate change and its related consequences on populations of pathogenic *Vibrio* for humans in marine and aquaculture environments has been extensively studied. However, a significant gap exists in the study of the impact of global warming in the seafood processing plants, from the entry of raw materials to the finished products. A promising research avenue would involve assessing the potential impact of temperature variations during seafood processing processes. This would include monitoring the phenotypic and genetic evolution of pathogenic *Vibrio* populations at each stage of the food supply chain. This approach would provide better insights into how environmental conditions, such as temperature fluctuations, can influence food safety and the quality of seafood products. Furthermore, this research could contribute to the establishment of early warning systems for extreme weather events, such as heat waves, to prevent potential food safety risks. Additionally, by demonstrating the impact of climate change on seafood processing plants, it could motivate governments and regulatory bodies to strengthen their environmental sustainability requirements. This could lead to the implementation of new regulations aimed at reducing the climate footprint of these seafood processing plants.

AUTHOR CONTRIBUTIONS

Thomas Brauge: Funding acquisition; writing—original draft; conceptualization; investigation; visualization; writing—review and editing. **Julia Mougin and Timothy Ells:** Writing—review and editing; investigation; writing—original draft. **Graziella**

Midelet: Writing—review and editing. **Julia Mougin:** Visualization.

ACKNOWLEDGMENTS

This study was supported by Haut de France region with VIBRATO project. Thomas Brauge acknowledges the receipt of a fellowship from the OECD Co-operative Research Programme: Sustainable Agricultural and Food Systems in 2023 (TAD/CRP PO 500120218). The Structure Fédérative de Recherche (SFR) Campus de la Mer and the embassy of France in Canada have also financially supported this work.

CONFLICTS OF INTEREST STATEMENT

No, there are no conflicts of interest.

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How to cite this article: Brauge, T., Mougín, J., Ells, T., & Midelet, G. (2024). Sources and contamination routes of seafood with human pathogenic *Vibrio* spp.: A Farm-to-Fork approach. *Comprehensive Reviews in Food Science and Food Safety*, 23, 1–25. <https://doi.org/10.1111/1541-4337.13283>