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Bivalves and microbes: a mini-review of their relationship and potential implications for human health in a rapidly warming ocean

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Heatwaves have become increasingly frequent and intense, posing a significant threat to the survival and health of marine bivalves. The temperature fluctuations associated with heatwaves can cause significant alterations in the composition and quantity of microbial communities in bivalves, resulting in changes to their immunological responses, gut microbiome, oxidative stress levels, and other physiological processes and eventually making them more susceptible to diseases and mass mortalities. This is particularly concerning because some of these bivalves are consumed raw, which could represent a risk to human health. This paper provides an overview of the current state of knowledge regarding the impact of marine heatwaves on bivalves and their microbial communities, demonstrating the intricate relationship between heatwaves, microbial ecosystems, and bivalve health. Our analysis highlights the need for additional research to establish the underlying mechanisms of these reactions and to develop appropriate conservation and management strategies to limit the impact of heatwaves on bivalves and their microbial ecosystems.

KEYWORDS

bivalve, microbial communities, climate change, heatwaves, human health

1 Introduction

Marine heatwaves have been widely recognized as one of the most significant drivers of change in the marine environment in recent years (Oliver et al., 2018). These heatwaves, defined as prolonged and intense periods of elevated water temperature, have become more frequent and intense with global warming, leading to severe impacts on the marine ecosystem (Frölicher et al., 2018; He et al., 2022a; Xu et al., 2022). One of the areas of particular concern is the effect of marine heatwaves on bivalve microbial communities, which are an essential component of the marine ecosystem and play a critical role in maintaining its stability and health. The diversity of microbial communities in bivalves has been extensively studied recently.

A growing body of literature demonstrates the presence of various bacteria, archaea, and eukaryotic microorganisms (Haygood et al., 1999; Fiore et al., 2010; Robledo et al., 2019). Bivalves harbor a diverse community of bacteria, including *Proteobacteria, Firmicutes*, and *Bacteroidetes. Vibrionaceae, Pseudomonadaceae*, and *Flavobacteriaceae* families (Leite et al., 2017; Akter et al., 2022). The structure of microbial communities in bivalves is highly variable, with different regions of the bivalve's body harboring distinct microbial communities. For example, the gills of clams contained a different microbial community than the digestive tract, with the gills being dominated by *Proteobacteria* and the digestive tract being dominated by *Firmicutes* (Zhang et al., 2016). Similarly, the gut of mussels contained a different microbial community, with the gut being dominated by *Bacteroidetes* and the gills being dominated by *Proteobacteria* (Musella et al., 2020). The function of microbial communities in bivalves is not well understood. However, recent studies have suggested that they play essential roles in the survival and growth of these organisms. For example, the microbial communities *Vibrio, Bacteroides, and Pseudomonas* in oysters play a crucial role in the digestion of food, including the breakdown of complex carbohydrates and the production of essential amino acids (Pierce and Ward, 2019). Similarly, the microbial communities *Gammaproteobacteria*, and *Alphaproteobacteria* in mussels play crucial roles in detoxifying pollutants, including heavy metals and organochlorines (Milan et al., 2018; Wang et al., 2020). In recent years, the effects of marine heatwaves on the bivalve microbial communities have become a focus of scientific research. This is because the microbes present in these bivalve mollusks play an essential role in the health and survival of the host and are thought to play a significant role in mediating the effects of heat waves on the bivalve mollusks (Ertl et al., 2016).

Mortality events affecting adult and juvenile bivalves have been reported throughout history (Jones et al., 2017; Alfaro et al., 2019). These events have been observed across all ages and production stages (Lattos et al., 2020; Soon and Zheng, 2020), some attributed to pathogens favored by temperature increase. One such disease affecting farmed Pacific oysters on the West Coast is the Protistan parasite *Mikrocytos mackini* (Denman Island Disease), firstly reported in the 1960s on Vancouver Island and has resulted in mortality events (Sweet and Bateman, 2016; Garcia et al., 2018). In addition, another parasite, *Haplosporidium nelsoni*, was associated with mortality events in *Crassostrea virginica* in 2007 (Matt et al., 2020).

However, despite the growing interest in this area, a comprehensive review of the existing research is yet to be conducted. This review paper aims to provide a comprehensive overview of the current state of knowledge on the effects of marine heatwaves on bivalve microbial communities. To do this, we conducted a thorough literature search covering articles and studies published in peer-reviewed journals, conference proceedings, and technical reports. The review paper will provide valuable insights into the current understanding of the effects of heatwaves on the bivalve microbial communities. It will inform future research efforts and potential human health risks *via* bivalve consumption. The results of this review will also have important implications for the management and conservation of marine ecosystems, as well as for developing mitigation strategies to deal with the impacts of these heat waves on bivalves.

2 Bivalve microbiome

The microbiome of bivalves consists of a diverse community of microorganisms, including bacteria, viruses, and fungi (Rey-Campos et al., 2022). The bacterial community is the most well-studied component of the bivalve microbiome. It plays a critical role in host health and disease (Figure 1). The composition of the bivalve microbiome can vary significantly depending on several factors, including habitat, water quality, and host species (Paillard et al., 2022). Bivalves inhabit a wide range of aquatic habitats, from freshwater streams to deep-sea hydrothermal vents (Zgouridou et al., 2022). The microbiome of bivalves is known to vary depending on the habitat in which they are found. For example, bivalves that inhabit polluted waters may have a different microbiome than those found in unpolluted waters (Martinez-Colon et al., 2009). Similarly, bivalves that live in close proximity to hydrothermal vents may have a different microbiome, such as *Methanoperedens* and *Endoriftia*, found in the gill tissue of the hydrothermal vent mussel *Bathymodiolus thermophilus*, which cannot be found in other marine environments (German et al., 2011; Smith and Wrighton, 2019; Lee D. Y. et al., 2021).

Water quality is an essential factor that can influence the microbiome of bivalves. A range of factors, including pollution, nutrient enrichment, and changes in temperature and salinity, can influence the quality of the water. Studies have shown that changes in water quality can lead to changes in the composition of the bivalve microbiome (Bentzon-Tilia et al., 2016; Michan et al., 2021). For example, bivalves living in nutrient-rich waters may have a different microbiome than those in nutrient-poor waters (Pusch et al., 1998; Bang et al., 2018). The microbiome of bivalves can also vary depending on the host species. Different bivalve species may have different requirements for their microbiome, which can result in differences in the microbiome composition (Vezzulli et al., 2018; Pierce and Ward, 2019). For example, some bivalve species may require specific bacteria to aid in the digestion of their food, such as *Spirochaetes* in clams; these bacteria are involved in the breakdown of complex carbohydrates (Harwood and Canale-Parola, 1984). In contrast, other species may require different bacteria to help with other aspects of their physiology.

The microbiome of bivalves is thought to play an essential role in host health and disease. The bacterial component of the bivalve microbiome is known to be involved in a range of functions,

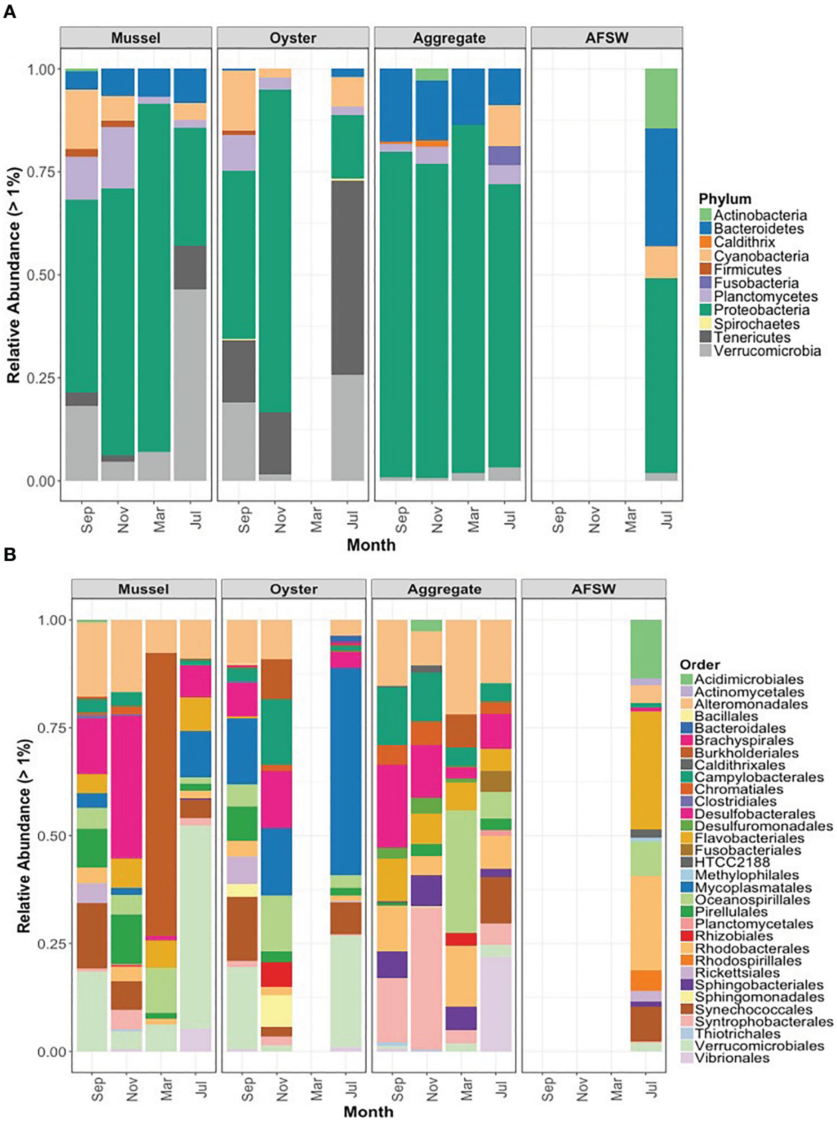

FIGURE 1
Microbial Community composition of each sample type by phylum and order. **(A)** Showing the relative abundance of each taxonomic group >1% of the total for mussel gut, oyster gut, aggregate, and aggregate-free seawater (AFSW) samples, categorized by phylum. Colors correspond to different phyla, as indicated in the legend. **(B)** Showing the relative abundance of each taxonomic group >1% of the total for each sample type, categorized by order. Colors correspond to different orders, as indicated in the legend. Data were obtained from (Pierce and Ward, 2019).

including digestion, nutrient cycling, and immune defense (Pierce and Ward, 2018; Timmins-Schiffman et al., 2021). Studies have shown that some bacteria in the bivalve microbiome produce antimicrobial compounds that help protect the host from pathogens (Destoumieux-Garzón et al., 2020; Balbi et al., 2021). Additionally, certain bacteria in the bivalve microbiome are associated with increased resistance to disease. *Bacteroidetes* and *Rhizobiales* exemplify this (Dubé et al., 2019). These bacteria produce enzymes that break down complex carbohydrates and have been shown to contribute to the immune response of bivalves. The microbiome of bivalves is also involved in nutrient cycling, an essential process for maintaining healthy ecosystems (Moruf et al., 2020). Additionally, the bivalve microbiome can play a role in transferring pathogens between different organisms in the ecosystem (Paillard et al., 2022).

3 Role of bivalve-microbe symbioses in mediating heatwave effect

Heatwaves are a frequent and growing problem in many parts of the world due to the effects of climate change (He et al., 2022b). These extreme weather events can devastate marine and freshwater ecosystems, leading to declines in biodiversity and changes in ecosystem function (Smale et al., 2019). In recent years, the study of bivalve-microbe symbioses has become increasingly important in understanding how these organisms can mediate the effects of heatwaves on aquatic ecosystems. The microbiome of bivalves has important implications for the ecology of aquatic ecosystems. Bivalves are filter feeders that can remove large amounts of organic matter from the water column, which can help to improve water quality. Bivalves and microbes are critical to water quality management as they are essential in maintaining the balance of dissolved oxygen, pH, and nutrient levels (Zhou et al., 2009; Mohapatra et al., 2013). This balance is essential for aquatic organisms' survival and helps mitigate the adverse effects of heatwaves on these ecosystems (Table 1).

Microbes such as *Pseudomonas* and *Aspergillus* play a critical role in decomposing organic matter in water (Zhou et al., 2009), which releases nutrients essential for the growth of aquatic plants and animals. During heatwaves, the decomposition of organic matter can accelerate, increasing nutrient levels that can cause harmful algal blooms and other adverse effects on water quality. However, some types of bacteria and fungi can also help break down harmful substances in the water, such as pollutants and toxins, improving water quality and protecting aquatic life (Chaturvedi et al., 2015). By regulating nutrient and toxin levels, microbes help to maintain the delicate balance of water quality that supports healthy aquatic ecosystems (Hlordzi et al., 2020).

One of the most critical roles of bivalve-microbe symbioses in mediating the effects of heatwaves is heat stress protection (Turner et al., 2016). During heatwaves, bivalves can experience thermal stress that can damage their tissues and impair their physiological functions (Masanja et al., 2022; Liu et al., 2023). However, some species of bivalves have been found to host microbial communities that protect against heat stress. For example, the bivalve *Crassostrea virginica* and *Mytilus coruscus* have been found to harbor a diverse and stable microbial community such as *Vibrio spp*, *Rhizobiales*, *Endozoicomonas* that can protect the host from thermal stress by producing compounds that act as heat shock proteins, chaperones and antioxidants (Lokmer and Mathias Wegner, 2015; Li et al., 2018). Bivalves rely on microbes for the acquisition of essential nutrients, such as nitrogen and phosphorus, which are often limited in their environment. During heatwaves, the availability of these nutrients can be further reduced, which can have adverse effects on bivalve growth and survival. However, some species of bivalves have been found to host microbial communities that can increase the availability of nutrients during heatwaves. For example, the bivalve *Mercenaria mercenaria* has been found to host a diverse microbial community, *Rhizobiales* and *Planctomycetes*, that can increase nitrogen availability during heatwaves by fixing atmospheric nitrogen (King et al., 2019; Soon and Zheng, 2020).

Bivalves rely on their immune system to defend against pathogenic microbes and other harmful agents (Rahman et al., 2019). However, during heatwaves, the immune system can be impaired, increasing the susceptibility of bivalves to disease (Nascimento-Schulze et al., 2021). Some species of bivalves have been found to host microbial communities that can enhance the host's immune defense during heatwaves (Allam and Espinosa, 2016). For example, bivalves have been found to harbor *Vibrionaceae* and *Rhodobacteraceae* that can produce antimicrobial compounds that can protect the host from pathogenic bacteria during heatwaves (Leite et al., 2017; Baden et al., 2021; Scanes et al., 2021b).

Bivalves are critical in carbon cycling in aquatic ecosystems (Hakenkamp and Palmer, 1999). However, their ability to do so can be influenced by heatwaves. During these extreme weather events, bivalves may experience changes in feeding behavior and metabolism (Liu et al., 2023), which can ultimately affect their contribution to carbon cycling. Despite these challenges, some species of bivalves have been found to host microbial communities that can enhance their ability to participate in carbon cycling during heatwaves. For instance, studies have shown that bivalves host a microbial community of *planctomycetes* that can enhance the host's ability to assimilate and recycle organic matter during heatwaves

TABLE 1 Summarizes the diverse beneficial functions performed by microbial communities associated with bivalves.

Microbe	Function	References
Bacillus spp.	*Bacillus sp.* is a beneficial bacterium in bivalves, which helps improve nutrient absorption, reduce ammonia toxicity, and enhance immune response.	Nayak, 2021
Flavobacterium spp.	*Flavobacterium spp.* is beneficial bacteria in bivalves that helps improve digestive enzyme activity and nutrient uptake.	Mi et al., 2022
Marinobacter spp.	*Marinobacter sp.* is a beneficial bacterium in oysters, which helps in improving the immune response and reducing pathogen load.	Clerissi et al., 2020
Pseudoalteromonas spp	*Pseudoalteromonas sp.* is a beneficial bacterium in clams, which helps in improving growth and survival rate.	Laroche et al., 2018
Planococcus spp	*Planococcus sp.* is a beneficial bacterium in clams, which helps improve growth and reduce the mortality rate.	Pushparaj et al., 2022
Rhodobacteraceae spp	*Rhodobacteraceae sp.* is a beneficial bacterium in bivalves, which helps reduce pathogen load and improve immune response.	Wan-Mohtar et al., 2022
Roseobacter spp	*Roseobacter denitrificans* is a beneficial bacterium in oysters that helps in the detoxification of pollutants and nitrogen metabolism.	Collins, 2014
Shewanella spp	*Shewanella colwelliana* is a beneficial bacterium in mussels, which helps reduce heavy metal toxicity and improve growth.	Pavan et al., 2020
Vibrio spp	*Vibrio tubiashii* is a beneficial bacterium in Pacific oysters, which helps in improving the immune response.	Rajeev et al., 2021

These functions include nutrient cycling, waste removal, pathogen suppression, and production of essential metabolites. The table also highlights the specific microbial taxa that contributed to each part. Overall, this review emphasizes the critical role of bivalve-associated microbial communities in promoting the health and productivity of bivalves and their surrounding ecosystems.

(Doni et al., 2023). Another example of a bivalve species that can benefit from microbial communities is the giant clam *Tridacna maxima.* This bivalve has been found to host symbiotic algae, which can increase the clam's photosynthetic capacity and carbon uptake even during periods of high-temperature stress (Soo and Todd, 2014).

Overall, understanding the complex relationships between bivalves, their microbial communities, and the carbon cycle is critical for accurately predicting the impacts of climate change on aquatic ecosystems. Bivalves are known for their ability to produce calcified structures, such as shells, that are important for their survival and ecology (Ysebaert et al., 2019). However, the biomineralization process can be affected by heatwaves (He et al., 2022a), which can alter these structures' chemical and mechanical properties. Some species of bivalves have been found to host microbial communities that can enhance the process of biomineralization during heatwaves. The bivalve *Crassostrea gigas*, commonly known as the Pacific oyster, has been found to harbor a diverse and stable microbial community that can regulate the chemical composition of the shell and enhance its mechanical properties during heatwaves (Lokmer et al., 2016).

4 Bivalve microbial community changes due to heatwave events

Heatwaves have been found to alter the microbial diversity of bivalve communities (Green et al., 2019; Alma et al., 2020).

Changes in microbial interactions due to heatwaves have been found to alter the interactions between bivalve microbial communities and their hosts (Scanes et al., 2021). A decrease in symbiotic relationships and an increase in pathogenic relationships have been observed, suggesting a shift from a mutualistic to a parasitic interaction (Willing et al., 2011). This may be due to changes in the microbial community structure and function in response to heatwave events. Heatwaves have been found to alter the transport of nutrients and organic matter in bivalve microbial communities (Wetz and Yoskowitz, 2013). An increase in nutrient uptake and a decrease in organic matter export have been observed, suggesting a shift from a source to a sink (IPCC, 2018). This adaptation may be an attempt to maintain energy balance and avoid thermal stress. Heatwaves have been found to alter the production of toxins by bivalve microbial communities (Zgouridou et al., 2022). An increase in toxin production has been observed, potentially as a response to increased competition and changes in microbial interactions. This adaptation may threaten the health of the bivalve host and the surrounding ecosystem.

Heatwaves have been found to alter the aggregation of bivalve microbial communities (Neu et al., 2021). An increased aggregation has been observed, potentially as a response to increased competition and changes in microbial interactions. This adaptation may affect the transport and processing of nutrients and organic matter in the bivalve microbial community (Paillard et al., 2022).

5 Ocean warming and the emergence of bivalve food poisoning

Seawater and bivalve hosts may harbor pathogenic microorganisms that significantly threaten human health (Table 2). These microorganisms can survive and reproduce under specific physiochemical conditions (Chahouri et al., 2022). Bivalve shellfish is a popular food source worldwide, with consumption reported across all five continents, as documented by the United Nations Food and Agricultural Organization (FAO, 2000). Despite its popularity, only a few nations, precisely 12, have recorded instances of bivalve-associated illnesses. These cases are distributed evenly across the continents, with four countries from Europe, Asia, North America, and Australia each reporting outbreaks. Among these, the largest-ever recorded outbreak occurred in Shanghai, China, in 1988, affecting 290,000 individuals infected with hepatitis A after consuming clams (Tang et al., 1991). This outbreak is particularly noteworthy for the high number of deaths it caused, with 47 fatalities recorded. Additionally, three other significant outbreaks of bivalve-associated illnesses were documented in Australia in 1979, the United States in 1986, and Japan in 1991, involving over 800 patients in each case (Murphy et al., 1979; Morse et al., 1986; Otsu, 1999).

Escherichia coli strains, including Shiga toxin-producing ones, can cause severe symptoms, such as stomach cramps, vomiting, and bloody diarrhea (Cabrera-Sosa and Ochoa, 2020; Vishram et al., 2021; Butt et al., 2022). Research shows that increased temperatures can modify *E. coli* gene expression, leading to the emergence of more hazardous strains (Kinghorn et al., 2002; Chung et al., 2006; Kumar and Libchaber, 2013). Studies on temperature adaptation indicate that mutations in genes that affect cellular processes can enhance *E. coli's* fitness at elevated temperatures (Hirota et al., 1970; Rudolph et al., 2010). *Salmonella* is another pathogen that can cause gastroenteritis, leading to severe dehydration, especially in children and the elderly (Dennehy, 2005; Barrett and Fhogartaigh, 2017). While large outbreaks of *Salmonella* make headlines, most cases go undiagnosed and are not part of any known outbreak. *Salmonella* infections result in an estimated 93.8 million cases of gastroenteritis and 155,000 deaths globally every year (Moura et al., 2018; Gong et al., 2022).

It is vital to comprehend the factors that can influence the emergence and spread of these pathogenic microorganisms to prevent future outbreaks and safeguard public health. Studies consistently show that the incidence of *Salmonella* infection is positively associated with higher ambient temperatures (Yun et al., 2016; Wang et al., 2018). This is likely because warmer temperatures facilitate more rapid bacterial replication, increasing infection rates. In South Korea, 17,638 cases of the Hepatitis A virus were reported (Lee D. Y.et al., 2021; Jeong et al., 2021); the primary source was Jogaejeot, seasoned *Venerupis philippinarum*, a traditional fermented food of Korea, and Jogaejeot is eaten raw. According to the Korean Centers for Disease Control and Prevention (KCDC), the *Hepatitis A* virus resists high temperatures.

Therefore, it is associated with considerable risk during times of ocean warming. Ocean warming has been identified as a significant

TABLE 2 Provides a summary of harmful microbial communities identified in various bivalve species, including bacteria, viruses, and parasites.

Microbe	Function	References
Campylobacter	*Campylobacter* is a bacterium that can cause diarrhea, cramping, and fever and can be transmitted through contaminated bivalves.	Pereira et al., 2021
Clostridium botulinum	*Clostridium botulinum* is a bacterium that produces a powerful toxin that can cause botulism, a potentially life-threatening illness that contaminated bivalves can transmit.	Ziarati et al., 2022
Escherichia coli	*Escherichia coli* is a bacterium that can cause severe diarrhea and other symptoms and can be transmitted through contaminated bivalves.	Leoni et al., 2017
Hepatitis A virus	*Hepatitis A virus* can cause liver inflammation and is associated with contaminated bivalves.	Jeong et al., 2021
Listeria monocytogenes	*Listeria monocytogenes* is a bacterium that can cause severe illness, particularly in pregnant women and people with weakened immune systems, and can be transmitted through contaminated bivalves.	Bintsis, 2017
Norovirus	*Norovirus* is a virus that can cause vomiting and diarrhea and is commonly associated with bivalve shellfish such as clams and mussels.	Wright et al., 2018
Salmonella	*Salmonella* is a bacterium that can cause diarrhea, fever, and abdominal cramps and can be transmitted through contaminated bivalves.	Gökoğlu and Gökoğlu, 2021
Shigella	*Shigella* is a bacterium that can cause diarrhea, fever, and abdominal cramps and can be transmitted through contaminated bivalves.	Elbashir et al., 2018
Vibrio parahaemolyticus	*Vibrio parahaemolyticus* is a bacterium that causes human gastrointestinal illness and is commonly found in bivalves.	Normanno et al., 2006

The identified microbial communities and their associated health risks are described, highlighting their potential impact on human health and the bivalve aquaculture industry. The information presented in the table serves as a valuable reference for researchers and policymakers seeking to understand better and mitigate the risks associated with harmful microbial communities in bivalves.

factor in the emergence of bivalve food poisoning caused by harmful microbes. As ocean temperatures continue to rise, the distribution and abundance of these harmful microbes in bivalve populations may increase, leading to a greater risk of foodborne illness for humans who consume contaminated seafood. Therefore, continued monitoring of ocean temperatures and the presence of harmful microbes in bivalve populations is necessary to mitigate the potential health risks associated with consuming contaminated seafood.

6 Conclusion and implications for bivalve aquaculture and coastal ecosystem health in a changing climate

In conclusion, this scientific review paper highlights the significant impacts of heatwaves on bivalve microbial communities and their implications for both bivalve and human health. The review demonstrates that heatwaves have the potential to alter the composition and diversity of microbial communities within bivalves, leading to changes in nutrient cycling, metabolism, and immune function. These alterations can ultimately impact bivalve health and may have implications for human health through the consumption of contaminated shellfish. The evidence presented in this review suggests that heatwaves may increase harmful bacteria and toxins in bivalves, including *Vibrio* spp. and *norovirus*, which have been associated with foodborne illness outbreaks. Furthermore, the impacts of heatwaves on bivalve microbial communities may exacerbate existing stressors on bivalve populations, including pollution and habitat destruction, further threatening bivalve health and ecosystem resilience.

Therefore, further research is needed to understand better the complex interactions between heatwaves, bivalve microbial communities, and human health. This research should improve our understanding of the underlying mechanisms driving changes in microbial community composition and function and the implications for bivalve and human health. Overall, this review emphasizes the urgent need for action to address the impacts of heatwaves on bivalves and their associated microbial communities. This includes efforts to mitigate the effects of climate change, reduce pollution, and protect critical bivalve habitats. Such actions are critical not only for the health of bivalve populations and the ecosystems they support but also for the health and well-being of human populations that rely on these valuable shellfish as a source of food and nutrition.

Author contributions

FM: Writing – original draft, data curation, investigation, validation. KY: Data curation, writing – review & editing, validation. YX: Writing – review & editing, validation, data curation. GH: Data curation, writing – review & editing, validation. XLL: Writing – review & editing, validation, data curation. XX: Data curation, writing – review & editing, validation. XJ: Writing – review & editing, validation, data curation. XL: Writing – review & editing, validation. RM: Writing – review & editing. YD: Conceptualization, resources. LZ:

Conceptualization, writing-original draft preparation, project administration. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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